



Holocene environmental change at Lake Njulla (999 m a.s.l.), northern Sweden: a comparison with four small nearby lakes along an altitudinal gradient

Christian Bigler^{1,2,6,*}, Evastina Grahn^{1,3}, Isabelle Larocque^{1,4}, Adam Jeziorski⁵ and Roland Hall^{1,2,5}

¹Abisko Scientific Research Station, ANS, Climate Impacts Research Centre, Box 62, SE 981 07 Abisko, Sweden; ²Department of Ecology and Environmental Science, Umeå University, SE 901 87 Umeå, Sweden; ³Man-Technology-Environment Research Centre, Örebro University, SE 701 82 Örebro, Sweden; ⁴IGBP/PAGES, Bärenplatz 2, CH 3011 Bern, Switzerland; ⁵Department of Biology, University of Waterloo, 200 University Avenue West, Waterloo, Ontario N2L 3G1, Canada; ⁶Institute of Plant Sciences, Altenbergrain 21, CH-3013 Bern, Switzerland; *Author for correspondence (e-mail: christian.bigler@ips.unibe.ch)

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Abstract

We assess Holocene environmental change at alpine Lake Njulla (68°22'N, 18°42'E, 999 m a.s.l.) in northernmost Sweden using sedimentary remains of chironomid head capsules and diatoms. We apply regional calibration sets to quantitatively reconstruct mean July air temperature (using chironomids and diatoms) and lake-water pH (using diatoms). Both chironomids and diatoms infer highest temperatures (1.7–2.3°C above present-day estimates, including a correction for glacio-isostatic land up-lift by 0.6°C) during the early Holocene (c. 9,500–8,500 cal. yrs BP). Diatoms suggest a decreasing lake-water pH trend (c. 0.6 pH units) since the early Holocene. Using detrended canonical correspondence analysis (DCCA), we compare the Holocene development of diatom communities in Lake Njulla with four other nearby lakes (Lake 850, Lake Tibetanus, Vuoskkujávri, Vuolep Njakajaura) located along an altitudinal gradient. All five lakes show similar initial DCCA scores after deglaciation, suggesting that similar environmental processes such as high erosion rates and low light availability associated with high summer temperature appear to have regulated the diatom community, favouring high abundances of *Fragilaria* species. Subsequently, the diatom assemblages develop in a directional manner, but timing and scale of development differ substantially between lakes. This is attributed primarily to differences in the local geology, which is controlling the lake-water pH. Imposed on the basic geological setting, site-specific processes such as vegetation development, climate, hydrological setting and in-lake processes appear to control lake development in northern Sweden.

Introduction

Arctic regions are vulnerable to impacts of projected climate change (Watson et al. 1997). Lakes are directly affected by climate change via alteration of the length of the open water season, the stratification pattern, run-off regimes and water temperature (e.g., Magnuson et al. (2000)). In addition, indirect catch-

ment-based processes may affect lake-ecosystems. For example, altered rates of weathering or erosion and changes in soil properties or vegetation can exert a strong influence on acidity and nutrient availability in lakes (Sommaruga-Wögrath et al. 1997; Lotter 2001). Paleolimnological techniques are well suited to evaluate ecological effects of climate-related processes over long temporal scales (MacDonald et al.

2000). However, the development of aquatic communities over Holocene time-scales may also be influenced by processes related to primary succession following deglaciation of the landscape. These processes remain poorly understood at high latitudes (Engstrom et al. 2000).

The first aim of this paper is to provide a Holocene reconstruction of key environmental conditions at the alpine Lake Njulla (999 m a.s.l.) in northern Sweden. We aim to provide independent evidence at Lake Njulla in order to contribute to the debate about the environmental conditions during the early Holocene that arose based on climate reconstructions using plant megafossils (Kullman 1999) versus reconstructions using pollen and plant macrofossils (Barnekow 1999a, 1999b). To do this, we analysed diatoms and chironomids in a sediment core from the same lake where Barnekow (1999a, 1999b) and Kullman (1999) carried out their studies. Applying regionally developed calibration sets, we reconstruct mean July air temperature using chironomids and diatoms and lake-water pH using diatoms. Head capsules of chironomids deposited in lake sediments have shown to be valuable temperature indicators (Walker et al. 1991; Levesque et al. 1993; Brooks and Birks 2001). Furthermore, their sedimentary remains are used to investigate other environmental issues such as pollution (e.g., Ilyashuk and Ilyashuk (2001)) or anoxia (e.g., Little and Smol (2001)). Similarly, diatoms have been applied successfully for reconstructing environmental conditions such as lake-water pH and temperature in northern Scandinavia (e.g., Korhola et al. (2000), Rosén et al. (2001), Bigler et al. (2002)). Combined with multivariate statistical analyses, including transfer functions that are based on large modern calibration sets, these aquatic organisms allow quantitative estimates of past environmental conditions (Birks 1995, 1998).

The second aim of the paper is to assess whether the patterns of Holocene diatom assemblage development in Lake Njulla are similar with other regional subarctic lakes. We compare the diatom stratigraphy at Lake Njulla with four additional lakes in close proximity to Lake Njulla that are within or adjacent to the Abisko Valley. We assume that all lakes experienced a similar climatic regime due to their close geographic proximity, but that catchment conditions and lake-catchment interactions differ because they encompass different types of bedrock and terrestrial vegetation zones. By comparing lakes with a similar climatic regime but different catchment conditions,

we aim to identify the environmental factors that play important roles in regulating Holocene patterns of diatom community development in subarctic lakes.

Study sites

Lake Njulla (unofficial name; 68°22'N, 18°42'E) is a small (1.1 ha), shallow (max. depth = 4.4 m) lake located at an elevation of 999 m a.s.l., approximately 300 m above the present-day altitudinal tree-limit formed by mountain birch (*Betula pubescens* ssp. *tortuosa*) and 200 km north of the Arctic Circle (Figure 1). The lake lies in a depression between the two mountains Njulla (or Nuolja; 1169 m a.s.l.) and Slättatjåkka (1191 m a.s.l.), within the Abisko National Park. The catchment encompasses 78 ha and consists of sparse alpine-tundra vegetation and bare rock originating mainly from calcareous-rich mica-schists (Kulling 1964). A sporadic survey from 1936 to 1952 estimated the average ice-free period to be approximately three months and anoxic conditions in the water column were recorded before ice-off (Ekman 1957). As the lake has no official name, several names were introduced that may lead to some confusion. Ekman (1957) named it Lake Nuolja (Number B35), Barnekow (1999a), Rundgren and Beerling (1999) used the name Lake Njulla, whereas Kullman (1999) called it Lake Pompe. Berglund et al. (1996), Barnekow (1999a, 1999b), Kullman (1999) provide more details about Lake Njulla in context of tree-limit and vegetational setting.

The four additional lakes used to compare patterns of diatom community development are all situated at lower altitudes than Lake Njulla, and they span a broad altitudinal gradient with lakes situated above and below present tree-limit, at 348 m a.s.l. (Vuoskkujávri), 409 m (Vuolep Njakajaure), 560 m (Lake Tibetanus) and 850 m (Lake 850) (Figure 1). The prevailing bedrock types at Vuoskkujávri are quartzite, slate and dolomite, at Vuolep Njakajaure sericite-quartzite, schist and dolomite, at Lake Tibetanus mica-schist and at Lake 850 granite and syenite (Kulling 1964). The occurrence of calcite marble in the catchments of Lake Tibetanus and Vuolep Njakajaure supplies dissolved inorganic carbon to the lakes and elevates lake-water pH (Barnekow et al. 1998). Consequently, Vuolep Njakajaure and Lake Tibetanus are alkaline (Barnekow 1999a; Barnekow et al. 1998), whereas Vuoskkujávri, Lake 850 and Lake Njulla are circumneutral (Table 1).

