Palaeoenvironmental changes in the northern boreal zone of Finland: local versus regional drivers

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Stockholm 2014
Për familjen time.
Për nënën dhe babain, vëllezërit, motrat dhe Seadin e vogël.
Për gjethën, të cilen e kam në qell, dhe gjithë ata që ende më gëzojnë në jetë.
Abstract. In this work, a variety of geochemical and biotic proxies derived from the Lake Loitsana sediment sequence (NE Finland) are employed to i) determine the timing of deglaciation, ii) characterise an early Holocene proglacial lake stage, iii) reconstruct Holocene lake development, iv) identify local-scale/site-specific processes that could cause shifts in biological assemblages and v) assess the most probable Holocene mean July air temperature ($T_{jul}$) development. The use of multiple proxies limits the uncertainties related to single-proxy approaches and facilitates the discrimination between local and regional driving factors. The results are then used to assess possible implications for interstadial environmental and climate reconstructions derived from older deposits in the adjacent Sokli basin. Lake Loitsana and its surroundings were deglaciated prior to 10 700 cal. a BP. The sediment record reflects a shallowing lake with four local events; i) the presence of a deep glacial lake, ii) glacial lake drainage and formation of Lake Loitsana, iii) changes in fluvial input due to progressive wetland expansion and iv) the gradual infilling of the lake. The results suggest that local events have driven changes in fossil assemblages through a variety of processes, and that the biological assemblages reflect changes in different environmental parameters in a highly individual manner. This further emphasises the importance of using multiple proxies in palaeoenvironmental studies. Biological assemblages can themselves act as important driving agents promoting changes in the composition of other assemblages. It is therefore suggested that future studies should consider for instance macrophyte abundance as well as food-web interactions as equally important physical parameters/factors, when assessing changes in biological assemblages. This study also assesses the impact of locally driven changes on quantitative $T_{jul}$ reconstructions derived from different biological assemblages. While pollen-inferred temperatures follow the classical trend of gradually increasing early Holocene $T_{jul}$ with a mid-Holocene maximum July warming, the plant macrofossil and chironomid assemblages reconstruct highest $T_{jul}$ during the early Holocene, i.e. at the peak of summer insolation. The relatively low early Holocene July temperatures recorded by the terrestrial pollen are the result of site-specific factors possibly combined with a delayed response of the terrestrial ecosystem compared to the aquatic ecosystem. The diatom-based $T_{jul}$ reconstruction seems to be particularly affected by secondary variables and display minor variability throughout the Holocene. Local scale events have a potential to drive changes in both biological assemblages and water chemistry, which can be reflected in the transfer-function based regional temperature reconstructions. The minimum $T_{jul}$ reconstructed on the basis of indicator plant taxa seem to be reliable, however one should keep in mind that absence of a certain taxa during any stage of lake development cannot be interpreted directly as cooling climate.

Keywords: Palaeolimnology, Palaeoecology, Biological assemblages, Sediment geochemistry, Regional drivers, Local drivers, Quantitative temperature reconstructions, Transfer-functions, Holocene, MIS-5d-c, Northern boreal forest zone, NE Finland.
**Sammanfattning.** Eftersom instrumentella mätningar sällan sträcker sig längre tillbaka i tiden än 200 år behövs data som rekonsstruerar miljöförändringar på längre sikt för att vi ska kunna förstå miljö- och klimatförändringar samt särskilja den antropogena effekten. Exempel på användningsområden för resultaten av denna studie är utvärderingen av framtida klimatförändringescenarier samt hur långtidsförvaringen av avfall från kärrnarkraftsreaktorer kan påverkas av förändringar under glaciationscyklar. I denna studie har pollen, växtmakrofossil, chironomider (mygglarver) och diatoméer (kiselalger), i kombination med sedimentgeokemi, analyserats från en sedimentkärna tagen i sjön Loitsana (i Sokli, nordöstra Finland). Syftet var att i) bestämma tidpunkten för isavsmältningen, ii) karakterisera en tidig holocen proglacial sjö iii) rekonsstruera den holocena sjöns utveckling, iv) identifiera lokala processer som kan orsaka förändringar i den biologiska artsammansättningen och v) bedöma den mest troliga utvecklingen för julimedeltemperaturer under holocen. Genom att kombinera flera metoder begränsas de osäkerheter som uppstår vid användningen av en proxy och det underlättar differentieringen mellan de lokala och regionala processer som driver förändringar i den biologiska artsammansättningen. Resultaten från denna studie används även för att bedöma eventuella konsekvenser för tolkningen av sediment från MIS 5e-c (Brørup).

Deglaciationen vid sjön Loitsana och dess omgivningar ägde rum strax innan 10 700 kaliobravade år BP (kal. år BP, d.v.s. före 1950). Den holocena miljörekonstruktionen återspeglar en kompleks sjöutveckling med fyra lokala händelser; i) förekomsten av en djup glacialsjö, ii) dräneringen av sjön och upptomsten av sjön Loitsana iii) förändringar i fluvialt inflöde på grund av utbredning av närliggande våtmarker och iv) en successiv igenfyllning av sjöbassängen. Resultaten tyder på att dessa lokala händelser och deras associerade processer har drivit förändringar i biologiska artsammansättningar. Det påvisades även att varje biologisk proxy återspeglar miljöförändringar på ett individuellt sätt vilket ytterligare betonar vikten av att använda en kombination av dessa vid rekonsstruktioner av äldre miljöer. Studien visar också att akvatiska växter själva kan verka som drivande faktorer och främja förändringar i biologiska artsammansättningen. Av den anledningen föreslås att framtida studier även bör inkludera akvatiska växtmakrofossil vid bedömningen av förändringar i den biologiska artsammansättningen.

Denna studie granskar även effekterna av ovannämnda lokalt drivna förändringar för kvantitativa rekonsstruktioner av julimedeltemperaturer. Den pollenbaserade rekonsstruktionen följer den klassiska trenden med relativt låga temperaturer innan 8200 kal. år BP och en maximal uppvarmning under 1200-1400 kal. år BP. Temperaturrekonsstruktioner baserade på makrofossil och chironomider visar emellertid en nästintill motsatt trend med höga temperaturer (>dagens värde) även under den tidiga delen av holocen. De relativt låga temperaturerna som rekonsstrueras av pollendata kan vara resultatet av lokala faktorer, som påverkar den fossila datauppsättningen, eventuellt kombinerat med en fördröjd respons av det terresttra ekosystemet jämfört med det akvatiska ekosystemet. Diatomér är speciellt påverkade av lokala faktorer och upprvisar minimala temperaturförändringar genom hela holocen. Lokala processer har en potential att driva förändringar i biologiska artsammansättningar, vilket kan reflekteras i regionala temperaturrekonsstruktioner baserade på så kallade transfer-funktioner. Minimum julitemperaturer baserade på växtmakrofossil av indikationsarter från akvatiska och våtmarksmiljöer, verkar vara tillfälliga. Dock bör det hållas i minnet att frånvaro av en art under något stadium av sjöutvecklingen inte direkt kan tolkas som en indikation på kallare klimat.
Palaeoenvironmental changes in the northern boreal zone of Finland: local versus regional drivers

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List of papers *
This doctoral dissertation consists of this summary and the following papers, which are referred to by their Roman numerals in the text.


* Author contributions. The following people have contributed to this thesis: Jan Risberg (JR), J. Sakari Salonen (JSS), Jan Weckström (JW), Karin F. Helmens (KFH), Krister N. Jansson (KNJ), Ludvig Löwemark (LL), Malin E. Kylander (MEK), Minna Vääränta (MV), Peter Kuhry (PK), Stefan Engels (SE) and Tomi P. Luoto (TPL). SS = Shyhrete Shala. All co-authors are acknowledged for reading and commenting on the manuscripts.

I Conceived and designed by SS, KFH and JR. Written by SS and edited by KFH. KNJ is acknowledged for the DEM-based glacial lake reconstruction. MEK is acknowledged for assessing the quality of raw data obtained through XRF core scanning and the introduction to principal component analysis. JR is acknowledged for supervision and assistance during the diatom analysis. LL is acknowledged for assistance during the XRF core-scanning.

II Conceived and designed by SS and PK after discussions with KFH and MV. Written by SS under the supervision of PK and edited by KFH, MV and PK. TPL, JSS and JW are acknowledged for pollen analysis, chironomid analysis and producing the diatom-inferred pH reconstruction, respectively.

III Conceived, designed and written by SS after discussions with KFH and MV. TPL, JSS and JW are acknowledged for the transfer-function based temperature reconstructions and compositional distance estimations using chironomids, pollen and diatoms, respectively.

IV Conceived and designed by KFH. Written by KFH, MV and SE. SS responsible for diatom analysis and interpretation of results as well as preparation of the location figure.
### Abbreviations

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tr>
<td>AMS</td>
<td>accelerator mass spectrometry</td>
</tr>
<tr>
<td>C/N</td>
<td>carbon/nitrogen ratio</td>
</tr>
<tr>
<td>cal. a BP</td>
<td>calibrated years before present (BP = 1950)</td>
</tr>
<tr>
<td>CONISS</td>
<td>constrained incremental sum-of-squares</td>
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<tr>
<td>C&lt;sub&gt;org&lt;/sub&gt;</td>
<td>organic carbon</td>
</tr>
<tr>
<td>DEM</td>
<td>digital elevation model</td>
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<tr>
<td>DOC</td>
<td>dissolved organic carbon</td>
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<tr>
<td>FIS</td>
<td>Fennoscandian Ice Sheet</td>
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<tr>
<td>IPCC</td>
<td>intergovernmental panel on climate change</td>
</tr>
<tr>
<td>ka BP</td>
<td>kilo years before present</td>
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<tr>
<td>LOESS</td>
<td>locally weighted scatterplot smoothing</td>
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<tr>
<td>LOI</td>
<td>loss-on-ignition</td>
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<tr>
<td>LWWA</td>
<td>locally weighted weighted averaging</td>
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<tr>
<td>MIS</td>
<td>marine isotope stage</td>
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<tr>
<td>OSL</td>
<td>optically stimulated luminescence</td>
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<tr>
<td>PAR</td>
<td>pollen accumulation rates</td>
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<tr>
<td>PCA</td>
<td>principal component analysis</td>
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<tr>
<td>RMSEP</td>
<td>root-mean-square error of prediction</td>
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<tr>
<td>SCM</td>
<td>Sokli carbonatite massif</td>
</tr>
<tr>
<td>SKB</td>
<td>Swedish nuclear fuel and waste management company</td>
</tr>
<tr>
<td>T&lt;sub&gt;Jul&lt;/sub&gt;</td>
<td>mean July air temperature</td>
</tr>
<tr>
<td>TOC</td>
<td>total organic carbon</td>
</tr>
<tr>
<td>WA</td>
<td>weighted averaging</td>
</tr>
<tr>
<td>WA-PLS</td>
<td>weighted averaging-partial least squares</td>
</tr>
<tr>
<td>XRF</td>
<td>X-ray fluorescence</td>
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PALAEOENVIRONMENTAL CHANGES IN THE NORTHERN BOREAL ZONE

Introduction


The northern boreal forest is a wide vegetation zone that covers large parts of Alaska, Canada, the southern tip of Greenland, most of Iceland, northern Fennoscandia and large parts of northern Russia (Fig. 1). An extensive circum-arctic tree-line ecotone (13 500 km long) is situated between the boreal forest and the tundra to the north. Species diversity is higher in the boreal zone compared to the tundra but lower compared to the more southerly vegetation zones (Waide et al. 1999). In Fennoscandia, the northern boreal forest has relatively low tree species diversity and is dominated by pine, spruce and birch. The number of herbs and ferns is also low and the ground vegetation is usually richer in bryophytes and lichens than vascular plants (Esseen et al. 1997). A warming in climate is predicted to affect high latitudes by causing northwards shifts in the tree-line ecotone and migration of species from south to north, which would lead to higher species diversity in the northern boreal zone (Root et al. 2003). Such shifts are easily studied in Finland due to its relatively flat topography compared to the rest of Fennoscandia. Even small changes in altitude in such areas, would cause a more uniform latitudinal shift in climate and subsequent regional vegetational response (Esseen et al. 1997).

