The establishment of ecological and environmental reference conditions is needed in the assessment of global change and in lake management at the local scale. In the research of this thesis, I returned to basics in the interpretation of midge palaeolimnology, aiming to refine the understanding of midge distribution patterns and taphonomical processes for more reliable reconstructions of past environmental conditions. To do this, I examined surface sediment datasets at different geographical scales, used environmental screening, tested the potential of several calibration models and applied the developed models to sediment profiles. A special focus of this work was on the climate and environmental variability during the time periods of the Medieval Climate Anomaly, the Little Ice Age and the most recent anthropogenic era.
Spatial and temporal variability in midge (Nematocera) assemblages in shallow Finnish lakes (60–70 °N): community-based modelling of past environmental change

TOMI P. LUOTO

ACADEMIC DISSERTATION
To be presented, with the permission of the Faculty of Science of the University of Helsinki, for public examination in the auditorium E204, The Physicium building, on 21 May 2010, at 12 noon.
Cover photo: Newly frozen Lake Pieni-Kauro in October 2009

Author's address: Tomi P. Luoto
Department of Geosciences and Geography
P.O. Box 64
00014 University of Helsinki
Finland
tomi.luoto@helsinki.fi

Supervised by: Professor Veli-Pekka Salonen
Department of Geosciences and Geography
University of Helsinki
Finland

Reviewed by: Dr. Oliver Heiri
Institute of Environmental Biology
Utrecht University
The Netherlands

Associate Professor Roberto Quinlan
Department of Biology
York University
Canada

Opponent: Dr. Stephen J. Brooks
Department of Entomology
Natural History Museum
UK

ISSN 1798-7911
ISBN 978-952-10-4282-9 (PDF)
http://ethesis.helsinki.fi

Helsinki University Print
Helsinki 2010
Abstract

Multi- and intralake datasets of fossil midge assemblages in surface sediments of small shallow lakes in Finland were studied to determine the most important environmental factors explaining trends in midge distribution and abundance. The aim was to develop palaeoenvironmental calibration models for the most important environmental variables for the purpose of reconstructing past environmental conditions. The developed models were applied to three high-resolution fossil midge stratigraphies from southern and eastern Finland to interpret environmental variability over the past 2000 years, with special focus on the Medieval Climate Anomaly (MCA), the Little Ice Age (LIA) and recent anthropogenic changes. The midge-based results were compared with physical properties of the sediment, historical evidence and environmental reconstructions based on diatoms (Bacillariophyta), cladocerans (Crustacea: Cladocera) and tree rings.

The results showed that the most important environmental factor controlling midge distribution and abundance along a latitudinal gradient in Finland was the mean July air temperature ($T_{Jul}$). However, when the dataset was environmentally screened to include only pristine lakes, water depth at the sampling site became more important. Furthermore, when the dataset was geographically scaled to southern Finland, hypolimnetic oxygen conditions became the dominant environmental factor. The results from an intralake dataset from eastern Finland showed that the most important environmental factors controlling midge distribution within a lake basin were river contribution, water depth and submerged vegetation patterns. In addition, the results of the intralake dataset showed that the fossil midge assemblages represent fauna that lived in close proximity to the sampling sites, thus enabling the exploration of within-lake gradients in midge assemblages. Importantly, this within-lake heterogeneity in midge assemblages may have effects on midge-based temperature estimations, because samples taken from the deepest point of a lake basin may infer considerably colder temperatures than expected, as shown by the present test results. Therefore, it is suggested here that the samples in fossil midge studies involving shallow boreal lakes should be taken from the sublittoral, where the assemblages are most representative of the whole lake fauna.