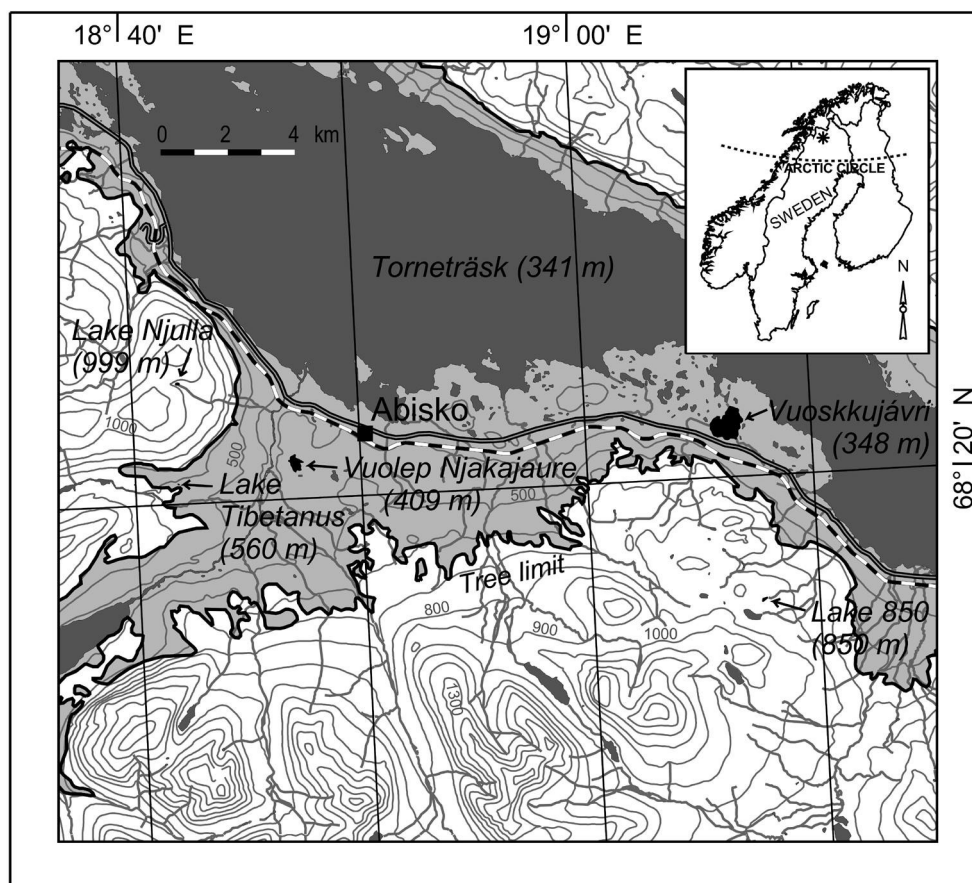


Figure 1. Map showing the location of Lake Njulla and the four other lakes that were compared with the diatom record from Lake Njulla. The shaded area indicates areas below the birch tree-limit (*Betula pubescens* ssp. *tortuosa*).

Methods

Coring, dating and chronology

The sediment core was retrieved from the deep region of Lake Njulla in March 1998, while the lake was ice-covered. Three overlapping core-segments (0–100 cm; 85–185 cm and 138–238 cm) were collected using a 1-m long Russian style corer with a diameter of 10 cm. The core segments were correlated using

measurements of coring depth, because loss-on-ignition (LOI) values did not reveal any significant changes over the Holocene that could be used for core correlation. The total sediment sequence collected was 238 cm and the distinct boundary between clay and gyttja occurred at 211–212 cm. The top long core section (0–100 cm) did not properly retrieve the uppermost 7 cm of unconsolidated sediment. Consequently, the surface sample (0–1 cm) was collected with a modified Kajak-corer (Renberg 1991). Except

Table 1. Selected characteristics of Lake Njulla and the four additional study lakes.

	Elevation (a.s.l.)	Lake-water pH (pH units)	Maximum lake depth (m)	Lake area (ha)	Catchment area (ha)
Lake Njulla	999 m	6.8	4	1.1	78
Lake 850	850 m	6.8	8	1.5	29
Lake Tibetanus	560 m	7.7	4	0.5	c. 2
Vuolep Njakajaure	409 m	7.5	14	13	c. 13
Vuoskkujávri	348 m	6.9	18	68	1122

for the topmost 7 cm, the sampling interval was set to 4 cm. The organic content of the sediment core was estimated by means of LOI, applying standard procedures (e.g., Heiri et al. (2001)).

Macroscopic remains of terrestrial plants were selected from five stratigraphic levels and dated at the Ångström Laboratory (Uppsala) by radiocarbon AMS

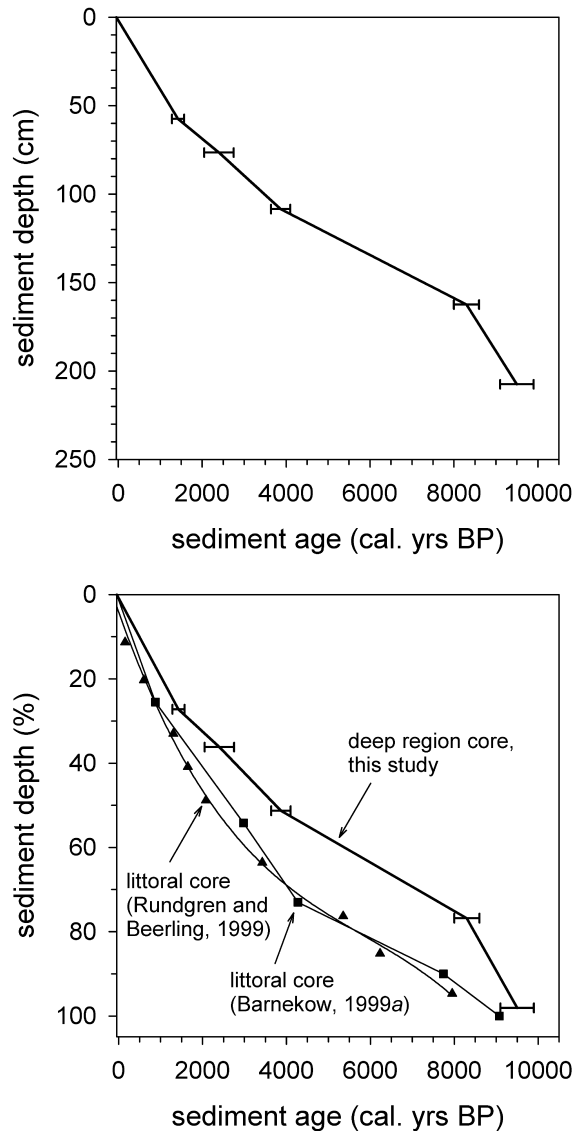


Figure 2. The depth-age relationship of Lake Njulla based on five AMS radiocarbon dates of plant macrofossils, with error bars representing 95.4% confidence intervals (upper panel). The depth-age curve is compared with two littoral cores from the same lake (Barnekow 1999a; Rundgren and Beerling 1999). To compare the cores, the depth from the sediment surface to the shift of basal clay to gyttja was set as 100% for each core.

methods. The resulting radiocarbon dates were converted into calibrated radiocarbon years before present (henceforth abbreviated as cal. yrs BP) using the program OxCal version 3.5 (Ramsey 2000). Linear interpolation of the mean calibrated dates was used to estimate the depth-age relationship.