Long-term natural environmental variability in Fennoscandia has been the subject of numerous palaeoenvironmental studies in the 20th century (e.g. von Post 1916, Cleve-Euler 1922, Renberg and Hellerberg 1982, Robertsson and García Ambrosiani 1988, García Ambrosiani 1991). While this has improved our understanding of e.g. vegetation successions through glacial-interglacial cycles (Iversen 1957, Andersen 1994) and related forcing factors, i.e. astronomical cycles (Imbrie et al. 1984), our understanding of driving mechanisms operating at smaller scales (centennial/millennial) remains relatively limited. Although the use of lake sediments, which has been the main source of palaeoenvironmental information, stretches far back in time (e.g. Agassiz 1850), most of the advancements in palaeolimnology (i.e. the study of lake deposits to infer past limnological changes) have taken place in the recent decades (e.g. Smol 1980, Hodgson et al. 1997, Battarbee 2000). Palaeoenvironmental studies on lake deposits have provided records of sediment geochemistry (LOI, TOC, C/N, XRF), biological assemblages (pigments, pollen, macrofossils, chironomids, cladocera, diatoms), stable isotopes ($^{18}$O, $^{13}$C, $^{15}$N) and lithological characteristics (grain-size, laminations). These records have in turn been used to reconstruct complex lake histories and to make conclusions of Holocene environmental and climate change and the effects of in-lake processes on biological assemblages (Birks et al. 2000, Velle et al. 2005, Anderson et al. 2008). Similar studies and especially studies including plant macrofossils are scarce in northern Fennoscandia, and notably few macrofossil records are available from both the northern boreal zone as well as the tree-line ecotone (Barnekow and Sandgren 2001, Bjune et al. 2004, Väliiranta et al. 2005, Väliiranta et al. 2011, Siitonen et al. 2011, Birks et al. 2012). Most studies in this region have focused on the Holocene climate development using primarily biotic proxies (e.g. Rosén et al. 2001, 2003), but often only one or two biological assemblages have been studied (e.g. Korhola et al. 2000, 2002, Larocque and Bigler...
2004, Larocque and Hall 2004, Seppä et al. 2009). It should also be noted that only few of these records date back to the earliest part of the Holocene, i.e. prior to 10 000 cal. a BP (Kujansuu et al. 1998, Szeroczyńska et al. 2007).

Research objectives

The overall aim of this thesis was to reconstruct palaeoenvironmental variations based on the Lake Loitsana sediment sequence (NE Finland), which is located in the northern boreal forest zone of Fennoscandia (Fig. 1), and covers most of the Holocene. Main focus is on the Holocene, particularly the early and mid-Holocene (prior to 4200 cal. a BP), but also include data derived from the adjacent ancient sediment basin where the sediment sequence represents MIS 5d-c (c. 110–94 BP; Martinson et al. 1987).

The present study is part of a larger project on the late Weichselian-Holocene climate and environment changes at nearby Sokli, funded by the Swedish Nuclear Fuel and Waste Management Company (SKB). The aim of this project is to reconstruct depositional environments, vegetation development and climate changes in northeastern Finland during a series of ice-free periods. Results from this study will contribute to assessments of long-term safety of a planned repository for used nuclear fuel in Sweden (SKB 2006), since these safety assessments focus on a time period of 100 000 years and more, thus covering the timescale upon which Quaternary ice-sheet cycles have operated. The effect of glacial conditions upon repository safety needs to be analysed and evaluated. In this context, characterising environmental conditions following deglaciation is of particular interest. Previous palaeoenvironmental studies at Sokli have focused on MIS 3 (c. 59–24 ka BP) and MIS 5d-c (c. 110–94 ka BP) interstadial stages (e.g. Helmens et al. 2007a, b, 2009, Vääränta et al. 2009). This work concentrates on a detailed multi-proxy environmental record of the Holocene epoch, which will provide important background information to understand the much longer-term, glacial-interstadial-interglacial, environmental changes. Questions that were addressed in this work included:
a) Lake development
   > What was the timing of early Holocene
deglaciation?
   > What were the characteristic biological
   and sedimentological features of the early
   Holocene glacial lake stage?
   > What local processes can be identified in
   the historical development of the subsequent
   Lake Loitsana basin?

b) Regional climate
   > Are locally driven changes in biological
   assemblages reflected in transfer-function
   based regional temperature reconstructions?
   > In light of proxy evidence, what is the most
   probable regional climate development dur-
   ing the Holocene?

c) Implications for glacial-scale environmental de-
velopment at Sokli
   > How does the Holocene record at Lake
   Loitsana support the interpretation of
   deposits from MIS 5d-c and other stages
   from the last glacial-interglacial cycle at
   nearby Sokli?

To achieve these goals high-resolution records of
sediment geochemistry (LOI, C/N, XRF), siliceous
microfossils (diatoms, phytoliths and chrysophyte
cysts) and macrofossils were compiled from an un-
usually thick (9m) lake deposit accumulated in Lake
Loitsana, NE Finland, that covers most of the
Holocene. The Holocene chronology is based on 14C
AMS dated terrestrial macrofossils from Lake Loit-
sana.

In order to comprehensively reconstruct lake ontogeny and to assess the potential local-scale/site-specific processes that drive changes in water chemistry and biological assemblages, the above mentioned data were incorporated with chironomid data (Engels et al.2013) and previously published
records of pollen (Salonen et al. 2013) derived from the
same sediment sequence. Quantitative $T_{jul}$ recon-
structions, based on pollen, chironomid and di-
atom records, were made using the transfer-function
approach whereas minimum $T_{jul}$ was inferred from
indicator plant species identified in the macrofossil
record (Salonen et al. 2013, this thesis). Biological as-
semblages are often used to infer past changes in tem-
perature, however, the complex nature of biotic re-
sponses to environmental change has made transfer-
function based reconstructions challenging to inter-
pret. In this work, particularly, the sensitivity of bi-
ological assemblages to different environmental vari-
able is assessed and the most probable Holocene
$T_{jul}$ development at and around Lake Loitsana is
discussed and evaluated against the evidence of local
development of the lake and the regional vegetation
development.

Study area

The study area, i.e. Lake Loitsana and the surround-
ing wetlands and the Sokli basin, is situated in the vicinity of the deserted mining hamlet of Sokli in NE
Finland (around 67°49’N, 29°17’E; Fig. 2). Regional
present-day vegetation is northern boreal forest with
birch (Betula pubescens and B. pendula), pine (Pi-
nus sylvestris) and spruce (Picea abies) as the dom-
inant tree species. The mean annual temperature in
the area is approximately -1 °C; mean January tem-
perature is -13.8 °C, mean July temperature is 13.4
°C, and mean annual precipitation is approximately
550 mm (Fig. 3). The Sokli area has in the last 40
years attracted numerous geology researchers due to
its rare local bedrock type (e.g. Paarma 1970, Pert-
tunen and Vartiainen 1992). The underlying bedrock
consists of a Palaeozoic carbonate-rich magma in-
trusion, the Sokli Carbonatite Massif (SCM; Fig. 2),
which is enriched in phosphorous, niobium, iron, sul-
phur and calcium and surrounded by bedrock consist-
ing of crystalline rocks of the Precambrian Shield
(Vartiainen 1980).

Previous research carried out on sediments recov-
ered from the Sokli basin have focused on geomor-
phology and stratigraphy (Johansson 1995, Helmens
et al. 2000), optically stimulated dating (Alexander-
son et al. 2008) and palaeoenvironmental reconstruc-
tions on various time scales (Helmens et al. 2007a, b,
et al. 2009). Extensive glacial lakes formed during the
latest deglaciation, in front of the retreating
ice margin of the Fennoscandian Ice Sheet (FIS),
have been reconstructed by Johansson (1995) using
raised shorelines, outlet channels, the distribution of
course-grained outwash and finegrained glacio-
lacustrine sediments, and topographic data. The re-
construction shows that glacial lakes covered vast ar-
eas in northern Finland. Most of the lakes, however,
were rather small and restricted to the deepest parts
of river valleys. The Sokli Ice Lake in NE Finland is
one of the glacial lakes reconstructed by Johansson
(1995). The main morphological features used in the
reconstruction, i.e. dry channels and deep canyons
carved out in the Precambrian crystalline rock, are
interpreted to represent glacial lake drainage sites or spillways. Minerogenic sediments underlying gyttja or peat are considered to be of glacio-lacustrine origin due to their relatively fine-grained lithology (Johansson 1995). The Sokli Ice Lake is the only ‘type 4’ glacial lake, i.e. a shallow lake with several meters thick bottom sediments and indistinct shore marks, reported from NE Finland (Johansson 1995). This type of glacial lake was, however, widespread in Sweden (Lundqvist 1972).

Lake Loitsana (67°48’18”, 29°16’56”E; 214 m a.s.l.) is situated in a former meltwater channel associated with northwest-southeast oriented eskers (Fig. 2C). Eskers situated northeast, northwest and south of the lake consist of sorted sands that were assum-

Figure 2. Orientation map showing A. the location of the study area; B. the regional setting; and C. the location of Lake Loitsana, coring site and geomorphology of the area (modified from Johansson (1995)). The light grey shading marks areas below 220 m a.s.l. whereas the darker grey shading marks higher elevations (10 m interval). X1 and X2 mark the location of sampling for basal peat dating from the Saunavuotso and Loitsana wetland, respectively. X3 marks the location of borehole 902 from which a basal peat age was inferred for the Sokli aapa.
Mean monthly temperature (°C)
Mean monthly precipitation (mm)
1971-2000
J F M A M J J A S O N D
-20
-10
0
10
20

Figure 3. Climatogram showing mean monthly precipitation and temperature for the time period of 1971-2000 for Savukoski, (67°17'N, 28°10'E, 193 m a.s.l.). Data were obtained from the Finnish meteorological institute.

The studies presented in this thesis are mainly based on down-core fossil data extracted from the Lake Loitsana sediment core (Papers I-III). Paper IV is based on the sediment record of the B-series borehole in the Sokli aapa. A summary of the methods that were used in each study (Papers I-IV) as well as the sample interval and the time period that each study covers are presented in Fig. 4. The methods and analyses employed to reconstruct palaeoenvironmental and palaeoclimatological variations from the Lake Loitsana sediment record are presented below.

### Sediment and sediment coring

Nine meters of lacustrine sediment were collected with a Russian peat corer (Jowsey 1966) from the ice-covered Lake Loitsana in spring 2008 (67°48'18"N, 29°16'56"E; 214 m a.s.l.). These sediments were used in the palaeoenvironmental reconstructions presented in papers I-III. The sediment succession consists of two major parts: a lower minerogenic unit (900–735 cm below sediment surface) and an upper organic unit (735–0 cm). The upwards-fining minerogenic unit consists mainly of fine sandy sediment (900–795 cm) and silt (795–735 cm) with increased clay content at 875–843 cm. The minerogenic unit at 900–795 cm contains nine sand layers (1–2 cm thick) and a 5 cm sand layer between 800 and 795 cm. The transition from the minerogenic to the organic-rich unit at 735–700 cm indicates a gradual change from silt with organic components to silty gyttja. The upper organic unit consists of 700 cm gyttja with alternating dark and light-brown layers and intervals with increased sand content at 700–635, 538–535, 377–340 and 70–35 cm below sediment surface. Diffuse laminations occur between 900 and 770 cm. Continuous laminations occur from 770 to 538 cm but are more distinct at 770–735 and 575–538 cm.