Transfer functions between midge assemblages and the environmental forcing factors that were significantly related with the assemblages, including mean air $T_{Jul}$, water depth, hypolimnetic oxygen, stream flow and distance to littoral vegetation, were developed using weighted averaging (WA) and weighted averaging-partial least squares (WA-PLS) techniques, which outperformed all the other tested numerical approaches. Application of the models in downcore studies showed mostly consistent trends. Based on the present results, which agreed with previous studies and historical evidence, the Medieval Climate Anomaly between ca. 800 and 1300 AD in eastern Finland was characterized by warm temperature conditions and dry summers, but probably humid winters. The Little Ice
Age (LIA) prevailed in southern Finland from ca. 1550 to 1850 AD, with the coldest conditions occurring at ca. 1700 AD, whereas in eastern Finland the cold conditions prevailed over a longer time period, from ca. 1300 until 1900 AD. The recent climatic warming was clearly represented in all of the temperature reconstructions. In the terms of long-term climatology, the present results provide support for the concept that the North Atlantic Oscillation (NAO) index has a positive correlation with winter precipitation and annual temperature and a negative correlation with summer precipitation in eastern Finland. In general, the results indicate a relatively warm climate with dry summers but snowy winters during the MCA and a cool climate with rainy summers and dry winters during the LIA.

The results of the present reconstructions and the forthcoming applications of the models can be used in assessments of long-term environmental dynamics to refine the understanding of past environmental reference conditions and natural variability required by environmental scientists, ecologists and policy makers to make decisions concerning the presently occurring global, regional and local changes. The developed midge-based models for temperature, hypolimnetic oxygen, water depth, littoral vegetation shift and stream flow, presented in this thesis, are open for scientific use on request.
Acknowledgements

I am very thankful to the Finnish Graduate School in Geology, the EPHIPPIUM project (Academy of Finland, grant no. 1107062), the Finnish Entomological Society, Nordenskiöld Foundation and the University of Helsinki Fund (Mathematics and Science Fund) for their financial support concerning this thesis.

My supervisor, Prof. Veli-Pekka Salonen, has given true support in my career and I am very grateful for the trust he has shown me. The reviewers, Dr Oliver Heiri and Dr Roberto Quinlan, provided critical and constructive comments that improved the value of this thesis.

I express my gratitude to the coauthors, Dr Kaarina Sarmaja-Korjonen, Dr Liisa Nevalainen, Dr Tommi Kauppila, Prof. Salonen and Dr Samuli Helama, for fruitful collaboration. I specifically want to thank Kaarina for her unselfish support, guidance and friendship. I thank Dr Seija Kultti for helping me numerous times and Dr Marjut Nyman for introducing me to chironomid palaeoecology. I also wish to acknowledge my other research colleagues and collaborators for all the discussions and their valuable advice on my work. Dr Roy Siddall is thanked for improving the english of the synopsis. The help and support of coworkers at the department, such as Mikko Haaramo MSc, Dr Mia Kotilainen, Frauke Kubischta MSc, Ilona Romu MSc, Elina Sahlstedt MSc, Tuija Vaahhtojärvi and Kirsi-Marja Äyräs, is deeply appreciated.

I thank my parents Sirpa and Mauri Luoto and my in-laws Riitta and Reijo Nevalainen for their support and help when needed. Special thanks go to my hairy friends at home: Onni, Helmi and Vilho. I just love you guys! The greatest and most heartwarming thanks belong to my dearly loved wife, Liisa, who guided, encouraged and kicked me in the buttocks during difficult times, but also provided me such comfort at home that it was always easy to forget all about the science.

I am among those who think that science has great beauty.
A scientist in his laboratory is not only a technician: he is also a child placed before natural phenomena which impress him like a fairy tale.

Marie Curie (1867 - 1934)
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This thesis is based on the following publications:


VI  **Luoto, T.P. & Helama, S.** Palaeoclimatological and palaeolimnological records from fossil midges and tree rings: the role of the North Atlantic Oscillation in eastern Finland through the Medieval Climate Anomaly and Little Ice Age. Submitted to *Quaternary Science Reviews*.