To relate our chironomid and diatom records to the pollen and plant macrofossil data from a littoral core (Barnekow 1999a), we used depth-age relationships that were developed based on individual radiocarbon dates of each core. To compare sedimentological patterns throughout the Holocene between cores collected from the littoral region of the lake (Barnekow 1999a; Rundgren and Beerling 1999) and the deepwater region (this study), we plotted the estimated radiocarbon ages from each of the cores as a percent of the total core depth (surface to basal shift from clay to gyttja; see Figure 2)

Chironomid and diatom analyses

For chironomid analysis, between 0.25–7 ml (in the lowest part of the core up to 30 ml) of wet sediment was deflocculated overnight in 10% KOH and then sieved through a 90- μm mesh. The retrieved chironomid head capsules were hand picked at 12–25x magnification using a stereomicroscope and a petri-dish divided into four chambers. Depending on the number of head capsules found in the first chamber, a subsample or alternatively the whole sample was picked. The head capsules were mounted onto microscope slides using Euparal[®] and dried at 70–80°C overnight. According to recent investigations (Heiri and Lotter 2001; Larocque 2001; Quinlan and Smol 2001), a minimum of 50 head capsules was identified in each sample, with exception of the lowest part of the sediment sequence that contained very few head capsules. Taxonomic identification was carried out at 100–1000x magnification and followed Wiederholm (1983). For the identification of the *Tanytarsini* tribe, an unpublished key by S.J. Brooks (The Natural History Museum London) was used. *Corynocera oliveri* and *Tanytarsus lugens* were differentiated when the mandibles were present. Otherwise, they were grouped as *Tanytarsus* spp. The differentiation of *Micropsectra* groups was based on the shape of the antennal pedestal and the spur. In case of split head capsules, two halves were counted as one unit.

Samples for diatom analysis were taken at the same stratigraphical intervals as for chironomids. Diatom

preparation followed standard methods including treatment with 30% H_2O_2 (Battarbee 1986), applying a preparation technique for large sample-sets (Renberg 1990). Cleaned diatom samples were dried onto coverslips and permanently mounted onto microscope slides using Naphrax[®]. Diatoms were identified at 1000x-magnification using phase contrast and at least 400 valves were counted from each sample. Taxonomic identification followed the guidelines of the SWAP project and Krammer and Krammer and Lange-Bertalot (1986–1991). Diatom concentrations (valves mg^{-1} dry sediment) were calculated by adding microspheres (Battarbee and Kneen 1982).

Stratigraphical chironomid and diatom data from Lake Njulla were zoned by optimal partitioning using sum-of-square criteria (Birks and Gordon 1985) within the computer program ZONE (Lotter and Juggins 1991). The number of significant zones was determined with the broken stick approach using the computer program BSTICK (Bennett 1996).

Numerical analyses

Quantitative inferences using diatoms and chironomids are based on a regional surface-sediment calibration set of 100 lakes from northern Sweden including broad climatic and environmental gradients (Larocque et al. 2001; Bigler and Hall 2002). Inference procedures are based on unimodal response models; specifically, weighted averaging partial least squares (WA-PLS; ter Braak and Juggins (1993)) using the computer program WA-PLS (version 1.0, unpublished program by S. Juggins, University of Newcastle). The chironomid-July T transfer function resulted in a coefficient of determination (r^2 , jack-knifed) of 0.65 and root mean square error of prediction (RMSEP, jack-knifed) of $1.1^\circ C$ (Larocque et al. 2001), whereas the diatom-transfer functions yielded $r^2=0.75$ and RMSEP= $1.0^\circ C$ for July T and $r^2=0.77$ and RMSEP= 0.19 pH units for lake-water pH (Bigler and Hall 2002). All quantitative inferences were smoothed using a LOESS smoother (polynomial degree=1, span=0.1).

We used detrended CCA (DCCA) to assess effects of environmental factors that may regulate Holocene patterns of diatom community change at each of the five study lakes. To do this, diatom samples from the Holocene cores were plotted as passive samples within the DCCA ordination space defined by surface sediment diatom assemblages from the calibration set. First, CCA of the calibration set data with forward

selection was carried out to select a set of environmental variables that could account for the variation in diatom assemblage composition almost as well as the entire environmental data set of all 19 variables (Bigler and Hall 2002). The selected variables (pH, sedimentary LOI, July T, lake depth, potassium concentration [K]) were then used in a DCCA ordination of the modern diatom calibration set samples, and the fossil samples from each core were added as passive samples. The resulting trajectories, smoothed with a five-point running mean, illustrate long-term patterns of Holocene development of diatom assemblages at each lake in the context of modern taxa-environment relationships identified with the calibration set. All ordinations were performed with the computer program CANOCO version 4 (ter Braak and Smilauer 1998) with square root transformed species data and rare species down-weighted.

Results

Dating, chronology and sedimentation rates

We found the shift from basal clay to gyttja between 211–212 cm core depth, while Barnekow (1999a), Rundgren and Beerling (1999) recorded this shift in two sediment cores retrieved from the littoral zone of Lake Njulla (water depth ~ 1.9 m) between 229–230 cm and 189–190 cm, respectively. Our established depth-age relationship reveals a mid-Holocene period (*c.* 8,300–3,900 cal. yrs BP) with relatively low sedimentation rate (1 mm yr^{-1}), whereas before and after this period the sedimentation rates are considerably higher (4 mm yr^{-1} and 3 mm yr^{-1} , respectively; Table 2, Figure 2). Although our depth-age relationship is based on five dates only, the observed pattern with relatively low sedimentation rates during the mid-Holocene is consistent with the chronology based on radiocarbon dates of the two littoral cores (Figure 2). In comparison, the depth-age relationships of the littoral cores show prior to *c.* 8,300 cal. yrs BP a less pronounced increase in sedimentation rates compared to our deep-region core (Figure 2).

When compared with other lakes in the near surroundings of Abisko village, the relatively low sedimentation rates during the mid-Holocene (*c.* 8,300–3,900 cal. yrs BP) in Lake Njulla appear to be relatively uncommon. Other nearby lakes that have been investigated show relatively linear sedimentation

Table 2. AMS radiocarbon dates of plant macrofossils from Lake Njulla.

Sample depth	Laboratory nr	$\delta^{13}\text{C} \text{‰ PDB}$	^{14}C yrs BP	cal. yrs BP (95.4% probability)
57.5 cm	Ua-16003	-29.1	1520 \pm 80	1570 – 1280
76.5 cm	Ua-16002	-29.9	2295 \pm 85	2750 – 2050
108.5 cm	Ua-16001	-29.4	3585 \pm 80	4100 – 3640
162.5 cm	Ua-16199	-28.9	7520 \pm 135	8600 – 8100
207.5 cm	Ua-16000	-30.4	8505 \pm 130	9900 – 9100

rates throughout the Holocene, for example Lake 850 (Shemesh et al. 2001), Lake Tibetanus (Barnekow 1999a), Vuolep Njakajaure (Barnekow et al. 1998) or Vuoskkujávri (Bigler et al. 2002).

Chironomid stratigraphy of Lake Njulla

In Lake Njulla, Holocene changes in chironomid assemblages are divided into eleven significant stratigraphic zones. The first seven zones (prior to 9,000 cal. yrs BP) cover relatively short periods with rapid, marked shifts in composition of chironomid assemblages, whereas the last four zones (9,000 cal. yrs BP until present) include considerably longer time periods with more stable chironomid assemblages (Figure 3).