Six and a half meters of lacustrine sediment, situated 13.5–20.0 m below the wetland surface, were collected from the B-series borehole in the Sokli aapa in winter, 2002 (67°48'32"N, 29°18'28"E; ~220 m a.s.l.). These sediments were used in the environment-
Figure 4. The time span of each paper, methods and sample resolution used in respective study. MIS stages are taken from Martinson et al. (1987).

tatal reconstruction presented in paper IV. The succession consists of ~2 m silty-sandy sediments, which are overlain by a 2-m densely compacted laminated sandy gyttja. The gyttja unit is disrupted by a hiatus at 15.8–15.6 m depth. Layers of sand and gravel are found above and below this sediment succession.

Sediment geochemistry

**LOI measurements.** - In order to determine the organic and inorganic carbon content of the sediment, LOI was performed at 550 °C for four hours and 950 °C for five hours (Heiri et al. 2001) on samples of similar size (~1 cm³). The LOI (expressed as % dry weight) was calculated according to the following equations:

$$LOI_{550} = \frac{\left(DW_{105} - DW_{550}\right)}{DW_{105}} \times 100$$  \hspace{1cm} (1)

$$LOI_{950} = \frac{\left(DW_{550} - DW_{950}\right)}{DW_{105}} \times 100$$  \hspace{1cm} (2)

The dry weight (DW) of the sample, after drying at 105 °C, was measured before combustion (DW₁₀₅), after heating to 550 °C (DW₅₅₀) and after heating to 950 °C (DW₉₅₀).

**C/N analysis.** - Carbon and nitrogen concentrations were measured through combustion in a Carlo Erba NC2500 Elemental Analyzer at the Stable Isotope Lab at the Department of Geological Sciences, Stockholm University. Freeze-dried sediment samples were ground and the material weighed into tin capsules for C/N-analysis. To account for carbonates in the sediment, material was also taken from all samples for Corg-analysis. The material was weighed into silver capsules, treated with HCl (10%) and dried overnight before analysis. C/N ratios have proven effective in revealing the source of the organic matter. As the aquatic flora has a high nitrogen composition, samples with low C/N (<10) ratios are generally considered to indicate higher lake productivity while those with a high C/N ratio (>20) could be indicative of low lake productivity. However, this ratio is also affected by the amount of terrestrial remains transported into the lake and should therefore be interpreted with caution (Wetzel 2001).

**XRF core scanning.** – Recent advancements in the XRF technique have enabled nondestructive, in-situ XRF measurements at sub-millimetre scales.
This has made XRF core scanning increasingly popular during the last decade for the analysis of both marine and lacustrine sediment cores (Francus et al. 2009, Croudace and Rothwell 2010, Löwemark et al. 2011). The increasing number of studies focusing on XRF core scanning data derived from lacustrine sediment has linked sediment geochemistry to a wide array of variables such as minerogenic input, grain-size changes, lake level and productivity, and redox processes (Moreno et al. 2007, Kylander et al. 2011, 2012, 2013, Vasskog et al. 2012).

The ITRAX XRF core scanner, which was used in this study, produces ‘relative’ elemental data expressed in peak area rather than ‘absolute’ measurements (i.e. concentrations) like those acquired using conventional XRF analysis of distinct samples. In a palaeoenvironmental context, however, it is the relative changes in the elemental profiles, which are of interest. Nevertheless, in order to avoid the closed sum effect, normalisation of elemental data is required (Calvert 1983, Rollinson 1993, Weltje and Tjallingii 2008). When working with homogenous sediments, normalisation by the incoherent + coherent scattering has been used to correct for various instrumental parameters such as dead times and tube aging. When dealing with sequences with highly variable matrices however, dilution effects from e.g. carbonates and organic matter (Löwemark et al. 2011, Kylander et al. 2013) require data normalisation with an element that is conservative and biologically unimportant. One such element is Ti, which has been utilised to reveal patterns that are undetectable in single elemental profiles (Moreno et al. 2007, Kylander et al. 2011).

In this study, XRF-data are used to detect environmental and catchment changes recorded in the Lake Loitsana sediments during the early Holocene. The cores were scanned using a molybdenum-tube at 2 mm resolution (voltage 30 kV, current 45 mA) and 30 s measuring time (cf. Croudace et al. 2006). Focus lies on the minerogenic unit and the transition to more organic sediments.

**Biotic proxies**

Fossil assemblages of pollen, macrofossils, diatoms and chironomids were extracted from the Lake Loitsana record and used to reconstruct the lake ontogeny (paper II) and make transfer-function based temperature reconstructions (paper III). The response of diatoms to environmental change was further assessed in paper I and IV. The analyses were performed following standard procedures as described in Fægri and Iversen (1989) for pollen, Birks (2007) for macrofossils, Battarbee (1986) for diatoms and Brooks et al. (2007) for chironomids. A combination of these proxy assemblages was used in order to avoid uncertainties related to single-proxy approaches and to facilitate the discrimination between local and regional drivers of changes in species distribution and abundance.

Pollen records are commonly employed to reconstruct vegetational history and to infer past climate changes. The interpretation of pollen rain can be challenging, however, as it is composed of different proportions of local vegetation and long-distance transported pollen (Birsks and Birks 2000), and local presence of certain species is difficult to deduce. This relationship is particularly important in areas where pollen production is low (e.g. the artic or alpine areas) and where the long distant transported pollen may dominate the pollen record.

Using a combination of macrofossils with pollen facilitates not only the interpretation of local vegetation development but often also yields a higher taxonomic resolution as plant macrofossils can often be identified to genera or even species level (Birks and Birks 2000; Birks 2007). Macrofossil records are apart from being useful to reconstruct local vegetation, also a valuable tool when addressing lake development, particularly when aquatic macrophytes, chironomids, diatoms and cladocera data are combined. These organisms are often found interacting with each other (van Donk and van de Bund 2002, Velle et al. 2005, Siitonen et al. 2011, Vääränta et al. 2011). In this study, macrofossils are also used to reconstruct minimum $T_{jul}$ based on presence of wetland and aquatic indicator taxa and their current northern limit (Iversen 1954, Kolstrup 1979, Vääränta et al. 2009). Minimum $T_{jul}$ values of these taxa are inferred from current species distribution maps (Lampinen and Lahti 2013) and the mean July air temperatures (1961–2000) calculated from daily measurements by Finnish Meteorological Institute (Venäläinen et al. 2005).

Diatoms have a long track record in palaeoenvironmental studies (e.g. Holst 1899, Sundelin 1917, Cleve-Euler 1922) and have been used to infer a wide range of environmental variables (pH, DOC, TOC, minerogenic turbidity, temperature) as they are particularly sensitive to water body conditions and respond rapidly to environmental change (e.g. Renberg and Hellerberg 1982, Fritz et al. 1991, Wumsam and Schmidt 1995, Smol and Cumming 2000).

While it has become evident that diatom-based Holocene temperature reconstructions can be relatively ambiguous (Bigler 2001), chironomids have shown a particular prominence in this aspect and are currently widely used to reconstruct Holocene July
Data analysis

Principal Component Analysis (PCA). – Detecting trends in compositional data is often not particularly straightforward. In such cases, using ordination techniques can be useful as they reveal relationships among the data. There are several ordination techniques available, with or without stratigraphical constraint of the data. Stratigraphically constrained ordination techniques such as PCA, work by identifying the first few axes, which capture the major variability of the data (Birks 2012 and references therein). This can be particularly useful when working with large data-sets such as the geochemical record obtained through high-resolution XRF core-scanning. To handle this data-set and detect potential correlations between different elemental profiles, a PCA was made using JMP 9.0.0 software (correlation mode, varimax rotation). Since the original data were initially normalised, the data-set became subsequently ‘closed’. All elemental profiles were therefore log transformed prior to analysis in order to avoid the closure effect of compositional data (e.g. Aitchison 1982).

Transfer-functions. – The most commonly used method to infer past changes in various environmental variables (e.g. temperature) is the multivariate calibration-function (Imbrie and Kipp 1971, Birks et al. 1990, ter Braak and Juggins 1993) more commonly referred to as the ‘transfer-function’ approach (Birks et al. 2010). Shortly, this method involves two steps: the regression and the calibration. The former involves the establishment of modern relationships between taxa and the parameter to be reconstructed. This requires a modern calibration set (c-set) with a number of calibration sites (for instance lakes) for which various environmental characteristics (e.g. depth, temperature, pH, conductivity, alkalinity, number of taxa) have been measured. These sites are chosen along a gradient that covers changes in the parameter of interest (pH, temperature, TOC). During the calibration step, the established relationship is used in combination with the fossil data to infer past changes in e.g. temperature.

The calibration site where the modern assemblage resembles the fossil assemblage most yields the inferred temperature. The temperature estimate can be based on assemblages from one calibration site or it can be a weighted average estimate of several calibration sites. The transfer-function approach has 5-6 basic assumptions. One of these assumptions is that variables other than the one to be reconstructed, have insignificant influence (Birks et al. 2010 and references therein, Juggins 2013). This is, however, not always the case when working with biological assemblages, which can complicate transfer-function based reconstructions of e.g. $T_{jal}$ (Anderson 2000, Rosen et al. 2003, Juggins 2013).

There are a number of various regression calibration models available for quantitative reconstructions (Birks et al. 2010). Transfer-function based $T_{jal}$ reconstructions presented in paper III are prepared according to Salonen et al. 2013 (pollen) and Luoto et al. in press (chironomids). The diatom inferred $T_{jal}$ make use of a combined c-set (Weckström 2001, Weckström et al. 2003, Solovieva et al. 2005, 2008) with 178 calibration sites. A LWWA regression model with a selection of the 50 calibration sites that were most similar to the fossil data in terms of species composition is used in this reconstruction.

Zonation. – When working with stratigraphical sequences, large data sets are common. In order to facilitate the description and highlight correlations, fossil data are usually divided into zones. The techniques available today are divided in two categories; splitting or divisive and agglomerative techniques. The former works by splitting the data set into smaller groups, while the latter clusters stratigraphically adjacent samples into larger groups (Birks 2012). In this study, an agglomerative technique (constrained incremental sum-of-squares: CONISS) was used for pair-wise clustering of samples with the highest compositional similarity. While zonation of the MIS 5c diatom record was performed in Tilia 1.7.16 (Grimm 2011), numerical analyses related to the zonation of all Holocene records were carried out using R 2.12.2 (R Development Core Team 2011) with the additional packages Rioja (Juggins 2009) and Vegan (Oksanen et al. 2011). The broken-stick model was employed to estimate the number of potentially significant zones in the record (Bennett 1996). Although numerical techniques provide results that are repeatable and less subjective than the traditional approach, i.e. visual examination of the data (Birks and Gordon 1985), the main patterns can be captured by both approaches. The zones obtained through numerical analyses were therefore used as
a guideline for the final zonation (i.e. lake stages), which was carried out visually in all studies.

Chronology

Dating control. – Age-depth estimations in lacustrine sediments are commonly established through radiocarbon dating. The method involves measurement of carbon isotopes from e.g. dead plant tissue, more particularly the procedure measures the relation between unstable $^{14}\text{C}$, which decreases at a constant rate, and the stable isotopes $^{12}\text{C}$ or $^{13}\text{C}$. These three isotopes are naturally occurring in the atmosphere and are incorporated into plants through uptake of CO$_2$ during photosynthesis (Hajdas 2006). The ratio of $^{14}\text{C}$ to $^{12}\text{C}$ or $^{13}\text{C}$ in the plant tissue is therefore in equilibrium with that of the atmosphere until the time of death (Libby et al. 1949) after which $^{14}\text{C}$ is reduced with time. As the half-life of $^{14}\text{C}$ is known, it is possible to date the timing of death by measuring the ratio of $^{14}\text{C}$ against the stable forms of carbon. However, variations in the production of these isotopes vary both geographically and over time and calibration curves need to be used to convert radiocarbon ages to calendar years (Olsson 1991). This conversion is often challenging due to wiggles on the $^{14}\text{C}$ calibration curve. Moreover $^{14}\text{C}$ age plateaus can cause converted ages that have a probability distribution spanning over several hundred years (Hajdas 2006, Reimer et al. 2009). Other possible problems with the radiocarbon dating method include contamination by old inorganic carbon or soil carbon from the catchment that is incorporated in the tissues of aquatic macrophytes and brown mosses thereby resulting in too old ages (MacDonald et al. 1991).