The publications are referred to in the text by their roman numerals.
### Abbreviations

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<th>Description</th>
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<tr>
<td>$\lambda_1, \lambda_2$</td>
<td>ratio of the eigenvalues</td>
</tr>
<tr>
<td>CCA</td>
<td>canonical correspondence analysis</td>
</tr>
<tr>
<td>CPET</td>
<td>chironomid pupal exuvial technique</td>
</tr>
<tr>
<td>DCA</td>
<td>detrended correspondence analysis</td>
</tr>
<tr>
<td>DLV</td>
<td>distance from littoral vegetation</td>
</tr>
<tr>
<td>DO</td>
<td>dissolved oxygen</td>
</tr>
<tr>
<td>GIS</td>
<td>geographical information system</td>
</tr>
<tr>
<td>LI</td>
<td>lotic index</td>
</tr>
<tr>
<td>LIA</td>
<td>Little Ice Age</td>
</tr>
<tr>
<td>LOI</td>
<td>loss-on-ignition pyrolysis</td>
</tr>
<tr>
<td>LWWA</td>
<td>locally-weighted weighted averaging</td>
</tr>
<tr>
<td>MAT</td>
<td>modern analogue technique</td>
</tr>
<tr>
<td>MCA</td>
<td>Medieval Climate Anomaly</td>
</tr>
<tr>
<td>MS</td>
<td>magnetic susceptibility</td>
</tr>
<tr>
<td>$N$</td>
<td>number of observations</td>
</tr>
<tr>
<td>N2</td>
<td>Hill’s (1973) effective number of occurrences</td>
</tr>
<tr>
<td>NAO</td>
<td>North Atlantic Oscillation</td>
</tr>
<tr>
<td>$P$</td>
<td>level of statistical significance</td>
</tr>
<tr>
<td>P:L</td>
<td>ratio between planktonic and littoral species</td>
</tr>
<tr>
<td>PCA</td>
<td>principal components analysis</td>
</tr>
<tr>
<td>PLS</td>
<td>partial least squares</td>
</tr>
<tr>
<td>$r$</td>
<td>Pearson product-moment correlation coefficient</td>
</tr>
<tr>
<td>$r^2$</td>
<td>apparent coefficient of determination</td>
</tr>
<tr>
<td>$r^2_{\text{boot}}$</td>
<td>bootstrapped coefficient of determination</td>
</tr>
<tr>
<td>$r^2_{\text{jack}}$</td>
<td>jackknifed coefficient of determination</td>
</tr>
<tr>
<td>RMSEP</td>
<td>root mean squared error of prediction</td>
</tr>
<tr>
<td>$S$</td>
<td>taxon richness</td>
</tr>
<tr>
<td>SqRL</td>
<td>squared residual length</td>
</tr>
<tr>
<td>TCE</td>
<td>total chyadorid ephippia</td>
</tr>
<tr>
<td>$T_{\text{Jul}}$</td>
<td>July temperature</td>
</tr>
<tr>
<td>TN</td>
<td>total nitrogen</td>
</tr>
<tr>
<td>TP</td>
<td>total phosphorus</td>
</tr>
<tr>
<td>TWINSPAN</td>
<td>two-way indicator species analysis</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>WA_{\text{tax}}</td>
<td>weighted averaging with taxon tolerance weighting</td>
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<tr>
<td>WFD</td>
<td>Water Framework Directive of the European Union</td>
</tr>
<tr>
<td>WMAT</td>
<td>weighted modern analogue technique</td>
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<tr>
<td>YD</td>
<td>Younger Dryas</td>
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<td>VI</td>
<td>TPL, SH</td>
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</table>