Zone I (237–234 cm sediment depth) has high relative abundance of *Diamesa*, *Tanytarsus* spp., *Corynocera ambigua*, *Psectrocladius sordidellus* gr. and *Sergentia*. *Cricotopus/Orthocladius* dominates (i.e., relative abundances exceed 50%) zone II assemblages (234–228 cm), whereas assemblages during zone III (228–222 cm) are dominated by the cold-water indicator (Larocque et al. 2001) *Micropsectra radialis* (Figure 3). Zone IV (222–214 cm) has relative high abundances of *Micropsectra insignilobus*, *Corynocera oliveri*, *Heterotrissocladius* group, *Tanytarsus* spp. and *Procladius* spp. *Corynocera ambigua* dominates assemblages in zone V (214–210 cm), while in zone VI (210–202 cm; 9,600–9,300 cal. yrs BP) *Oliverdia* prevails. Zone VII (9,300–9,000 cal. yrs BP) is dominated by *Tanytarsus* spp., *Corynocera ambigua*, *Paratanytarsus* and *Psectrocladius sordidellus* gr. (Figure 3). During the transition from zone VII to zone VIII (c. 9,000 cal. yrs BP), relatively high abundances of the warm-water indicator *Microtendipes* (Larocque et al. 2001) are recorded.

Zone VIII (9,000–8,400 cal. yrs BP) assemblages are dominated by *Corynocera oliveri*, which contributes up to 60% of chironomid assemblages, with *Micropsectra insignilobus*, *Tanytarsus* spp., *Paratanytarsus* and *Psectrocladius sordidellus* gr. as

sub-dominants. The shift from zone VIII to zone IX (8,400–4,700 cal. yrs BP) is characterised by a decrease of *Corynocera oliveri*, with coincident increases of *Corynocera ambigua* to >60%. In zone X (4,700–900 cal. yrs BP), *Micropsectra radialis* reappears, a species that is relatively abundant in zones II–IV. During zone X, relative abundances of *Sergentia* and *Trissocladius* increase while *Corynocera ambigua* decreases, although it remains as the most abundant taxon (30%). The most recent zone XI (900 cal. yrs BP until present) continues the trend within zone X with further decreasing abundance of *Corynocera ambigua* and a concomitant increase of *Sergentia*. *Zalutschia lingulata pauca* appears and reaches abundances of up to 10% during zone XI. Interestingly, the surface sample shows a relatively high abundance of *Paratanytarsus* (almost 50%).

Diatom stratigraphy of Lake Njulla

Diatoms are abundant and well preserved throughout the organic portion of the sediment core. However, below the sediment transition from clay to gyttja (211–212 cm; 9,600 cal. yrs BP) the organic content of the sediment (as LOI) is between 3–4% of sediment dry mass and diatom abundance is very low (Figure 4). Relatively high diatom concentrations (valves mg^{-1} dry sediment) occur from 8,500–5,000 cal. yrs BP (Figure 4). Overall, 171 different diatom taxa were identified and the diatom assemblages consist mostly of benthic taxa throughout the entire Holocene (Figure 4).

Numerical zonation procedures divide the diatom stratigraphy into five significant stratigraphic zones (Figure 4). Different *Fragilaria* species dominate the three oldest zones. *Fragilaria construens* var. *venter* and *Fragilaria brevistriata* dominate assemblages during zone I (9,600–9,200 cal. yrs BP), whereas *Fragilaria pseudoconstruens* dominates during zone II (9,200–8,700 cal. yrs BP). Zone III covers the period from 8,700–4,000 cal. yrs BP and the most common *Fragilaria* species include *F. construens*

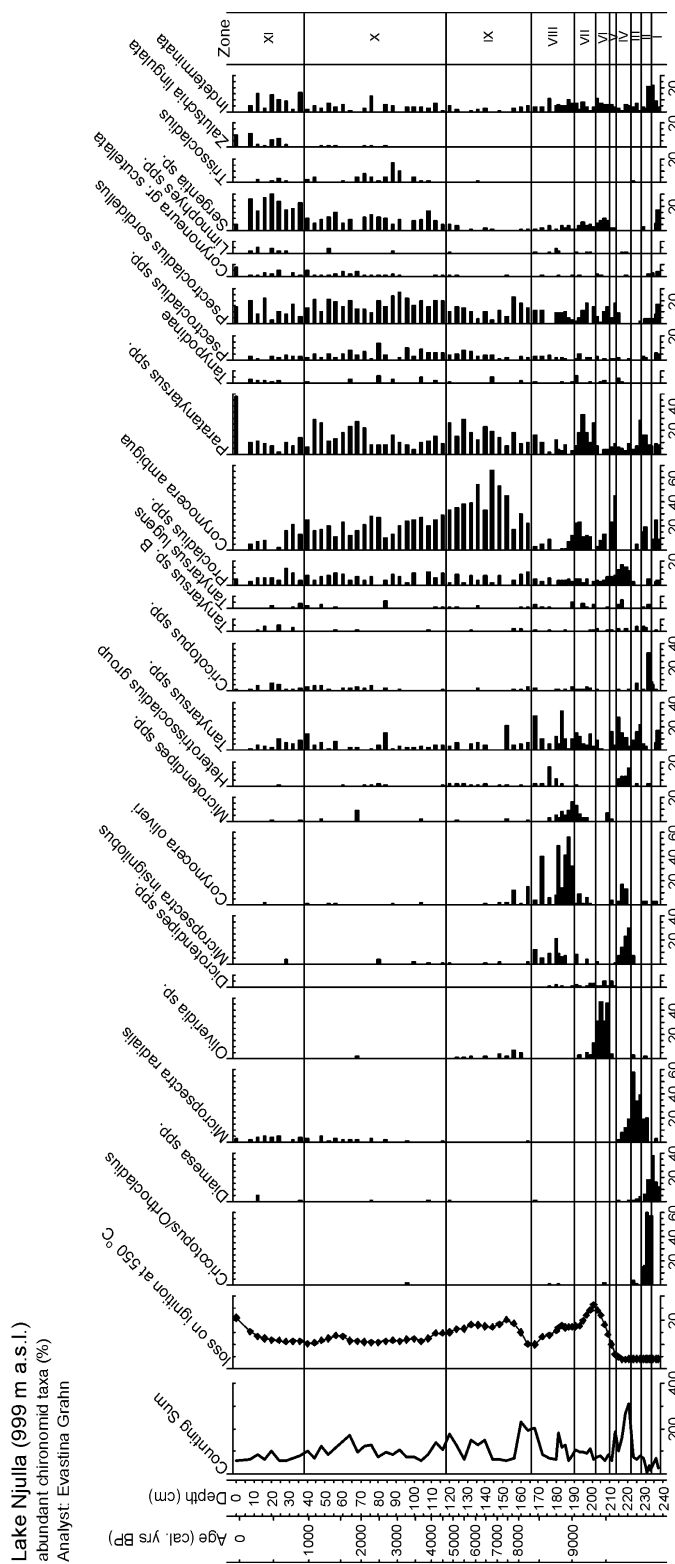


Figure 3. Changes in percent abundances of abundant chironomid taxa in the sediment core from Lake Njulla. Horizontal lines represent significant zone boundaries.

var. *venter*, *F. pinnata*, *F. pseudoconstruens* and *F. brevistriata*. In addition, *Achnanthes minutissima*, *Achnanthes pusilla* and *Navicula seminulum* attain relatively high abundances within zone III. Overall, diatom assemblages during zones I–III (9,600–4,000 cal. yrs BP) show a gradual decline in dominance by *Fragilaria* taxa from >90% to ~40% of the diatom sum and development of more diverse assemblages of benthic taxa belonging mainly to the genera *Achnanthes* and *Navicula*.