The radiocarbon calibration curve for the northern hemisphere (IntCal09) that now extends back to 50 000 cal. a BP, is based on empirical tree ring data, which provide a direct measure of atmospheric $^{14}\text{C}$, and reservoir-age-corrected marine data (Reimer et al. 2009). Age determination for the Holocene sediment succession was therefore established through the use of AMS radiocarbon dating. The age of the MIS 5c-d sediment record, however, was determined using OSL dating, as its age beyond the limit of radiocarbon dating (Alexanderson et al. 2008). OSL dating has developed rapidly over the last decades (e.g. Murray and Wintle 2000, Alexanderson 2002, Duller 2006, Preusser et al. 2009, Blomdin et al. 2012). Basically, OSL dating works by measuring a luminescence signal, in minerals such as quartz and feldspars, which is sensitive to both light and heat. When sediments are exposed to sunlight or heat this signal begins to deteriorate and is eventually erased (also known as sediment bleaching). In order for OSL dating to work, it is essential for the sediments to become completely bleached and then buried. The OSL date is then derived from the luminescence signal, which begins to accumulate once the sediment is buried and yields the age of sediment burial (Preusser et al. 2008). The dating of the MIS 5d-c sediments was performed on quartz grains extracted from samples consisting of fine medium sand (Alexanderson et al. 2008).

Calibration and age-depth modelling. – Radiocarbon dating was performed by accelerator mass spectrometry (AMS) on plant macrofossil remains in Poznań Radiocarbon Laboratory, Poland. Samples were washed in a fine jet of water through a 100-µm sieve. The residue was analysed in a Petri-dish for appropriate dating material, which was put in glass vials filled with distilled water and a small drop of 10% HCl for preservation purposes. The radiocarbon dates were calibrated into calendar years before present (cal. a BP) using IntCal09 (Bronk Ramsey 2009, Reimer et al. 2009) in R 2.12.2 software (R Development Core Team 2011). A smooth spline model was applied to the dates using the CLAM 2.1 package (Blaauw 2010) for R. Weighted average estimates and sediment accumulation rates (cm a$^{-1}$) are based on both the entire calibrated distribution of all dates and the applied model. These point estimates are, according to Blaauw (2010), more likely to give a robust age estimate than e.g. the median as all dating information is taken into consideration. The Lake Loitsansa chronology is compared with two basal peat dates from the adjacent Saunavuotso and Loitsana wetlands (Fig. 2C: X1 and X2, respectively) and one inferred date from borehole 902 (Helmens et al. 2000) in the Sokli aapa (Fig. 2C: X3).

Results

The next chapters provide summaries of four papers presented in this thesis.

Paper I

Palaeoenvironmental record of glacial lake evolution during the early Holocene at Sokli, NE Finland

Shyhrete Shala, Karin F. Helmens, Krister N. Jansson, Malin E. Kylander, Jan Risberg and Ludvig Löwemark

A palaeoenvironmental record of glacial lake development, following the ice-marginal retreat of the FIS in NE Finland, is presented in this study. A 3-m-thick
Figure 5. Summary of palaeoenvironmental data and stages during the early Holocene glacial lake development and initiation of Lake Loitsana. For lithology legend see Fig. 6.
silt eroded from exposed shorelines were deposited into the lake during the shallow water glacial-lake stage, diatom abundances sharply decreased and pioneering Staurosira venter dominated the turbid waters. A change to higher diatom abundances and increased species richness marks the final drainage of the glacial lake and initiation of gyttja deposition in Lake Loitsana.

**Paper II**

**Evaluating environmental drivers of Holocene changes in water chemistry and aquatic biota composition at Lake Loitsana, NE Finland**

Shyhrete Shala, Karin F. Helmens, Minna Väleranta, Tomi P. Luoto, Jan Weckström, J. Sakari Salonen and Peter Kuhry

This comprehensive study based on sediment characteristics, geochemical data and biological assemblages (pollen, macrofossils, chironomids and diatoms) was conducted to reconstruct the development of Lake Loitsana and evaluate driving agents to changes in water chemistry and biological assemblages throughout the Holocene. Exhaustive records of macro- and microfossils of aquatic and wetland plants, zoological taxa and diatoms are here compared to chironomid records (Engels et al. submitted) to facilitate the discrimination between local and regional factors and study potential interactions between the aquatic biota. The presence of an early Holocene proglacial lake makes this study particularly interesting, as there are few studies from the northern boreal forest zone of Fennoscandia that include such an initial development stage and deal with multiple biological assemblages.

Ten samples from the Lake Loitsana sediment sequence were dated (Fig. 6). Two samples were considered to be too old and were excluded from the age-depth model. In contrast to the other dated samples, which were performed exclusively on terrestrial plant
remains, these two samples also contained unidentified epidermal remains, most likely of aquatic origin and were thus most probably contaminated by old carbon as Loitsana is a hard water lake with carbonates in circulation (MacDonald et al. 1991). The lowermost radiocarbon date (760–755 cm) of the remaining eight samples provided an age of c. 10 730 cal. a BP, thus confirming that the core represents most of the Holocene epoch. No material suitable for dating was obtained from the lowermost 140 cm of minerogenic sediment (900–760 cm). It can, however, be assumed that these sandy sediments were deposited at relatively high sedimentation rates and most likely represent a short time period. The sediment record suggests that the lake development was complex and included i) a proglacial lake stage ii) the subsequent glacial lake drainage and formation of Lake Loitsana, iii) a history of fluvial input affected by nearby wetland expansion, which caused the redirection of a major streamlet and iv) lake in-filling in an eventual groundwater-fed shallow lake (Fig. 7). These three local factors have in turn driven changes in the fossil assemblages by influencing water body conditions (pH, stratification, trophic state, turbidity, and turbulence), available substratum, fluvial activity, rate of sediment influx, water depth and shore erosion.

The biological assemblages reflect changes in different environmental parameters in a highly individual manner, which emphasises the importance of using multiple proxies in palaeoenvironmental studies. The results further suggest that biological assemblages can themselves act as important driving agents in providing habitat and food thus promoting changes in the composition of other assemblages. This is particularly evident in Lake Loitsana when considering aquatic macrophyte abundance, more exactly Myriophyllum, which in this study appears to be an important driving factor for Corynocera ambigua, a chironomid with a modern distribution in

Figure 6. Age-depth model, lithology and accumulation rate for the Lake Loitsana sediment sequence.
Figure 7. Summary of multi-proxy record of the Holocene Lake Loitsana sediment sequence (modified from paper II). Diatoms are grouped according to living habitat and reworked/Tertiary taxa; the abundance of phytoliths and chrysophyte cysts is relative to the sum of all siliceous microfossils. Chironomids are grouped according to their trophic state preference (Luoto 2011b); oligotrophic = 5–15, mesotrophic = 15–25 and eutrophic = 25–100 TP µg/l. The percentage of stream taxa includes semi-terrestrial taxa (<2% abundance). Plant macrofossils are presented as bars showing concentrations per 10 cm$^3$ or as relative abundance of remains. For a detailed lithology see Fig. 6.
Finnish lakes related to cold oligo-mesotrophic waters (Luoto 2011b). It is concluded that even though lake and catchment development are linked to regional-scale factors, observed changes in lake biota also reflect local-scale processes within the lake (proper stream re-direction and infilling) and the immediate surrounding catchment area (wetland initiation and forest development). Taking local environmental factors into account when conducting quantitative environmental/climatic reconstructions based on biological assemblages is therefore not only necessary in order to assess their impact on these reconstructions but might also provide an explanation to the different responses of these proxies.

**Paper III**

**Assessment of quantitative Holocene temperature reconstructions using multiple proxies from the Lake Loitsana sediment record**

Shyhrete Shala, Karin F. Helmens, Tomi P. Luoto, J. Sakari Salonen, Minna Väätäinen and Jan Weckström

Four mean July air temperature ($T_{jul}$) reconstructions, based on biotic proxies extracted from the Holocene sediment sequence of Lake Loitsana, were in this study evaluated in relation to each other and local-scale/site-specific processes in the lake development. These latter factors have been shown to significantly influence the species distribution of the fossil assemblages. The aim was to assess the reliability of each reconstruction and the most likely Holocene development of $T_{jul}$, particularly the timing of highest $T_{jul}$. Similar approaches were used where possible in order to make the transfer-function based reconstructions comparable with each other. Pollen and chironomid-based $T_{jul}$ was reconstructed using a two-component WA-PLS regression calibration model (ter Braak and Juggins 1993) and the diatom-based $T_{jul}$ was reconstructed using a LWWA regression model with classical deshrinking (see Juggins and Birks 2012). The reliability of the reconstructions was assessed using the compositional fit (squared chord distance) between fossil samples and their closest modern analogues in the c-set, the temperature optima (WA-optima) of the dominating taxa as well as the distribution of lakes along the temperature gradient of the c-set. Minimum $T_{jul}$ values were inferred based on the presence of indicator plant taxa. The reconstructed $T_{jul}$ display highly differentiating patterns throughout the Holocene (Fig. 8).

While pollen-based temperatures follow the classical trend of relatively low early Holocene $T_{jul}$ and a mid-Holocene maximum in July warming, the plant macrofossils and chironomids reconstruct high $T_{jul}$ already during the early Holocene, i.e. at the peak of summer insolation. The diatom-based reconstruction displays least variability, (only 0.6 °C amplitude) throughout the entire Holocene. The evaluation in relation to local-scale/site-specific processes revealed that the reconstructions are influenced at least to some extent by local factors, which further emphasises the advantage of using multiple proxies when reconstructing climate variables. The poor compositional fit and low pollen-based $T_{jul}$, reconstructed during the early Holocene, is attributed to an over-representation of locally produced pollen of Cyperaceae, Equisetum and Gramineae (syn. Poaceae) in the fossil samples. These taxa are commonly found in tundra vegetation and have thus low temperature optima in the c-set. Minimum $T_{jul}$ values of 15 °C are inferred from the presence of plant macrofossils (Typha and Glyceria lithuanica) during the early Holocene. These temperatures might have prevailed until 6500 cal. a BP if the presence of Typha pollen is interpreted as local. The chironomid-based $T_{jul}$ reconstruction appears to have been mainly affected by processes such as macrophyte abundance, DOC and the general infilling of the lake. While shallow water conditions, resulting from the general lake infilling, caused an overestimation of $T_{jul}$ values during the late Holocene, macrophyte abundance and DOC appears to have favoured the abundance of cold water Corynocera ambigua and cold stenotherm C. olivieri thus causing underestimation of the reconstructed $T_{jul}$ during mid-Holocene. However, maximum warming based on chironomids is found consistently in the early Holocene irrespective of local lake development. The diatom-based $T_{jul}$ values were found to be underestimated mainly due to two factors; the mass-occurrence of Fragilariaceae, which constitute more than 90% of the total abundance and have a low WA-optima (~11.5–12.5 °C), and the uneven distribution of calibration sites along the temperature gradient of the c-set with the majority of the c-sites within the range of 11.1–13.0 °C (Fig. 9).