KSK = Kaarina Sarmaja-Korjonen (Department of Geosciences and Geography, University of Helsinki, Finland)
LN = Liisa Nevalainen (Department of Geosciences and Geography, University of Helsinki, Finland)
SH = Samuli Helama (Arctic Centre, University of Lapland, Rovaniemi, Finland)
TK = Tommi Kauppila (Geological Survey of Finland, Kuopio, Finland)
TPL = Tomi P. Luoto (Department of Geosciences and Geography, University of Helsinki, Finland)
VPS = Veli-Pekka Salonen (Department of Geosciences and Geography, University of Helsinki, Finland)
1. Introduction

1.1. State of the world address

Climate forcings include variations in solar activity and the Earth’s orbit, plate tectonics and changes in greenhouse gas concentrations, which are amplified or diminished by multiple climate change feedbacks. Our planet is undergoing accelerated warming due to dramatic increases in anthropogenic emissions of greenhouse gases into the atmosphere (International Panel on Climate Change (IPCC) 2007). In the present climatic change there are multiple stressors, the effects of which are not well understood and which will culminate in ways that are difficult to predict. The global change scenarios for Finland in the 21st century project major problems, including increased temperatures, precipitation and surface runoff (Boer et al. 1990, Carter et al. 2004, Jylhä et al. 2004). The expected changes in Finland will be more severe during winters than summers (Fig. 1), critically affecting factors such as the development and duration of the snow cover, which is an important climate change feedback mechanism and provides a critical ecological threshold for ecosystem health.

The projected global warming will also have numerous other serious consequences for ecosystems and mankind: the sea level rise will endanger coastal areas and the frequency and severity of extreme weather events will increase. To reduce the effects of human-induced climate change, global greenhouse gas emissions must be reduced significantly.

Increased primary productivity resulting from an elevated availability of nutrients leads to harmful eutrophication processes, which are probably the greatest threat to global freshwater ecosystems and resources (UNEP 1999). The eutrophication processes are accelerated by the increased atmospheric concentrations of carbon dioxide through its direct influence on plant and algal growth and indirect influence through increased temperatures, which promotes plant metabolism and boosts the growth of planktonic algae (Chapman 1996). Progressive eutrophication inevitably leads to dramatic changes in biota and biodiversity, massive blue-green algal blooms, late-winter/summer hypolimnetic oxygen depletions and winter fish kills in Finnish lakes. In addition to its influence on aquatic ecosystems, eutrophication creates problems for human societies through an increase in unwanted fish species, the deterioration of water supplies and a decrease in the recreation status of lakes. Although eutrophication is in many cases a natural phenomenon, anthropogenic activities have strikingly increased its occurrence and magnitude in lakes (Räike et al. 2003, Smol 2008). In Finland, this is especially a problem in the southern part of the country (Valpola 2006, Luttor 2007), where the population is focused. The European Union (EU) aims to control the eutrophication problem through the Water Framework Directive (WFD, European Commission 2000), which obligates member countries to monitor the ecological status and water quality of surface waters and to estimate the natural reference conditions (European Commission 2003).

The self-perpetuating process of eutrophication, probably by internal (autochthonous) loading of accumulated nutrients redissolved into the water, makes it difficult to remedy water bodies even if the external (allochthonous) loads of nutrient sources are reduced or eliminated (Alhonen 1985). Restoration of lakes is possible by removing nutrients from the ecosystem through the removal of unwanted fish, such as roach (Rutilus rutilus L.), and excess plant growths. In addition, oxygenation of the hypolimnion (cf. Lappalainen 1994) when the lake is frozen and oxygen exchange with the atmosphere is prevent-
ed slows the release of nutrients from the sediments. More drastic restoration measures include chemical treatment of the lake water or sediment, dredging and covering the lakebeds with various membranes. However, in lake restoration projects it is difficult or even impossible to remedy the lake in such way that the ecological status returns to the previous natural state. Rather, alternative communities can exist under similar nutrient conditions (Langdon et al. 2006), and a different faunal composition may therefore be expected in “restored” lakes compared to the ecological reference conditions. Moreover, the present climate change complicates ecological restorations, because under warming climatic conditions, water quality, e.g. hypolimnetic oxygen conditions, can strongly deteriorate (Stefan et al. 1993), making it difficult to identify the effectiveness of restoration efforts.