A marked shift in community composition is observed around 4,000 cal. yrs BP. Abundances of the *Fragilaria* species decrease substantially to <10% and are largely replaced by *Navicula digitulus* and a more diverse community consisting of many other benthic taxa. These changes coincide with the onset of more rapid sedimentation rates. The transition from zone IV to zone V occurs at 600 cal. yrs BP, when *Navicula digitulus* and *Navicula seminulum* almost disappear with coincident increases of *Achnanthes marginulata*, *Achnanthes kriegeri*, *Navicula minima*, *Pinnularia biceps*, *Pinnularia microstauron* var. *microstauron* and *Aulacoseira distans* var. *nivalis*. Towards the end of the zone, percent abundances of *Brachysira brebissonii*, *Brachysira vitrea* and *Surirella linearis* also increase substantially.

Holocene temperature trends at Lake Njulla inferred from chironomids and diatoms

As the sample resolution is relatively coarse and sample-specific prediction errors are relatively large (~1.0°C) compared to the magnitude of Holocene temperature changes, our interpretation emphasises the long-term trends rather than individual data points. Prior to 9,600 cal. yrs BP, when the shift from clay to gyttja occurs, uncertainties in the chronology and the low counting sums make the interpretation of July T rather tentative. After the shift from clay to gyttja and with the onset of organic sedimentation, chironomids suggest the warmest July T of the entire Holocene (c. 9,500–8,500 cal. yrs BP; Figure 5). Similarly, diatoms infer the warmest temperatures during the early Holocene. However, the magnitude of temperature inferred based on the three oldest diatom samples is likely to be erroneous, as the assemblage consists almost entirely of *Fragilaria construens* var. *venter*, a species that did not show a well-defined optimum to temperature in the calibration set (Bigler and Hall 2002). During this early Holocene period, July T is inferred to be 2.3–2.9°C

above the estimated present-day temperature at Lake Njulla, ignoring samples with ‘poor’ fit to the calibration set or effects of glacio-isostatic land-uplift. As glacio-isostatic land-uplift (half-life period >2,000 years) of about 100 m since deglaciation has occurred (Ingólfsson and Norddahl 2001), our earliest inferences of July T should be corrected by c. 0.6°C, applying a regional temperature lapse rate (Laaksonen 1976).

Since c. 8,800 cal. yrs BP, a moderate long-term climatic deterioration is inferred both by chironomids and diatoms, showing the most pronounced decrease from c. 8,800–8,300 cal. yrs BP. Interestingly, both aquatic indicators show a cold period around c. 8,300 cal. yrs BP. Considering the few radiocarbon dates of our stratigraphy, this cold phase may be related to the widespread cold event in the Northern Hemisphere at c. 8,200 cal. yrs BP (e.g., Alley et al. (1997)). Diatoms suggest a pronounced cooling from c. 5,000–4,000 cal. yrs BP, which is not in agreement with the chironomid-based inference. From c. 2,800–1,200 cal. yrs BP, both indicators are in close agreement, while during the last 1,000 cal. yrs BP the inferences are almost opposite (Figure 5). The present-day temperature at Lake Njulla as estimated based on interpolation using Climate Normals 1961–1990 from the nearest climate stations is in close agreement with the chironomid-inferred temperature, while diatoms overestimate it considerably (>1°C).

The diatom-based lake-water pH reconstruction suggests a long-term acidification pattern during the Holocene (Figure 5). The lake was, according to the diatoms, slightly alkaline (c. pH=7.2) during the early Holocene, and underwent a gradual pH decrease, to slightly acidic conditions (c. pH=6.5). A reversal of the long-term decreasing trend is inferred between c. 2,500–1,500 cal. yrs BP. Diatom-based pH inferences suggest that Lake Njulla experienced the lowest lake-water pH of the entire Holocene during the past 500 years.

Comparison of Holocene diatom development at Lake Njulla with other nearby lakes

Ordination of fossil diatom assemblages from Lake Njulla by DCCA suggests that Holocene patterns of diatom community change are correlated overall with declines in lake-water pH and July T (Figure 6). After deglaciation, diatom assemblages from zones I–III develop mainly along DCCA axis 2, which is most closely correlated with gradients of physical variables

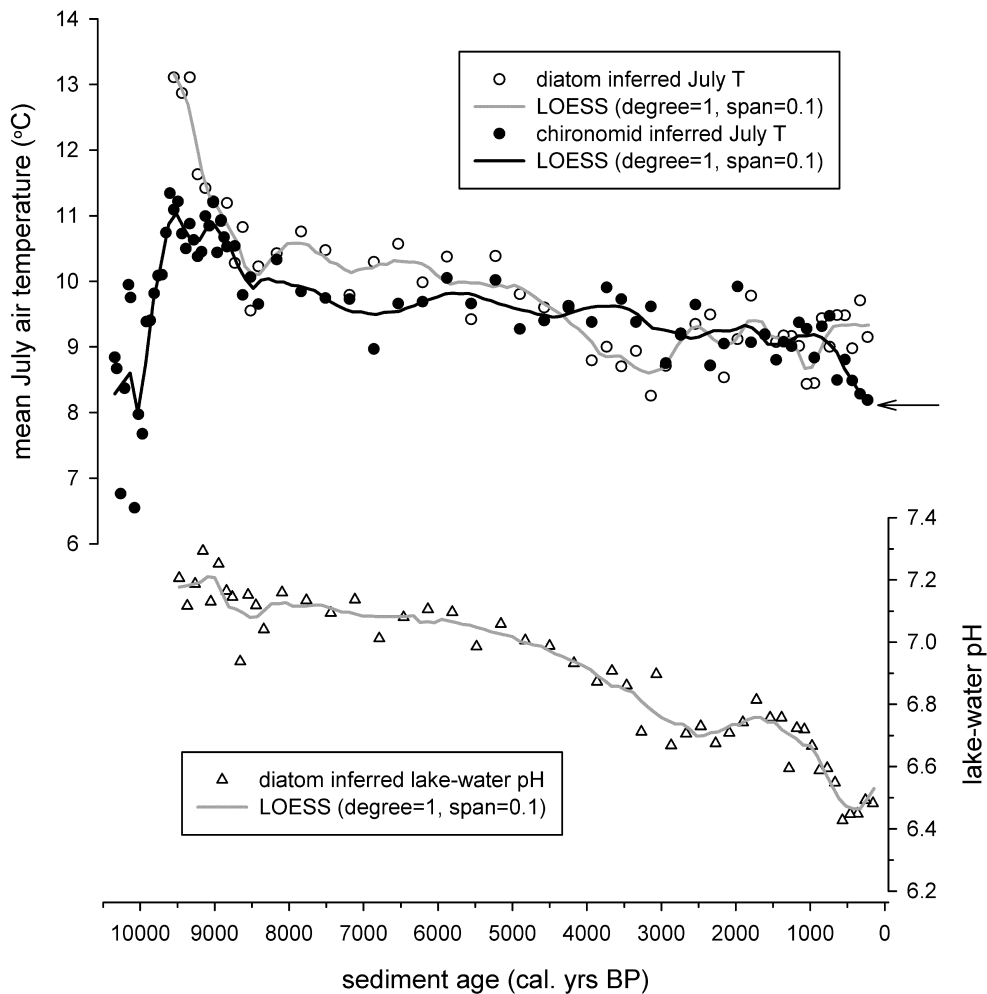


Figure 5. Quantitative reconstruction of mean July air temperature (July T) based on chironomids (solid circles) and based on diatoms (open circles) and of mean lake-water pH based on diatoms (open triangles). The solid lines represent LOESS smoothers (polynomial degree=1, span=0.1). The horizontal arrow indicates the present-day temperature (8.1°C) estimated by spatial interpolation of Climate Normals (1960–1990) from nearby meteorological stations and applying a lapse rate of 0.57°C per 100 m (Laaksonen 1976).