It is concluded that although site-specific processes have clearly had a large effect on the relatively low early Holocene pollen $T_{jul}$, this might further have been influenced by a delay in response of terrestrial vegetation to climate change at Lake Loitsana, NE Finland. The early-Holocene warming as suggested by the aquatic/wetland ecosystem in the Lake Loitsana sequence (chironomids, macrophytes) seems to be reliable, indicating a $T_{jul}$ about 2 °C higher, or more, compared to present-day.
Figure 8. Summary of the local development of Lake Loitsana (as reconstructed in paper I and II). Holocene pollen and chironomid-based $T_{jul}$ reconstruction using a two-component weighted averaging-partial least squares (WA-PLS) regression. LOESS smoother (span 0.25, one robustifying iteration) is added to both $T_{jul}$ reconstructions. The diatom-based reconstruction using locally weighted weighted average (LWWA) with classical deshrinking is displayed with a LOESS smother. Summary diagram of Holocene development of terrestrial vegetation extended after Salonen et al. (2013). Selected pollen (grey silhouette) and macrofossil remains (dashed line) of taxa displaying local presence are also included. The 60°N summer and winter insolation (Berger and Loutre 1991).
**Figure 9.** The distribution of lakes along the sampled temperature gradients of the diatom calibration set (7.9-15.7 °C), chironomid calibration set (7.9-17.0 °C) and pollen calibration set (9.0-17.3 °C).

**Paper IV**

**Large shifts in vegetation and climate during the Early Weichselian (MIS 5d-c) inferred from multi-proxy evidence at Sokli (northern Finland)**

Karin F. Helmens, Minna Väliiranta, Stefan Engels and Shyhrete Shala

In this paper, an extensive record consisting of multiple proxies (macrofossils, chironomids, siliceous microfossils, loss-on-ignition and lithological characteristics) is integrated and combined with chironomid and indicator plant species-based palaeotemperatures. The record was extracted from sediments of MIS 5d-c age preserved in the Sokli basin and used to infer the vegetation, depositional and climate history at Sokli (NE Finland). The chronology was constrained with two OSL dates. The samples were taken at 14 m and 15 m depth from sediment surface, and yielded ages of 94±16 and 94±19 ka BP (Alexander et al. 2008). The results suggest highly dynamic landscape changes. During MIS 5d the landscape was characterised by a braided-river environment, steppe-tundra vegetation and strong continental conditions. This was followed by the development of an oxbow lake during MIS 5c; the ongoing terrestrialisation as a result of the gradual infilling led to a return to stream-channel deposition during the late part of MIS 5c. A mixed boreal forest was developed as birch, pine and spruce (in that order) established in the area. The vegetation gradually opened up during the late part of MIS 5c, which was followed by the MIS 5b stadial. This study also suggests mean $T_{jul}$ of at least 12–14 °C during MIS 5d and of several degrees higher than present day (13.4 °C) during MIS 5c. The diatom assemblage presented in this study was extracted from the laminated unit of sandy gyttja deposited during early and mid-MIS 5c (Fig. 10). The record is characterised by mass-occurrence (>20%) of *Staurosira venter* and *S. construens* throughout the record and high abundances of *Staurosira binodis, Staurosirella lapponica, S. pinnata, Pseudostaurosira brevistriata, Fragilariforma neo-producta, Martyana martyi* and *Staurosira binodis* (henceforth Fragilariaceae). Fragilariaceae species are generally considered to be opportunistic and pioneering due to their wide range of ecological preferences (Smol 1983, Anderson 2000). They are favoured by relatively high alkalinity (Battarbee, 1986) and are often found in lakes that have some sort of disturbance such as proglacial environments (Bigler et al. 2002, Risberg et al. 1999). Relatively high abundances of phytoliths, chrysophyte cysts and Tertiary diatoms during the early stages of MIS 5c are associated with low concentrations of diatoms, most likely due to erosion caused by flooding during the earliest phase of infilling of the oxbow lake. The on-going infilling of the lake eventually initiated terrestrialisation and a more diverse diatom flora developed. An increased nutrient availability, reflected by increasing abundances of e.g. *Stephanodiscus parvus* and *Cocconeis placentula v. euglypta*, and continuous fluvial influx (*Meridion circulare*) is recorded throughout MIS 5c. Supplementary information associated to this paper is available online at doi: 10.1016/j.quascirev.2012.02.008.

**Discussion**

**Holocene development of the Sokli Ice Lake and Lake Loitsana**

As the margin of the FIS retreated towards the north-west during the early Holocene deglaciation, meltwater was trapped between the ice-sheet and the higher terrain to the east, and a glacial lake was formed. The time period during which this glacial lake existed has been estimated to less than 100 years (Johansson 1995). Although the timing of deglaciation around Lake Loitsana roughly corresponds with the early Holocene regional deglaciation pattern reconstructed for northern Finland (Johansson et al. 2011), due to the low accuracy of the available dates from Lake Loitsana, which hampers precise age estimation, it is difficult to estimate the exact the life...
span of the glacial lake itself. In general, the Lake Loitsana sediment record suggests a shallowing lake with four limnological phases that had major impacts on the Holocene sedimentation dynamics, water chemistry and composition of biotic assemblages. These stages are i) a deep glacial lake phase ii) the drainage of this glacial lake, which led to the formation of a smaller and shallowing glacial lake and eventually the much smaller Lake Loitsana, iii) a phase with changes in fluvial input affected by nearby wetland expansion, which caused the redirection of a major streamlet and iv) a gradual infilling of an eventual principally groundwater-fed lake.

Deep glacial lake phase. – The presence of a proglacial lake makes this study interesting as few studies from the northern boreal forest zone of Finland include such an initial developmental stage (Kujansuu et al. 1998; Fig. 1B: 1, Szeroczyńska et al. 2007; Fig. 1B: 2). These sediments are of importance as they allow us to conduct high-resolution studies of environmental and climate conditions directly following the latest deglaciation. At high northern latitude sites, such as Lake Loitsana, this event coincides with the period of high summer insolation (Fig. 8). The aquatic flora (i.e. siliceous microfossils, bryozoa) was during this time, mainly affected by physical factors such as rate of sediment influx, turbulence and possibly reduced light penetration caused by suspended minerogenic material (i.e. turbidity). For example, low diatom abundances, associated with high accumulation rates, have been recorded in sediments of Lake Inarijärvi in NE Finland (Kujansuu et al. 1998), the Baltic Ice Lake (Kabailienė 1995; Fig. 1B: 3) and Lake Agassiz in North America (Risberg et al. 1999; Fig. 1A: 4). Cold and deep-water associated chironomid taxa Heterotrissocladius maeeri-type and Tanytarsus lignens-type and bryozoan Fredericella indica inhabited the glacial lake; the former is also reported to have dominated the deep waters of the late-glacial Baltic Ice Lake (Luoto et al. 2010; Fig. 1B: 5). The surrounding vegetation of the newly deglaciated land was initially relatively open and characterised by shrubs (Betula nana, Salix) and wetland taxa (Carex, Equisetum, Glyceria lithuanica, Juncus and Sphagnum). Tree Betula was present already during the early Holocene, corresponding with previous finds from northern Finland (Väliranta et al. 2005; Fig. 1B: 6) and northern Sweden (Barnekow and Sandgren 2001; Fig. 1B: 7).

Glacial lake drainage. – The glacial lake drainage initiated at c. 10 500 and was completed at c. 10 200 cal. a BP, which corresponds roughly to that of Lake Inarijärvi further north (Kujansuu et al. 1998). As the proglacial lake was progressively drained, Lake Loitsana was confined to a topographical depression and was affected by shore erosion from the newly exposed areas. The subsequent more abundant presence of littoral/wetland (Callitriche spp, Potamogeton...
aton spp, *Myriophyllum, Typha*) and terrestrial (*Betula, Salix*) taxa in the macrofossil record might reflect the closer proximity of the coring site to the shore (Hannon and Gaillard 1997). In the case of Lake Loitsana, however, changes in distance of the coring site to the shore, appear not have been important for the presence of different macrofossils in the sediment record, probably due to the steep-sloped nearby esker facing the lake. The increased abundance in macrofossils might thus also be the effect of shore erosion. Relatively rich early Holocene aquatic vegetation was also found in the alpine Lake Njargajavri further north (Väiranta et al. 2005). The reduction in lake volume following the final drainage of the glacial lake, combined with an increased input of sediment, caused a morphometric eutrophication (cf. Hofmann 1998). This is mainly reflected by the continuous occurrence of the hypereutrophic diatom *Stephanodiscus parvus*. High relative contributions of trace elements in the sediment support the interpretation of increased input from the local Sokli Carbonatite Massif.

Changes in fluvial input affected by nearby wetland development. – Changes in surface inflow patterns into to Lake Loitsana, have clearly affected the species composition of macrofossils, chironomids and diatoms directly (input of rheophilic species) and indirectly (input of minerogenic particles/DOC). The influx was particularly pronounced between 10 200 and 6800 cal. a BP. Fluvial input to Lake Loitsana diminished after 6800 cal. a BP and is reflected as a marked reduction in stream indicators in the sediment record. Input reduction corresponds with a wetland expansion along the lake’s southern shores, which resulted in a diversion of the Soklija. The high carbon content, lack of fluvial influx (i.e. rheophilic diatoms and chironomids) and high amount of chrysophyte cysts further suggests that the lake might have been temporarily isolated between 6800 and 6300 cal. a BP. This time period corresponds roughly with lowest lake levels recorded in Lake Jierstivaara and Lake Njargajavri, Finnish Lapland (cf. Korhola et al. 2005; Fig. 1B: 8; Väiranta et al. 2005). In the Lake Loitsana record, however, there is no clear stratigraphical evidence indicating a shallow lake phase. Therefore, it may be that the temporarily isolated phase is caused by local hydrological changes at the surroundings. Lake Loitsana became a mainly groundwater fed lake from c. 6300 cal. a BP and received almost no surface inflow after c. 4300 cal. a BP.

Lake infilling. – The progressively infilling Lake Loitsana initially derived its sediments from a large catchment area stretching beyond the boundaries of the local bedrock. Following the proglacial lake drainage, these sediments originated from a much more confined catchment with strong carbonatite imprint. The mid-Holocene stream diversion resulted in a further confinement of the catchment area; after this the sediment input was mostly of very local origin and sedimentation rates decreased significantly. The long-term natural acidification that is typical for most tree-line lakes in northern Fennoscandia (Korhola and Weckström 2004, Sarmaja-Korjonen et al. 2006; Fig. 1B: 6) was not observed in Lake Loitsana where the pH remained at ~7.2–7.7 throughout the Holocene. It is possible that the alkaline nature of the bedrock kept the lake well buffered; however, pH >7 is not unique for Lake Loitsana as this has also been observed in other high latitude lakes such as alpine Lake Somaslampi (Szeroczyńska et al. 2007) and boreal Lake Kipojärvi (Väiranta et al. 2011; Fig. 1B: 9).