The instrumental records of meteorological and especially limnological parameters are very short. For example temperature measurements in Finland did not start until the mid-18th century (Vesajoki & Holopainen 1998), and no measured data therefore exist for the distinct late Holocene climate events, the Medieval Climate Anomaly (MCA) and Little Ice Age (LIA), or events prior them. In addition, the observational records are often fragmentary and coincide with the time when human activities have increasingly contaminated the environment on a global scale (Bradley 2000). Because we have entered a time period during which major changes in the biosphere are primarily the result of human activities (Crutzen (2002) coined the term “Anthropocene”), and we live in a strongly modified
biosphere, we need to put present-day conditions into context (Pienitz et al. 2004). Thus, longer indirect interpretations from geological and other natural archives are needed for assessments of long-term climate dynamics to refine the understanding of the presently occurring changes (Caseldine et al. 2010). In addition to environmental scientists and policy makers, ecologists require long-term monitoring data to make effective assessments, because regime shifts are reported and many lakes have already passed critical ecological thresholds due to recent warming (Smol et al. 2005; Smol & Douglas 2007a, 2007b).

Methods of palaeoenvironmental reconstruction include stratigraphic sequencing, palaeomagnetism, radiometric dating, oxygen isotope studies and many other methods. The palaeoclimatic records can be tested against proxies of potential climatic forcings, such as solar activity (Jirikowic & Damon 1994; Solanki et al. 2004), the North Atlantic Oscillation (NAO) (Cook et al. 2002; Luterbacher et al. 2002; Trouet et al. 2009) and the strength of the thermohaline circulation (Bianchi & McCave 1999; Chapman and Shackleton 2000; Bond et al. 2001), and interpreted in the context of long-term synoptic climatology. This is particularly important in the North Atlantic sector, where the natural climatic changes originating from the Atlantic Ocean seem to drive multi-decadal variations (Enfield et al. 2001; Sutton and Hodson 2005; Knight et al. 2005). These natural variations can be then compared with the more recent changes induced by human activity.

1.2. Ecosystem-based reconstruction of environmental change

Palaeolimnology plays an important role in the study of long-term environmental change, providing information on past changes and also giving insights into the effects of present and future environmental changes. Palaeolimnology is a diverse and rapidly developing field and new methods and applications are frequently presented (Sarmaja-Korjonen 2003, 2004; Wooller et al. 2004; Kurek & Cwynar 2009; Pienitz & Lotter 2009, van Hardenbroek et al. 2010). Commonly used palaeolimnological methods include the development of transfer functions (i.e. the training set or calibration set approach), which are multivariate statistical models relating modern organisms to environmental conditions (Pienitz et al. 1995, Weckström et al. 1997; Quinlan and Smol 2001a; Rühland and Smol 2002; Brooks and Birks 2004; Seppä et al. 2004). These functions can be applied to fossil species assemblages from deeper sediment layers and used to reconstruct past environmental changes (Fig. 2). Thus, quantitative palaeolimnology provides a useful tool for characterizing the pristine state of a lake and thus eases the determination of goals for conservation, preservation or restoration projects (Räsänen et al. 2006). Additionally, the high-resolution records obtained from lake deposits are ideal for applications to problems in ecology, since they provide temporal and spatial scales for ecological experiments and ecosystem monitoring.