(i.e., July T, LOI, lake depth) and not correlated with lake-water pH. From 8,300–4,800 cal. yrs BP, which corresponds closely to diatom assemblage zone III (Figure 4), DCCA scores show only minor changes, indicating a period of relatively stable environmental conditions. Subsequently (4,800–2,700 cal. yrs BP), movement of diatom sample scores in DCCA paralleled the vector for lake-water pH and, interestingly, diatoms change from assemblages that occur most commonly in lakes of the present-day birch forest zone to those that occur typically in alpine tundra environments. During *c.* 2,700–800 cal. yrs BP, DCCA scores indicate relatively stable conditions while the DCCA scores increase on both axes since *c.* 800 cal. yrs BP.

To assess whether the pattern of diatom community development in Lake Njulla is representative for other subarctic lakes, we compared results from Lake Njulla with Holocene diatom records from four additional lakes in and adjacent to the Abisko Valley (Figure 7). Lake 850 is situated on the opposite side of the Abisko Valley at an elevation 150 m lower than Lake Njulla (Figure 1). Sediments from Lake 850 show a pattern of Holocene diatom development which is similar to that from Lake Njulla, with increasing DCCA scores on the first axis and decreasing scores on the second axis (Figure 7). The trajectory of sample scores appears to correlate most strongly with decreasing lake-water pH and July T from *c.* 9,200–8,300 cal. yrs BP, and mainly with decreasing lake-

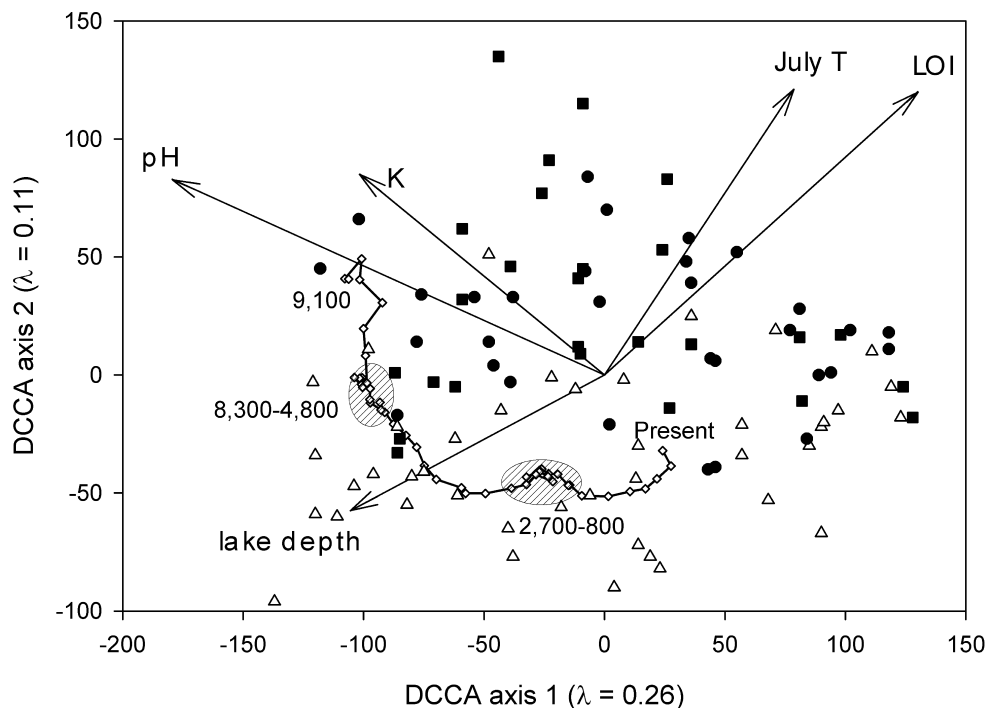


Figure 6. Detrended canonical correspondence analysis (DCCA) with forward selected environmental variables of modern diatom calibration set samples. Samples from the calibration lakes are classified according to present-day catchment vegetation including alpine tundra (open triangles), birch forest (closed circles) and birch-conifer and conifer forest (closed squares) zones. The fossil sample scores of sedimentary diatom assemblages from Lake Njulla are projected as a trajectory (running mean, $n = 5$) onto the biplot of the modern diatom calibration set data by adding them as passive samples. Presented dates are in calibrated radiocarbon years BP (cal. yrs BP).

water pH, but not July T, between *c.* 8,300 cal. yrs BP and present. During the period *c.* 8,600–8,300 cal. yrs BP, however, movement of sample scores at Lake 850 appear to respond most strongly to declining July T, which corresponds to the period of most rapid declines of July T as inferred from both chironomids and diatoms at Lake Njulla. Even though the pattern is similar between Lake Njulla and Lake 850, the timing of developmental patterns differs substantially. Diatoms at Lake Njulla show a long-term pattern of change with two periods of relatively constant composition (*c.* 8,300–4,800 and *c.* 2,700–800 cal. yrs BP; Figure 6). In contrast, diatom assemblages from Lake 850 developed more quickly and reached relatively stable DCCA scores that are similar to present-day values already at *c.* 7,200 cal. yrs BP.

The pattern of DCCA sample scores from Vuoskkujávri also shows similarities with patterns from Lake Njulla and Lake 850, except during the early Holocene period (*c.* 10,100–9,300 cal. yrs BP), which includes a period that was not recovered from the two other lakes. During this earliest period (before 9,300 cal. yrs BP) DCCA scores at Vuoskkujávri increase

sharply along the July T vector (Figure 7), which is consistent with the warming trend inferred from chironomids at Lake Njulla (Figure 5). Since *c.* 9,300 cal. yrs BP, when the direction of DCCA scores changes distinctly, the pattern matches overall patterns observed at Lake Njulla and Lake 850 relatively well, indicated by increasing scores on the first axis and decreasing scores on the second axis. The timing of the development is intermediate between that of Lake Njulla and Lake 850, and Vuoskkujávri reaches similar DCCA scores to the present-day sample at *c.* 6,000 cal. yrs BP. Interestingly, DCCA sample scores from Vuoskkujávri lie above those from Lake Njulla and Lake 850. This pattern is consistent with the lower elevation of Vuoskkujávri, and corresponding warmer July T, compared with the other two lakes.

In contrast to the three lakes Vuoskkujávri, Lake 850 and Lake Njulla, Vuolep Njakajaure and Lake Tibetanus show completely different patterns of diatom community development, both in trajectory of DCCA scores and the timing of changes in assemblage composition. Vuolep Njakajaure shows increasing DCCA scores on both axes from *c.* 8,600–1,750