Detected changes in biological assemblages and potential driving factors

High abundances of Fragilariaceae characterised both the Holocene (papers I-II) and the MIS 5d-c sediment records (paper IV). Observed genera of this family are generally considered to be opportunistic and pioneering due to their wide range of ecological preferences and often dominate alkaline lakes that have some sort of disturbance, e.g. alpine proglacial lakes or recently deglaciated lakes with shallow photic zones (e.g. Battarbee 1986, Anderson 2000, Battarbee 2000, Bigler et al. 2002; Fig. 1B: 7; Ampel et al. 2009). In this study the mass-occurrence of Fragilariaceae appears to be favoured by the alkaline water and disturbances through fluvial/minerogenic influx as well as groundwater inflow from the esker. *Martyana martyi* in particular, has a preference for high ion content (Witkowski et al. 1995/96). As boreal conditions have prevailed almost since Lake Loitsana’s initiation, the length of the growing season or deficiency of nutrients have probably not been restricting factors affecting the aquatic macrophyte prevalence (cf. Väiranta 2006a, b; Fig. 1A: 10-13). In general, factors such as distance of the coring site to the shore and fluvial activity appear to be of greater importance to the macrophyte assemblages in the sediment record. This further highlights that absence of certain species in the fossil record should be carefully interpreted as it does not necessarily reflect its actual absence from the local vegetation (Birks 1973, Hannon and Gaillard 1997, Väiranta 2005). In Lake Loitsana, however, changes in water depth did not result in a marked
alteration of the distance to the nearest shore due
to the presence of an esker in the vicinity of the
coring site with a steep side facing the lake. Thus,
previously, any changes in water level had no sig-
nificant effect on macrophyte abundance. This is fur-
ther supported by the more or less consistent pres-
ence of littoral zone species such as Myriophyllum,
Potamogeton and large terrestrial remains such as
Betula throughout the record. An important aspect
of aquatic macrophytes is that they can themselves
act as environmental drivers by providing habitat
and food for other organisms. This is particularly
evident in the case of Corynocera ambiguus, which
is associated with higher abundances of Myriophyl-
tum. Corynocera ambiguus has a modern distribution
in Finnish lakes related to cold oligo-mesotrophic wa-
ters but is known to have a complex ecology (Broder-
sen and Lindegaard 1999). Pectocladus sordidellus-type is another example of taxa associated with
littoral vegetation and water depth (Tolonen et al.
2001; Fig. 1B: 14, Luoto et al. in press; Fig. 1B: 15)
and appear also in the Lake Loitsana record to have
been affected by macrophyte abundance. Other local
factors affecting chironomids species distribution in-
clude water body conditions (e.g. streaming water,
DOC). The presence of cold stenotherm Corynocera
oliveri-type in the sediment record coincides with in-
creased fluvial activity and might thus be driven by
increased DOC contents as allochthonous carbon con-
sists mainly of DOC (Jansson and Broberg 1994).
Corynocera oliveri-type has, though generally con-
idered a cold water indicator, also been found in
warmer lakes (Palmer et al. 2002) as well as associ-
ated to higher DOC concentrations in Canadian Arct-
ic lakes (Gajewski et al. 2005, Medeiros and Quinlan
2011).

Holocene climate development in NE Finland based on different proxy records

The rich and diverse fossil record extracted from the
Lake Loitsana sediment sequence allowed for $T_{jul}$
reconstructions dating back to c. 10 800 cal. a BP. A
comparison of the reconstructed $T_{jul}$ deviation from
present day mean July air temperature revealed that
both the absolute values and the general trends differ
considerably between the different proxies (Fig. 8).
It is inferred that changes in biological assemblages, i.e.
pollen, plant macrofossils, chironomids and diatoms,
driven by local scale/site-specific processes have had
an influence on quantitative reconstructions (paper
III). The diatom-based $T_{jul}$ displays a stable tem-
perature around 12 °C (i.e. below the present day
value of 13.4 °C). Only a minor dip occurs during
the early stages of Lake Loitsana correspond-
ing to the morphometric eutrophication phase (Fig.
8). Although diatoms have been shown to capture
Holocene climate variability (e.g. Bigler 2001), their
sensitivity to other variables (e.g. pH, trophic state)
complicates temperature reconstructions especially
during time periods when the other variables are not
constant (Battarbee 2000, Bigler and Hall 2003; Fig.
1B: 7). Paper III shows that the diatom-based $T_{jul}$
reconstruction is hampered throughout the Holocene
by the mass-occurrence of Fragilariaaceae as well as
by the design of the calibration set where the ma-
jority of the calibration-sites are within the range
of 11.1-13.0 °C. Diatom-inferred temperature recon-
structions are therefore not discussed further. Below
I will evaluate how local-scale/site-specific processes
may have hampered the temperature signal. The re-
construction outcomes are discussed against previous
studies from the region. Three focus time-windows
are used; the early Holocene; prior to 8200 cal. a
BP, the mid-Holocene; 8200–4200 cal. a BP and the
late Holocene; 4200 cal. a BP–present (Walker et al.
2012).

Early Holocene (prior to 8200 cal. a BP). – The
reconstructed early Holocene temperatures display
contrasting patterns (Fig. 8). Pollen-based recon-
structions display low $T_{jul}$ values (~2 °C be-
low present-day) while chironomids reconstruct high
$T_{jul}$ of at least 2 °C higher than present. The high
early Holocene $T_{jul}$ is further supported by indepen-
dent data provided by plant macrofossils, which sug-
gest minimum $T_{jul}$ of at least 2 °C above present
prior to 10 000 cal. a BP. The low pollen-based
$T_{jul}$ temperatures reconstructed by Seppä and Birks
(2001; Fig. 1B, 9) for NW Finnish Lapland and
Seppä et al. (2009), seem to be in accordance with
the Lake Loitsana pollen reconstructions. Both of
these records are, however, shorter than the Lake
Loitsana record and do not extend prior to 10 000
cal. a BP. The pollen reconstruction from Lake Loit-
sana, however, seems to be influenced by tapho-
nomic differences between the fossil data in rela-
tion to the calibration set (Salonen et al. 2013; pa-
per III). As the c-set is designed to delimit the
amount of local pollen in the modern samples, the
high abundance of locally produced pollen (Cyper-
aceae, Equisetum and Gramineae (syn. Poaceae))
in the early Holocene fossil samples of Lake Loit-
sana becomes a limiting factor for the pollen tem-
perature reconstruction. These taxa in the c-set are
commonly found in tundra vegetation and therefore
may result in too low $T_{jul}$. Warmer than present
chironomid-inferred $T_{jul}$ values are reconstructed
during the early Holocene. The taxa, which yield
these high temperatures (i.e. *Polypedilum nubeculo-

sum-type, *Chironomus anthracinus*-type, *Cricotopus cylindraceus*-type and *Procladius*) have been associated with both vegetation and trophic state in previous studies (Raunio et al. 2010, Eggemont and Heiri 2012). As parts of this time period were characterised by littoral vegetation and morphometric eutrophication, one might argue that the reconstructed temperatures are driven mainly by these factors. If these species were indeed driven by the local vegetation and higher trophic state, their highest abundance would be expected to be restricted to the time periods when these factors prevailed. This, however, is clearly not the case in the Lake Loitsana sediment record as higher abundances of these taxa occur also outside these phases (paper II). It seems, thus, unlikely that these factors have had a major impact on the species distribution and thus the reconstructed high $T_{jul}$ values, which prevailed already during the deep glacial lake phase and start to decline halfway through the morphometric eutrophication phase. Macrofossil inferred minimum $T_{jul}$ is based on the local presence of wetland/aquatic plant taxa. As such, this reconstruction is mainly restricted by taphonomic factors that affect the representation of remains in the fossil sample. Temperatures higher than present are inferred for the earliest part of the record. Macrofossil remains suggest present day temperatures from c. 10 000 cal. a BP onwards. Moreover, pollen of aquatic/wetland plants is generally said to have relatively local dispersal range (Krattinger 1975, Birks and Birks 2000, Ahee 2013). Accordingly the occurrence of *Typha latifolia* pollen supports the interpretation of warmer than present early Holocene July conditions. A similar pattern with high chironomid inferred $T_{jul}$ and low pollen inferred $T_{jul}$ have also been recorded in tree-line ecotone lakes (Jones et al. 2011; Fig. 1A: 16, Paas et al. 2011; Fig. 1A: 17, Salonen et al. 2011; Fig. 1A: 16, Luoto et al. in press, Paas 2013), while in northern boreal lakes on the Kola Peninsula high chironomid inferred $T_{jul}$ were reconstructed (Ilyashuk et al. 2013; Fig 1B: 18-19). Minimum $T_{jul}$ warmer than present have also been inferred from the boreal Lake Kipojärvi, northern Finland (Välirantta et al. 2011). The suggested very early Holocene warming, reconstructed by macrofossils and chironomids, is consistent with the contemporary high summer insolation (Berger and Loutre 1991) and also increased sunspot activity (Solanski et al. 2004) as well as high summer sea-surface temperatures (SST) from the Barents Sea (Hald et al. 2007; Fig 1A: 20).

**Mid-Holocene (8200–4200 cal. a BP).** Throughout this time period the pollen-based reconstruction displays $T_{jul}$ values higher than present day (i.e. 13.4°C). The temperature gradually increases until c. 7000 cal. a BP after which it remains around 14°C (Fig. 8). This increase is in accordance with the plant macrofossil reconstruction, which suggests at least present day temperatures during mid-Holocene. Chironomid inferred $T_{jul}$, however, display values below present day (13.4°C) with the exception between 6800 and 6000 cal. a BP when conditions slightly warmer than today, are reconstructed. The increase in pollen-inferred temperatures coincides with the migration and establishment of pine forest in the area, which is based on PAR, as well as occurrence of *Alnus, Filipendula* and long-distance transported *Corylus*. Warmer temperatures are generally driven by the occurrence of tree pollen such as *Pinus, Tilia, Ulmus, Corylus, Carpinus, Fraxinus*. With the exception of *Pinus*, these taxa are presently only found in the southernmost part of the calibration set (Salonen JS, personal communication). The low $T_{jul}$ values (>13°C) inferred from the chironomid assemblages between 8600 and 6800 cal. a BP as well as 6000 and 5000 cal. a BP, appear to be driven by high occurrences of *Corynocera ambigua* and *C. olivieri*-type, whose abundance/presence in this record appear to be driven by local-scale processes. Similarly, an influence of the river diversion on the chironomid assemblage and thus reconstructed $T_{jul}$ around 6500 cal. a BP cannot be ruled out as the observed change in species distribution appears to be related to locally driven changes in water body conditions (e.g. lack of fluvial input). To summarise, pollen and plant macrofossil-based $T_{jul}$ reconstruction seems to be least influenced by local-scale factors and thus they most probably reflect the regional mid-Holocene climate most reliably. Temperatures higher than present are in accordance with earlier regional temperature reconstructions (e.g. Renssen et al. 2009, Seppä et al. 2009).

**Late Holocene (4200 cal. a BP to present).** While plant macrofossils suggest at least comparable $T_{jul}$ throughout the late Holocene, pollen and chironomid reconstructions indicate higher than present $T_{jul}$ temperatures (Fig. 8). Relatively low spruce pollen percentages are encountered since c. 4000 cal. a BP in comparison to other sites in Finnish Lapland (Salonen et al. 2013). The WA-optima of *Picea* (15.2°C) is 4th highest among the dominating taxa in the e-set and this may to some extent have led to an overestimation of the reconstructed $T_{jul}$ values during the late Holocene, despite its underrepresentation in the fossil samples. Increasing chironomid-inferred temperatures from c. 4200 cal. a BP until present are clearly related to declining abundances of cold-indicating *Corynocera ambigua* and *Paratanytarsus.*
The most recent rise in $T_{jul}$ values from c. 1800 cal. a BP onward seems to be driven by increased abundances of warm indicating Cladotanytarsus mancus-type and Tanytarsus mendax-type (Eggermont and Heiri 2012). These taxa, however, have also a preference for shallow waters and nutrient-rich conditions (Brooks et al. 2007, Luoto 2011a). The inferred temperature of 15.2 $^\circ$C is therefore probably unrealistically high and driven by the further shallowing of the lake.