For the purposes of modern ecology, the palaeoecological training sets can be very informative, because they are able to provide large amounts of data on the modern distribution of species. The fossil (or subfossil) assemblages in surface sediment samples are beneficial compared with traditional ecological monitoring, because single sampling provides integrated species data from a time period of several recent years. In the case of organisms that vary seasonally in their occurrence, such as larval midges (Insecta: Diptera: Nematocera) and water fleas (Crustacea: Cladocera) (Einarsson et al. 2002; Tátosová and Stuchlík 2006; Nevalainen 2008a; Nevalainen &
Sarmaja-Korjonen (2008), the use of ecological monitoring to establish modern distribution data for the purposes of training sets would be very time- and resource-consuming and would also provide information on fewer taxa than the calibration set approach (Saros 2009). However, the traditional single-sample and multilake calibration set approach does not allow the distinguishing of which species inhabit particular habitats within a lake basin and in many cases it is difficult to identify the effect of different environmental variables, due to covariance (Korhola et al. 2000; Saros 2009). Nevertheless, it is possible to clarify the influence of correlating environmental variables using experimental approaches/modern ecology and merging this information quantitatively with the paleolimnological calibration set data (Brodersen et al. 2004), although this approach is also labour-intensive. Nevertheless, different modern ecological approaches and perspectives, such as establishing temperature or oxygen sensitivity of reproduction patterns in organisms (Nevalainen & Luoto 2010, Nevalainen et al. subm. a), are clearly needed to increase the level of understanding and to serve as reliable bases for the development of ecosystem-based calibration sets and for consequent environmental reconstructions.

Midges and especially chironomids (Chironomidae), also known as the non-biting midges, are a diverse insect group in freshwater environments (Lindegård 1997) and they have been successfully used as indicators of contemporary water quality (Sæther 1979, Armitage et al. 1983, Kansanen et al. 1984, Paasivirta 1984), but also as palaeoindicators of lake productivity (Brodersen & Quinlan 2006), climate (Brooks 2003, Walker & Cwynar 2006), salinity (Walker et al. 1995; Heinrichs et al. 2001; Eggermont et al. 2006) and pollution (Meriläinen et al. 2001, 2003; Ilyashuk et al. 2003; Ilyashuk & Ilyashuk 2004; Brooks et al. 2005). Midges are holometabolic (complete metamorphosis) insects that go through egg (embryo), larval, pupal and adult (imago) life stages (Tokeshi 1995; Fig. 3). The remains of the larval stage (mainly the third and fourth instars) are preserved in lake sediments as fossil head capsules and mouth parts, such as mandibles (Fig. 4). Midges are stenotopic, ubiquitous, abundant, identifiable, species-rich, complementary and sensitive, making them especially well suited to the needs of palaeolimnology (Brooks 2003; Brooks et al. 2007). Developments in numerical techniques in palaeolimnology have enabled the use of midges as quantitative indicators of environmental conditions, especially regarding air/water temperature (in northern Europe by Olander et al. 1997,
1999, Brooks and Birks 2001, 2004, Larocque et al. 2001 and Seppä et al. 2002). Although the distribution of midges is most often found to be driven on a broad scale by temperature, other factors also affect their distribution, such as lake trophic conditions, hypolimnetic oxygen content and water depth, and these parameters have also been used to develop quantitative calibration models (Lotter et al. 1998, Quinlan et al. 1998; Brodersen & Lindegaard 1999; Korhola et al. 2000; Brooks et al. 2001; Little & Smol 2001; Quinlan & Smol 2001a; Barley et al. 2006; Zhang et al. 2006; Kurek & Cwynar 2009). Furthermore, fossil midge assemblages are high potential tools for the implementation of the WFD of the EU as a lake type classification technique (Nyman & Korhola 2005), and for the establishment of the ecological and limnological reference conditions for lake management projects (Salonen et al. 1993; Luoto & Nevalainen subm.).