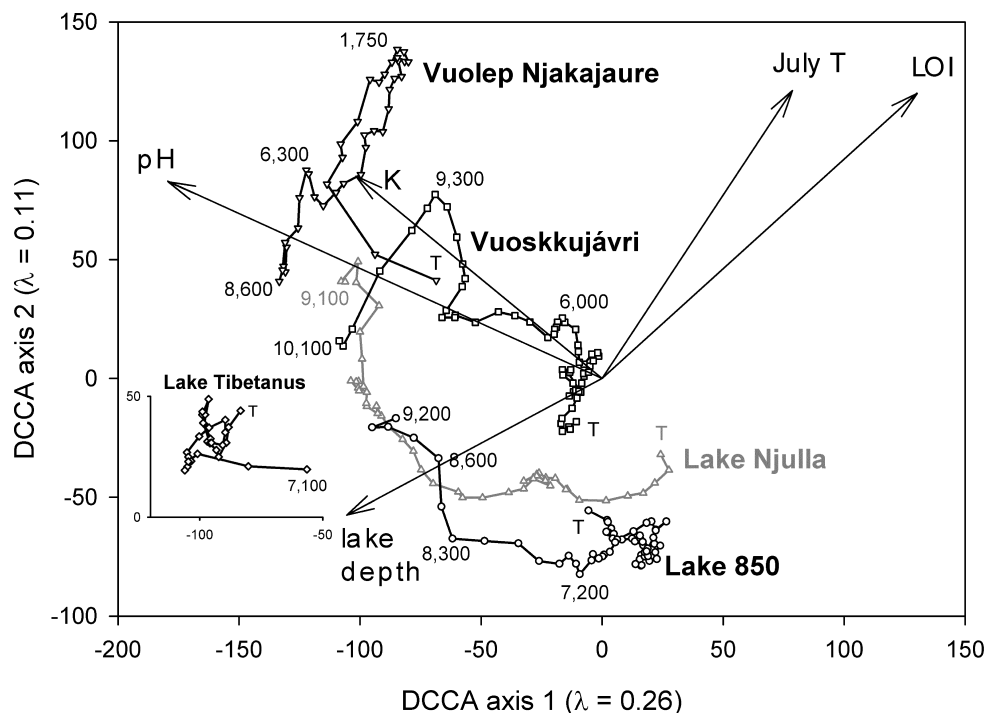


Figure 7. Comparison of Holocene development of diatom assemblages from all five study-lakes by detrended canonical correspondence analysis (DCCA). The trajectories (running mean, $n = 5$), including selected dates (cal. yrs BP) and the top of each core (T), of the five lakes are projected onto the biplot of the modern calibration set data (not shown) by adding the DCCA scores to the analysis as passive samples.

cal. yrs BP, with a reversal from *c.* 6,300–5,500 cal. yrs BP. Overall, the pattern of diatom change shows very little, if any, correlation with changes in lake-water pH (Figure 7), which is the environmental variable that explains the greatest amount of variance within the modern diatom calibration set (Bigler and Hall 2002). Instead, the changes seem primarily related to weaker variables in the calibration set such as temperature, LOI or related environmental variables. At *c.* 1,750 cal. yrs BP, the trajectory reaches a reversal point and subsequent changes are characterised by decreasing DCCA scores mainly along axis 2. Interestingly, the two most recent samples show a distinct change along the lake-water pH axis, suggesting a marked recent lake-water pH decrease. Finally, the trajectory of diatom sample scores from Lake Tibetanus shows only minor changes since *c.* 7,100 cal. yrs BP and indicates that diatom assemblages maintained remarkably stable composition since *c.* 7,100 cal. yrs BP, which are dominated by *Amphora libyca* and a few *Navicula* species (Jezioriski, unpublished data). Overall, the trajectory is most similar to that of Vuolep Njakajaure, with relatively little change along the vector for lake-water pH, but

here only minor changes are recorded even along the second DCCA axis.

Discussion

Holocene climate changes at Lake Njulla

The pattern of our quantitative July T reconstruction at Lake Njulla based on chironomids and diatoms with warmest temperatures after deglaciation (9,500–8,500 cal. yrs BP) is supported by estimates based on tree megafossils at Lake Njulla. Tree megafossil remnants of *Pinus sylvestris*, *Betula pubescens* ssp. *tortuosa* and *Alnus incana* have been recovered close to shoreline at Lake Njulla and were dated to 8,500–8,100 ^{14}C yr for specimens from all three species, and also to 5,400–4,500 ^{14}C yrs for specimens of *Betula* and *Alnus* (Kullman 1999). The calibrated ages for the megafossils are 9,600–8,800 cal. yrs BP and 6,400–5,000 cal. yrs BP, respectively. Based on this megafossil evidence, Kullman (1999) inferred that the early Holocene climate in northern Sweden was dominated by continental conditions with strong seasonal

variations and summers that were 2.4°C (corrected for the glacio-isostatic land-uplift) warmer than today. Barnekow (1999a) collected and analysed a littoral sediment core for plant macrofossils (e.g., leaves, fruits) and pollen, but found no pine needles during the early Holocene that could support the findings by Kullman (1999), but the concentration of *Betula pubescens* fruits and catkin scales was highest during the early Holocene (Barnekow 1999a). Based on plant macrofossil evidence, Barnekow (1999a) suggests open vegetation with sparse mountain birch and estimated summer temperatures to c. 1.5°C warmer during the early Holocene than today (corrected for glacio-isostatic land-uplift).

Our inference based on chironomids and diatoms (corrected for glacio-isostatic land-uplift) suggests July T was warmer by 1.7–2.3°C during the early Holocene (9,500–8,500 cal. yrs BP), which lies intermediate between the value inferred by tree megafossils (2.4°C; Kullman (1999)) and the value inferred from plant macrofossils (1.5°C; Barnekow (1999a)). However, the pattern of our inferences with a cooling trend at Lake Njulla since 9,500 cal. yrs BP is more consistent with estimates based on tree megafossil findings at Lake Njulla and a more comprehensive postglacial tree-limit chronology from the southern Scandes (Kullman and Kjällgren 2000) than with pollen and macrofossil evidence from Lake Njulla and other sites in northern Fennoscandia (Sonesson 1974; Berglund et al. 1996; Barnekow 1999a, 1999b; Seppä and Birks 2001). Our inferences and the megafossil evidence suggest that highest temperatures and altitudinal tree-limits occurred during the early Holocene, whereas pollen and macrofossil evidence infer that peak summer temperatures occurred during the mid-Holocene. The inferred climatic pattern is consistent with forcing of summer temperatures by Milankovitch sun-earth cycles that provided greatest solar insolation during the early Holocene at high latitudes (Bradley 1999).

During the mid- and late Holocene, our temperature reconstructions using chironomids and diatoms at Lake Njulla show a long-term trend of gradual cooling and compare, in general, relatively well with other regional evidence. Comparable temperature reconstructions were suggested based on a multi-proxy study using diatoms, chironomids, pollen and near-infrared spectroscopy from the Sarek Mountains (Rosén et al. 2001), based on reconstructions using glacier movements in Scandinavia (Karlén 1988; Dahl and Nesje 1994) and from sedimentological

studies of nearby pro-glacial lakes of the Kårsa glacier (Snowball 1996; Karlén 1998).

Effects of environmental changes on diatom assemblages in Lake Njulla

During the early Holocene, diatom assemblages in Lake Njulla are dominated by different *Fragilaria* species (Figure 4). These species often occur in newly deglaciated terrain (Smol 1983), favour relatively high alkalinity (Battarbee 1986), may tolerate relatively poor light conditions (Anderson 2000) and are characterised as adaptable and competitive (Lotter et al. 1999). Consequently, we suggest that the *Fragilaria*-dominated assemblages developed after deglaciation when rates of minerogenic erosion were high due to low retention of mineral grains by sparse terrestrial vegetation and effective erosive forces. These conditions provided adequate growing seasons with extensive habitat availability and low light conditions in the water column, favouring *Fragilaria* taxa. This conclusion is supported by results from ordination of fossil diatom assemblages by DCCA, which shows developmental patterns of early Holocene *Fragilaria*-dominated assemblages are most strongly correlated with physical variables (e.g., July T, LOI).

After 8,300 cal. yrs BP, more diverse benthic diatom assemblages developed and community composition became more stable at Lake Njulla as illustrated by relatively similar DCCA sample scores (Figure 6,7). These changes may have resulted from lower sedimentation rates, likely as consequence of increased catchment stability and reduced erosion. This appears to correlate with lower precipitation inferred from oxygen isotopes at nearby Lake 850 and Lake Tibetanus (Shemesh et al. 2001; Hammarlund et al. 2002) and only moderate changes in chironomid-inferred temperature (Figure 5). Resulting lower mineral turbidity in Lake Njulla appears to have increased light availability and permitted development of more diversified habitats that supported a diverse benthic diatom community with *Navicula*, *Achnanthes* and other genera.