**Implications for interstadial environment reconstructions**

Palaeoenvironmental records extracted from older deposits at Sokli have provided evidence of a more dynamic Weichselian glaciation and warmer interstadial temperatures than previously thought (e.g. Helmens et al. 2007a, b, 2009, Vääranta et al. 2009). To date the interpretation of these older sediment deposits in the Sokli basin have lacked the reference baseline environment development succession description that is provided by this Holocene study. The lacustrine sediment sequence of Lake Loitsana is particularly interesting since most of the older deposits in Sokli also have a lacustrine facies. A particular issue that should be brought up in the study of Sokli deposits is the influence of the special type of bedrock in the area (Vartiainen 1980). The carbonatite deposit is richer in nutrients (e.g. phosphorous) than the surrounding Precambrian bedrock. This could possibly result in a local ‘fertilisation’ effect and anomalous ecosystem response. Accordingly, also the high temperatures reconstructed based on plant macrofossils and chironomids for the previous interstadial(s) can be speculated to be a result of the “fertilisation” effect. In the Holocene record of Lake Loitsana the reduction in lake size and volume following glacial lake drainage and the subsequent morphometric eutrophication, could have led to such a ‘fertilisation effect’ and anomalous environmental conditions due to the relatively large input of local carbonatite bedrock material. This appears, however, not to have been the case as the chironomid-based $T_{jul}$ reconstruction in the early Holocene does not show any specific response to marked local changes in the glacial lake to Lake Loitsana transition. The same is valid also for pollen and macrofossil reconstructions, which do not show anomalous values for this period. Lake Loitsana proxy evidence consistently shows no major deviations from the environmental and climate reconstructions derived from other boreal or even subarctic sites in Fennoscandia (Vääranta et al. 2005, Vääranta 2006a, b, Larsen et al. 2006; Fig. 1B: 21, Jones et al. 2011, Vääranta et al. 2011, Birks et al. 2012; Fig. 1B: 22). Furthermore, several of the plant taxa recorded in the early Holocene sediments as well as the MIS 5d-c are presently not found in the surroundings of Lake Loitsana despite the local bedrock. It seems most plausible therefore, that the long records derived from the Sokli area provide reliable information about climate changes during the last Interglacial-Glacial cycle in NE Finland.

**Conclusions**

- Lake Loitsana and its surroundings were deglaciated prior to 10 700 cal. a BP. This is in agreement with the wider deglaciation history of NE Finland.

- The glacial lake that formed following deglaciation was initially deep and characterised by high input of minerogenic influx from a wider catchment area. The continuing ice-marginal retreat of the FIS, lowered the glacial lake level due to the deglaciation of a major spillway, leaving the coring site in a relatively sheltered embayment dominated by shore erosion that created turbid water conditions.

- Four limnological/hydrological events were identified based on the Lake Loitsana sediment record: the presence of a proglacial lake, the drainage of this lake and eventual formation of Lake Loitsana, adjacent wetland expansion and subsequent river diversion, and the general infilling of the lake.

- In addition to regional climate and catchment changes, the Lake Loitsana development was affected by local-scale/site-specific processes including changes in fluvial input, influx rate of eroded material, turbidity, turbulence, water chemistry and water depth. These changes resulted in marked shifts in local aquatic and wetland assemblages. Aquatic macrophytes were also identified as potential drivers to changes in chironomid species distribution.

- The transfer-function based regional temperature reconstructions derived from different biotic assemblages can be influenced by these locally driven environmental changes. The different proxies, however, respond individualistically to various processes and inferred $T_{jul}$ appears to be reliable in varying level during different time intervals.

- Summer temperatures in the Lake Loitsana area seem to have been warm already during the
early Holocene but relatively warm conditions prevailed until the mid-Holocene, i.e. until c. 6000 cal. a BP. During the latter part of the Holocene, $T_{jul}$ were close to present day value.

Future prospects

The complex nature of biotic response to environmental change that is being increasingly emphasised in palaeolimnological/ecological studies (Birks and Birks 2006, Smol 2010) is further verified by this study. The Lake Loitsana record has shown that the early Holocene lake sediments are of importance and should be further investigated if we are to reconstruct changes occurring in direct connection to the deglaciation phase. In northern Finland these changes are often recorded in glacial lake sediments and as demonstrated in this study, even shallow glacial lakes have a potential for palaeoenvironmental reconstructions. For regional climate reconstructions the use of lakes where gyttja accumulation started directly following deglaciation should be preferred. This delimits the effects of marked local environmental changes. Possible future sites for early Holocene palaeoenvironmental reconstructions have been recognised in the nearby Värrösjönturati area (Fig. 2B). Finely laminated lacustrine sediments derived from one of the lakes has been dated using terrestrial macrofossils, and the initiation of deposition dates prior to 10000 cal. a BP. As emphasised in this study, macrofossil records from the boreal forest zone of Fennoscandia dating back to the earliest part of the Holocene are scarce. Aquatic macrophytes are predicted to react quickly to climate change (e.g. Alahuhta et al. 2011) and have been found to occur in both northern boreal and tundra sites prior to 10000 cal. a BP (Väliwanta 2005, 2006a, b). As the aquatic species disperse quickly (Barrat-Segretain 1996 and references therein, Sawada et al. 2003) and are not restricted by factors such as soil development, aquatic macrophytes can be successfully used to reconstruct post-glacial environmental conditions (Väliwanta et al. in prep). In combination with pollen studies, this proxy might also further improve our understanding of migration dynamics of terrestrial vegetation. Furthermore, as highlighted in this study, macrophyte abundance appears to be related to changes in chironomid species distribution. Aquatic vegetation has long been acknowledged to be an important component in the food-web chain as they e.g. provide refuge for zooplankton which graze upon phytoplankton, reduce nutrient availability through uptake of nutrients from the water and are themselves important as food for various zooplanktons (e.g. van Donk and van de Bund 2002, Siitonen et al. 2011). The effects of food web interactions on the aquatic biota are being increasingly stressed (van Donk and van de Bund 2002, Anderson et al. 2008, Furey et al. 2012, Luoto et al. 2012). Although not fully addressed in this study, future studies should thus consider also this as an essential tool in the assessment of changes in biological assemblages. The initiation and subsequent expansion of wetlands surrounding Lake Loitsana has clearly influenced the development of Lake Loitsana. Several cores were collected from these wetlands and they bear evidence of changing environmental conditions throughout the Holocene. The Saunavuotso wetland situated north of Loitsana (X1 in Fig. 2C) is particularly interesting since it was once connected to Lake Loitsana. Peatland initiation occurred at c. 8500 cal. a BP (Fig. 7) and was following only a short period of gyttja accumulation after the glacial lake drainage. The peat record holds evidence of a complex Holocene development with an atypical succession from bog to fen (Väliwanta M, personal communication). This is contrasting to the succession of most wetlands, which commonly develop from groundwater fed fens into precipitation fed bogs (e.g. Gorham 1957, Hughes et al. 2000). Further studies on the cores collected from Saunavuotso might thus provide additional information on wetland development as well as how local hydrological changes occurring within the wetland might affect Holocene lake development.

Financial support

This PhD-project was funded by the Swedish Nuclear Fuel and Waste Management Company (SKB) and the Department of Physical Geography and Quaternary Geology, Stockholm University. Many thanks to the Bolin Centre for Climate Research (Stockholm University), BioCold and NEPAL projects, Carl Mannerfelt Foundation, Gerard De Geer fund, INTIMATE COST Action, K&A Wallenberg foundation, Margit Althin’s foundation and Swedish So-
ciety for Anthropology and Geography for the financial support I received throughout this project.

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PALAEENVIRONMENTAL CHANGES IN THE NORTHERN BOREAL ZONE


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Appendix A. Identified diatom taxa in the Holocene and MIS 5d-c record

<table>
<thead>
<tr>
<th>Diatom groups</th>
<th>Holocene</th>
<th>MIS 5c</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Planktonic taxa</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aulacoseira ambigua (Grunow) Simonsen</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Aulacoseira islandica (O. Müller) Simonsen</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aulacoseira subarctica (O. Müller) Haworth</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Cyclotella dubia (Fricke in A. Schmidt) Round</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Cyclotella meneghiniana Küttzing</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Cyclotella ocellata Pantocek</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Cyclotella radiosa (Grunow) Lemmermann</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Cyclotella roesi Hákansson</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Cymbella spp (Küttzing) Brebisson</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Stephanodiscus alpinus Hustedt</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Stephanodiscus cf. hantzschii Grunow (in Cleve &amp; Grunow)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Stephanodiscus medius Hákansson</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Stephanodiscus parvus Stoermer &amp; Hákansson</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Stephanodiscus spp Ehrenberg</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td><strong>Tychoplanktonic taxa</strong></td>
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<tr>
<td>Aulacoseira distans (Ehrenberg) Simonsen</td>
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<td>x</td>
</tr>
<tr>
<td>Aulacoseira hirata v. hirsuta (Grunow) Haworth</td>
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<td>x</td>
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<tr>
<td>Aulacoseira valida (Grunow) Krammer</td>
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<td>x</td>
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<tr>
<td>Fragilaria capucina Desmazières</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Fragilaria capucina v. mesolepta (Rabenhorst) Rabenhorst</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Fragilaria capucina v. rumpens (Küttzing) Lange-Bertalot</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Fragilaria capucina v. vaucheriae (Küttzing) Lange-Bertalot</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Melosira varians Agardh</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Nitzschia intermedia Hantsch</td>
<td>x</td>
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<tr>
<td>Tabellaria flocculosa (Roth) Küttzing</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Ulvaria ulna (Nitzsch) Compère</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td><strong>Benthic taxa</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Achnanthes bioretii Germain</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Achnanthes clevei Grunow</td>
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<td>x</td>
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<tr>
<td>Achnanthes conspica Mayer</td>
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<td>x</td>
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<tr>
<td>Achnanthes lanceolata (Brebisson) Grunow</td>
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<td>x</td>
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<tr>
<td>Achnanthes lanceolata spp biporoma</td>
<td>x</td>
<td>x</td>
</tr>
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<td>Achnanthes lanceolata spp frequensissima Lange-Bertalot</td>
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Cymbella subcuspidata Krammer
Didymosphenia geminata (Lyngbye) M. Schmidt
Diploneis elliptica v. elliptica (Kützing) Cleve
Diploneis oculata (Brébisson) Cleve
Diploneis parma Cleve
Ellerbeckia arenaria f. teres (Brun) Crawford
Encyonema brebissonis (Hustedt) Mann
Encyonema silesiacum (Bleisch in Rabenhorst) Mann
Epithemia adnata (Kützing) Brébisson
Epithemia frickei Krammer
Epithemia sorex, v. sorex Kützing
Epithemia spp Brébisson
Epithemia turgida v. granulata (Ehrenberg) Brun
Epithemia turgida v. turgida (Ehrenberg) Kützing
Eunotia curvata (Kützing) Lagerstedt
Eunotia implicata Norpel, Lange-Bertalot & Alles
Eunotia praerupta Ehrenberg
Eunotia praerupta v. papilio (Grunow) Norpel
Fallacia helensis (Schulz) Mann
Fragilaria bidens (Ehrenberg) Grunow
Fragilaria nitzschioides (Grunow)
Fragilariforma neoproducta Lange-Bertalot
Frustulia amphipleuroides (Grunow in Cleve & Grunow) Cleve-Euler
Frustulia vulgaris (Thwaites) De Toni
Geissleria paludosa (Hustedt) Lange-Bertalot & Metzeltin
Gomphonema acuminatum v. acuminatum Ehrenberg
Gomphonema angustatum (Kützing) Rabenhorst
Gomphonema clavatum Ehrenberg
Gomphonema gracile Ehrenberg
Gomphonema minutum (Agardh) Agardh
Gomphonema olivaceum (Hornemann) Brébisson
Gomphonema parvulum v. parvulum (Kützing) Kützing
Gomphonema spp Agardh
Gomphonema truncatum Ehrenberg
Gyrosigma acuminatum (Kützing) Rabenhorst
Hippodonta capitata (Ehrenberg) Lange-Bertalot, Metzeltin & Witkowski
Hippodonta baucheruggensis (Grunow) Lange-Bertalot, Metzeltin & Witkowski
Martyniana martyi (Héribaud) Round
Navicula absconensis Hustedt
Navicula absolata Hustedt
Navicula amphiola Cleve
Navicula carin Ehrenberg
Navicula centrioides Hustedt
Navicula centrizis Grunow
Navicula constans Hustedt
Navicula cryptocephala Kützing
Navicula cryptotenella Lange-Bertalot
Navicula decassia Ostrup
Navicula digitatoria (Gregory) Ralls
Navicula edrigeana (Carter)
Navicula eugua (Gregory) Grunow
Navicula ezplanata Hustedt
Navicula gastrum (Ehrenberg) Kützing
Navicula hambergii Hustedt in Hamburger
Navicula harders Hustedt in Breindmuhl
Navicula joubaudii Germain
Navicula laevissea Kützing
Navicula lapidosa Krasske
Navicula laterostriata Hustedt
Navicula meniscus Schumann
Navicula meniscus v. upsaliensis Grunow
Navicula placenta (Ehrenberg) Kützing
Navicula protracta (Grunow) Cleve
Navicula pseudoventralis Hustedt
Navicula pusilla W. Smith
Navicula radiosa Kützing
Navicula reichardtii Grunow
Navicula rhynchocephala Kützing
Navicula rosalis Hustedt
Navicula schoenfeldii Hustedt
Navicula scutelloides W. Smith ex. Gregory
Navicula spp Bory
Navicula submuralis Hustedt
Navicula subrotsundata Hustedt
Navicula varidula (Kützing) Ehrenberg
Navicula wetlands Hustedt
Navicula vulpesia Kützing
Neidium affine (Ehrenberg) Pfitzer
Neidium amplatum (Ehrenberg) Krammer
Neidium dubium (Ehrenberg) Cleve
Neidium tridens (Ehrenberg) Cleve
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<td><strong>Stauroneira lappenos</strong> (Grunow in Van Heurck) Williams &amp; Round</td>
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<td><strong>Stauroneira leptostauron</strong> (Ehrenberg) Williams &amp; Round</td>
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<td><strong>Stauroneira pinnata</strong> v. pinnata (Ehrenberg) Williams &amp; Round</td>
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<td><strong>Synedra parasitica</strong> v. subconstruct (Grunow in Van Heurck) Hustedt</td>
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<td><strong>Tetracyclus glans</strong> (Ehrenberg) Mills</td>
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<td><strong>Ulnaria capitata</strong> (Ehrenberg) Compère</td>
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**Aerophilic taxa**