Because temperature, pH, substrate, water depth, food, dissolved oxygen (DO), salinity and turbulence, among other gradients, affect midge distribution and abundance, it is also important to measure these when developing a training set. In addition, it is important to consider how these parameters affect the midges. The effect of water temperature on midge species compositions is probably greater than the effect of air temperature. However, when compared, air temperature inference models have most often demonstrated superior performance (Brooks & Birks 2001). There are also potential difficulties in the measurement of water temperature that may cause serious problems in applications (Seppälä 2001). Data on the minimal DO requirements of aquatic invertebrates is needed when studying low oxygen tolerances (Davis 1975). The minimal DO conditions in shallow lakes in Finland usually occur during late winter, and winter oxygen depletion is especially common in shallow and productive ponds and lakes, where decomposition consumes a great deal of oxygen (Brönmark and Hansson 2005). Therefore, when developing a midge-based transfer function for DO using shallow boreal lakes, DO should be measured during late winter in the hypolimnion, where the minimal values occur. In addition, the selection of the sampling point is crucial, because the fossil assemblages may have an uneven distribution within a lake basin (Heiri et al. 2003; Heiri

Figure 3. Chironomid larva from Kvaliroslaguna, Svalbard (a), and an adult midge laying eggs on the water surface in Lake Pielinen, eastern Finland (b). Photo credit T.P. Luoto.
This can cause bias in the performance of calibration models and in reconstructions, and the most representative sampling point should therefore be carefully assessed.

1.3. Where to draw the line? – Reliability of reconstructions

The signal of environmental parameters can be extracted from fossil records and statistically separated from extraneous noise by comparing modern observational records with records of proxy data. Because midge assemblages are influenced by many environmental factors, the inference of one particular variable, such as temperature, may be compromised if the midge response to secondary variables becomes stronger (Heiri & Lotter 2003; Velle et al. 2005; Brooks 2006; Brooks et al. 2007). However, in lakes with a high number of taxa, the reconstruction of multiple variables is potentially possible due to the elevated number of indicator taxa and by examining the community response, since the community as-
semblage is unique in a particular environment with multiple and varying forcing factors affecting the species composition. The factors to which midge assemblages are responding the most at a given time and the reliability of reconstructions can be evaluated using several approaches, including direct and indirect hypothesis testing (Birks et al. 1990; Birks 1998; Bigler et al. 2002, 2003; Velle et al. 2005). In addition to statistical tests implemented by using, for instance, the modern analogues of fossil taxa, the topmost inferred values can be compared with the modern observations and measurements from the study lakes to assess the accuracy of reconstructions in the most recent layer. However, care should be taken in the interpretation of these evaluation methods, since ‘poor’ fit samples may also represent the truth, while the ‘good’ fit samples may not always provide accurate estimates (Bigler et al. 2002). Moreover, reconstructing multiple variables from midge assemblages gives the opportunity to compare the reconstructions, thus possibly enabling the separation of correct and erroneous inferences. However, multiproxy investigations and comparison to other local studies, historical evidence and observational records (i.e. reproducibility) are probably the best means for estimating the reliability of reconstructions.

1.4. Objectives of the study

This study aimed to provide detailed taxon-specific ecological data on midge-environment relations in Finland using sedimentary death assemblages and to apply this data to produce reconstructions of past changes in climate, water quality and habitats (cf. Smol 1990, Saros 2009) that can be interpreted in case-specific and synoptic palaeoenvironmental contexts. Multi- and intralake perspectives together with geographical scaling and environmental screening approaches were used to seek the forcing factors behind midge distribution, diversity and abundance and different training set designs were tested. The developed models were applied to high-resolution sediment profiles from southern and eastern Finland, with a special focus on the time periods of the MCA, LIA and increased anthropogenic influence.

The present study area is located in a climatologically important region, because the North Atlantic has a direct influence on the climate of Northern Europe through the upper troposphere jet stream and strong westerly atmospheric circulation providing the heat and moisture transport from the Gulf Stream (Wallén 1970). These large-scale climatic patterns, teleconnections or modes, explain a major part of the variability in atmospheric circulation (Wallace & Thompson 2002). The developed models can provide essential knowledge on past environmental conditions (e.g. the baseline or reference conditions) and natural variability (e.g. spatiotemporal climate patterns and mechanisms, such as the NAO) that is needed by decision makers in local, regional and global environmental change assessments and in ecosystem management (Smol 1992).