At 4,700 cal. yrs BP, pollen and macrofossil analyses indicate the subalpine birch woodland tundra, which prevailed during early and mid-Holocene, was replaced with alpine tundra vegetation (Barnekow 1999a). Consistently, the diatom ordination by DCCA indicates that composition of diatom assemblages after 4,800 cal. yrs BP shifted from those typical of

lakes with forested catchments to those typical of lakes within alpine tundra vegetation. Interestingly, chironomid-inferred July T values do not show major temperature changes that could be responsible for the onset of diatom assemblage composition change at 4,800 cal. yrs BP. The responses of diatoms included marked declines of *Fragilaria* species and an increase in percent abundance of *Aulacoseira* taxa and *Navicula digitulus* (Figure 4). These changes are illustrated in the DCCA ordination as a transitional period from 4,800–2,700 cal. yrs BP (Figure 6). The DCCA sample scores move in a direction orthogonal to the July T vector, suggesting that the diatom responses are not primarily correlated with July T. Instead, they appear to be more strongly associated with gradually declining lake-water pH. Declining pH is consistent with inferred acidification of the catchment due to a consistent increase in abundance of *Empetrum* leaves that was recorded in the littoral sediment core since *c.* 4,000 cal. yrs BP (Barnekow 1999a). In addition, increasing sedimentation rates suggest that erosion of catchment materials increased following loss of trees and continuous vegetation cover. By 2,700 cal. yrs BP, *Fragilaria* species had almost completely disappeared and were replaced by a more diverse benthic flora containing high abundances of *Achnanthes* and *Navicula* among other genera. From 2,700–800 cal. yrs BP, relatively stable diatom assemblages were recorded. During this period, no major changes in composition of terrestrial vegetation were observed, and chironomids inferred relatively constant temperatures, even though the variability between single data points increased slightly. A marked $\sim 1^\circ\text{C}$ cooling in chironomid-inferred July T since *c.* 800 cal. yrs BP and a distinct diatom-inferred pH decrease are associated with considerable change in diatom assemblage composition. *Navicula digitulus*, which had abundances of 20% and more, disappeared quickly and was replaced by *Achnanthes marginulata*, *Achnanthes kriegeri*, *Navicula minima*, *Pinnularia*, *Brachysira* and *Aulacoseira* species.

Although diatoms have a relatively short generation time, the recorded assemblage changes appear to respond over relatively long time-scales (centuries to millennia) to climatic conditions and changes in catchment vegetation (MacDonald et al. 1993). This pattern is observed in the sediments from Lake Njulla, where development of diatom assemblages appears to be closely associated with terrestrial vegetation, catchment acidification, lacustrine habitat availability and climate. Based on the chironomid-inferred tem-

perature and pollen-based vegetation changes, we suggest that the earliest diatom assemblages were mainly controlled by physical variables, such as low catchment stability, high rates of erosional input and warm temperature (until 8,300 cal. yrs BP). From 8,300–4,800 cal. yrs BP relatively stable conditions prevailed. The transitional period of diatom assemblages from 4,800–2,700 cal. yrs BP was simultaneous with a vegetation change (loss of trees) and increasing acidification. Later on, a climatic deterioration as inferred by chironomids occurred and catchment erosion probably increased. The most recent diatom assemblage shift starting at *c.* 800 cal. yrs BP, we assign predominantly to responses of the diatom community associated with a pH decrease.

Possible mechanisms driving diatom developmental patterns in subarctic lakes near Abisko

Diatom communities from all five lakes had the most similar DCCA scores following deglaciation and during the early Holocene, suggesting that the initial environmental conditions may have been quite comparable for all lakes during early stages of primary succession. In fact, small *Fragilaria* species (e.g., *F. pseudoconstruens*, *F. pinnata*, *F. construens* var. *venter*, *F. brevistriata*) commonly dominate postglacial and early Holocene sediments of lakes throughout glaciated regions (Smol 1983, 1988). However, the *Fragilaria* assemblages were replaced within a few hundred years in Lake 850, Vuoskkujávri and Vuolep Njakajaure (Shemesh et al. (2001), Bigler et al. (2002); Bigler unpublished data), indicating that clear-water conditions were established relatively quickly after lake-formation. The different pattern in Lake Njulla, with relatively high abundances of *Fragilaria* species lasting until *c.* 4,000 cal. yrs BP, could reflect the local influence of prolonged snowfields in the catchment that may have remained at high altitudes as a consequence of relatively high winter precipitation. Consistent with this hypothesis, paleoecological studies indicate much higher regional precipitation based on pollen (Seppä and Birks 2001; Hammarlund et al. 2002) and oxygen isotopes (Shemesh et al. 2001; Hammarlund et al. 2002). The catchment setting of Lake Njulla, located in a small cirque close to the top of a mountain, could support long-lasting snowfields close to the lakeshore.

The replacement of early Holocene *Fragilaria*-dominated diatom assemblages by more diverse benthic communities was probably associated with

decreased mineral turbidity and natural acidification processes related to reduced rates of mineral erosion and base cation supply due to stabilisation of the catchment and development of terrestrial vegetation and soils, occurring similarly in most lakes. During the past 8,000 years, DCCA sample scores from Lake Njulla, Lake 850 and Vuoskkujávri move in a direction that is correlated with declining lake-water pH and orthogonal to the vector for July T, suggesting that Holocene changes in diatom assemblages are more strongly regulated by pH than by temperature in these lakes. These three lakes are characterised by circumneutral present-day lake-water pH, and the lake catchments do not contain the calcite marble, which elevates the pH of Vuolep Njakajaure and Lake Tibetanus (Table 1). In contrast, a different pattern of diatom development was observed at Vuolep Njakajaure and Lake Tibetanus, characterised by more constant community composition. Diatom assemblages were particularly stable in Lake Tibetanus, probably due to the influence of constant groundwater inputs and rapid flushing rates throughout the Holocene (Hammarlund et al. 2002).

Interestingly, the diatom assemblage trajectories in all lakes seem to be closely related to the vegetation in the lake catchment. For example, Lake Njulla shows a change in diatom assemblages from those characteristic of lakes with forested catchments to those that dominate in alpine tundra lakes. In contrast, diatom assemblages from Vuolep Njakajaure, Vuoskkujávri and Lake Tibetanus were always characteristic of lakes with forested catchments, which is an accurate reflection of vegetation that has existed in the catchments of each lake (Barnekow 1999b; Bigler et al. 2002).

Overall, differences in patterns of lake-water pH due to different supply of base cations from underlying geological substrates may account, to a large extent, for different patterns of diatom community development among lakes. During the early Holocene, diatom assemblages appear to have been similar in different lakes and most strongly controlled by environmental conditions of a mainly physical character (i.e., warm temperature, high erosion and mineral turbidity). Subsequently, diatom assemblages seemed to be regulated primarily by natural catchment acidification and changes in lake-water pH. Imposed on the basic development directed by the geological substrate, differences in the hydrologic setting, succession of vegetation, climate and in-lake processes may lead to variability in rate and scale of diatom

community development among lakes. The important role of climate is illustrated by the fact that modern relationships between diatoms and July T are strong in northern Scandinavia (Weckström et al. 1997; Rosén et al. 2000; Bigler and Hall 2002) and that sedimentary diatom assemblages of the past century might be strongly related to climatic factors (Sorvari et al. 2002).

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