*Achnanthes exigua* Grunow

*Planoecis oblongella* (Negeil) Cleve-Euler

*Hantzschia amphiovys* (Ehrenberg) Grunow in Cleve & Grunow

*Luticola mutica* (Kützing) Mann

*Navicula minima* Grunow

*Neidium bisulcatum* v. subampliatum Krammer

*Pinnularia borealis* v. scalaris (Ehrenberg) Rabenhorst

*Reimeria sinuata* (Gregory) Kociolek & Stoermer

**Rheophilic taxa**

*Amphora pediculus* (Kützing) Grunow

*Aulacoseira italica f. crenulata* (Ehrenberg) R. Ross in Hartley

*Caloneis naviculiformis* Aueswald

*Diatoma mesodon* (Roth) H. Huber

*Eunotia pectinalis* v. minor (Kützing) Rabenhorst

*Fragilaria versvens* Rafts

*Meridion circulare* v. circulare (Greville) Agardh

*Meridion circulare* v. construens (Rafts) van Heurck

**Reworked / Tertiary taxa**

*Cocconodiscus spp* Ehrenberg

*Hemiaulus spp* Ehrenberg

*Opehka geminata* (Grunow) Hustedt

*Paralia sulcata* (Ehrenberg) Cleve

*Paralia sulcata* v. biserrata Grunow

*Stephanopyxis* spp Ehrenberg

**Unknown ecology**

*Achnanthes spp* Bory

*Amphora spp* Ehrenberg

*Aulacoseira spp* Thaawites

*Caloneis spp* Cleve

*Cymbella spp* Agardh

*Diatoma spp* Bory

*Eunotia spp* Ehrenberg

*Fragilaria spp* Lyngbye

*Navicula sect. Minisculae*

*Neidium spp* Pilzter

*Nitzschia spp* Hassall

*Surirella spp* Turpin

*Tabellaria spp* Ehrenberg
Appendix B. List of synonyms

Taxon names used in this study

Achnanthidium minutissimum (Kützing) Czarnecki
Achnanthes minutissima (Ehrenberg) Mann & Stickle
Aulacoseira italica f. crenulata (Ehrenberg) Ross in Hartley
Caloneis ventricosa (Ehrenberg) Meister
Cricnula cuspidata (Kützing) Mann
Crymella brehmi (Hustedt) Mann
Encyonema siliceaum (Bleisch in Rabenhorst) Mann
Eunotia curvata (Kützing) Lagerstedt
Eunotia pectinatis v. minor (Kützing) Rabenhorst
Fallacia helensis (Schulz) Mann
 Fragilaria dilatata (Brébisson) Lange-Bertalot
 Fragilariforma neoproducta (Lange-Bertalot) Williams & Round
 Proratalia amphipleuroides (Grunow in Cleve & Grunow) A. Cleve-Euler

Geisleria paludosa (Hustedt) Lange-Bertalot & Metzeltin
Hippodonta capitata (Ehrenberg) Lange-Bertalot, Metzeltin & Witkowski
Hippodonta baenkeburgensis (Grunow) Lange-Bertalot, Metzeltin & Witkowski

Luticola mutica (Kützing) Mann
 Martyana martyi (Héribaud) Round

Pinnularia abaujensis (Pantoscek) Ross
 Placoces elipinensis (Gregory) Cox
 Pseudostaurosira brevisatria (Grunow in Van Heurck) Williams & Round
 Pseudostaurosira pseudoconstruens (Marciniak) Williams & Round
 Reimera sinuata (Gregory) Koçölek & Stoerner
 Sellaphora bacillum (Ehrenberg) Mann
 Sellaphora pupula (Kützing) Meerschekowsky
 Staurosira biunica (Ehrenberg) Lange-Bertalot

Staurosira construens Ehrenberg
 Staurosira venter (Ehrenberg) H.Kobayasi
 Staurosirella lapponica (Grunow in Van Heurck) Williams & Round
 Staurosirella leptostauron (Ehrenberg) Williams & Round
 Staurosirella pinnata (Ehrenberg) Williams & Round
 Synedra parasitica (W. Smith) Hustedt
 Unnaria ulna (Nitzsch) Compère

Basionyms

Achnanthes minutissima Kützing
Navicula pseudotuscula Hustedt
Navicula tuscula (Ehrenberg) Grunow
Aulacoseira crenulata (Ehrenberg) Thwaites
Caloneis silicula (Ehrenberg) Cleve
Navicula cuspidata (Kützing) Kützing
Cymella brehmi Hustedt
Cymella silicicola Bleisch
Eunotia bilunaris (Ehrenberg) Mills
Eunotia minor (Kützing) Grunow in Van Heurck
Navicula helensis Schulz
Unnaria capitata (Ehrenberg) Compère
Fragilaria neoproducta Lange-Bertalot
Frustulia rhomboides v. amphipleuroides (Grunow) De Toni
Navicula ignota var. palustris (Hustedt) Lund
Navicula capitata Ehrenberg
Navicula capitata v. lanceburgensis (Grunow) Patrick
Navicula mutica Kützing
Prapilaa leptostauron v. martyi (Héribaud) Lange-Bertalot
Pinnularia gibbe Ehrenberg
Navicula elipinensis (Gregory) Ralfs
Prapilaa brevisatria Grunow
Prapilaa pseudoconstruens Marciniak
Cymella sinuata Gregory
Navicula bacillum Ehrenberg
Navicula pupula Kützing
Prapilaa construens v. binodis (Ehrenberg) Hustedt
Prapilaa construens v. construens (Ehrenberg) Hustedt
Prapiliara construens v. venter (Ehrenberg) Hustedt
Prapilaa lapponica Grunow
Prapilaa leptostauron v. leptostauron (Ehrenberg) Hustedt
Prapilaa pinnata Ehrenberg
Prapilaa parasitica (W. Smith) Grunow
Prapilaa parasitica v. subconstricta Grunow
Prapilaa ulna (Nitzsch) Lange-Bertalot
Thank you...

I am very thankful for where I am today and the people I have met on my way here have played a large part in making it a wonderful experience.

To my supervisors Karin Helmens, Krister Jansson, Peter Kuhry and Jan Risberg (Stockholm University): thank you for giving me the opportunity to pursue this PhD project, for the support you have given me through the years and for always having your doors open for me when I needed advice. Pulling this through without your help would have been difficult. Special thanks to my co-supervisors Peter Kuhry and Jan Risberg who have been instrumental for my continued studies at PhD level. Peter’s inspiring lectures first stirred my interest for palaeoenvironmental studies, while Jan’s outstanding supervision during my master’s thesis, motivated me to continue my studies in Quaternary Geology.

I am also very thankful to my external supervisor Minna Välimäki (University of Helsinki) for her interest in my studies, the tremendous support she has given me during these past few years and for giving me the opportunity to spend three weeks at the Environmental Change Research Unit. My time at ECRU was made enjoyable to a large part by the wonderful ECRU members whose kindness, enthusiasm, team-work, excellence and impressive skills in Mölkky will always be an inspiration for me. Thank you for making me feel at home from day one.

During my studies I’ve had the pleasure of working alongside several collaborators whose enthusiasm and expertise has helped broaden the value of this work. Jan Weckström has always been of great support. His analytical thinking made him just the right kind of person with whom I could discuss the curious world of diatoms and transfer-functions. Malin Kylander; working with XRF-data never made much sense until you came into my life. Thank you for making everything easier and much more enjoyable, your are an inspiration. Sakari Salonen and Tomi Luoto, thank you for the countless discussions we’ve had this last year, for patiently answering all my questions and quickly responding to my e-mails. Collaborating with you has truly been a pleasure. I have also had the privilege of receiving support from Antonio Martínez Cortizas, Gavin Simpson, Liselott Wilin, Malin Johansson, Martin Margold and Päivi Kaislahti Tillman, which has undeniably made many of my days easier. Hilary Birks was kind enough to introduce me to plant macrofossil analysis for which I am deeply grateful.

INK would not have been the great working place it is were it not for the wonderful people who work here. I am particularly thankful to Susanna Blandman, Linus Richert, Björn Gunnarsson, Carina Henriksson, Erik Hansson, Helle Skånes, Stefan Wastegård, Sven Karlsson and Yanduy Cabrera who have always done a great job and been supportive in every way possible. To all my fellow PhD students both at INK and elsewhere in the Geobuilding; thank you for all the motivating chats, laughs, discussions, after-works and relentless efforts to win the pub-quiz, which unfortunately only ever resulted in 2nd place. Ewa, Alistair, Steve, Ping, Annika, Marika, Moo and Reto: you’ve made life a little lovelier for me.

To all my friends, especially Anna, Alba, Carolina and Nando; the good times and laughs that we shared, our long chats, wandering around, discovering new places and countless other little things have made this last year bearable. My arctic friends; Svalbard would not have been as amazing were it not for your company. Lewis, Iván, Isabelle; thanks for being an inspiration, for always answering my questions and for cheering me up.

I am beyond grateful to my family who has been with me on every step of this road. To mom, dad, Jeton, Enver, Edona, Qendresa, Qendrim, my brother-in-law, my lovely sisters-in-law and my beautiful nephew who has reoriented my life; thank you for supporting me through all my years at the university, for never doubting me, for always being there. Your love and support has pulled me through, this is for you.

Last but not least I’d like to thank all the wonderful people I’ve met at various courses, workshops and conferences, who have shared their inspiring work with me and taken interest in mine.