In particular, the research presented in this thesis aimed to:

1) develop a midge-based palaeotemperature inference model (paper I) and apply it to a late-Holocene sediment profile, with a special focus on the relationship between chironomid-inferred temperatures and diatom-inferred trophic conditions during the LIA (paper II);
2) examine the relationship between midge assemblages and late-winter hypolimnetic oxygen to produce quantitative estimations of past oxygen conditions (paper III);
3) develop a midge-water depth transfer function for the reconstruction of past lake levels (paper IV), which are sensitive indicators of effective
moisture variability; 4) investigate intralake gradients in midge assemblages for better understanding of midge ecology and taphonomy and with the aim of producing more reliable and novel environmental reconstructions, with a focus on hydrological variables (paper V); and 5) infer temperature and precipitation trends during the MCA and LIA using midge and tree-ring records and examine the long-term relationship between the NAO and climate (paper VI).

2. Regional setting

2.1. Multilake datasets

The study area is located in Finland, ranging from 60°13’ to 69°53’ N and 22°00’ to 30°13’ E (Fig. 5). The study sites span a 1080-km latitudinal transect, from boreal coniferous forests in the south to tundra vegetation in north. The examined 83 lakes are generally small and shallow and are remotely located. The altitude of the lakes varies from 11 to 404 m above sea level (a.s.l.) and the mean July air temperature ($T_{Jul}$) ranges from 11.3 to 17.0 °C. The mean annual precipitation varies within the area from 400 to 660 mm. The surface sediment dataset in paper I was collected from 82 of these sites. The dataset in paper III was collected from southern Finland (60°13’-63°05’ N, 22°00’-30°13’ E). The vegetation in the catchments of the 30 lakes in this dataset consists of boreal coniferous forests, underlain by Precambrian granitic bedrock and typically having a thin soil layer. Some of the lakes are located in urban areas. In general, the
study area in paper III is more influenced by human activity than that examined in paper I, although some sites have remained close to their pristine state. The dataset in paper IV comprises 68 lakes, which are mostly the same as in paper I, except for the omission of the human disturbed and deepest lakes to better assess the influence of water depth and focus on the study of shallow lakes (< 7 m).

2.2. Intralake dataset

The intralake dataset was derived from surface sediment samples of Lake Pieni-Kauro, situated in Kuhmo, eastern Finland (64°17’ N, 30°07’ E) (Fig. 5, paper V). The regional mean annual air temperature varies between 1 and 2 °C and the mean annual precipitation between 600 and 650 mm (climate normals 1971–2000). The mean air $T_{\text{Jul}}$ in the lake area is 15.3 °C. The catchment bedrock consists of Archean granitoids and migmatites (Mikkola 2008). The area is sparsely inhabited and the catchment is characterized by a drumlin landscape and wilderness-like coniferous forests. The northern shore is covered by wetlands and the Saavanjoki River enters the lake from the north, while the main outlet is on the western side. Lake Pieni-Kauro is part of a larger lake complex connected by small rivers that originates in Russia and eventually drains into the Gulf of Bothnia in the Baltic Sea. The ca. 30 ha lake lies at an elevation of 188.4 m a.s.l. The maximum water depth in the dystrophic Lake Pieni-Kauro is 7.9 m.

The emergent aquatic vegetation of Lake Pieni-Kauro and the Saavanjoki River mostly consists of the common reed (*Phragmites australis* (Cav.) Trin. ex Steud.), which is especially abundant on the lake’s western and southern shores. The mouth of the Saavanjoki River is characterized by floating-leaved yellow water-lily (*Nuphar lutea* L. Sm.), while the emergent water horsetail (*Equisetum fluviatile* L.) is common in the soft bottoms of the shallow shores in the river-lake transition zone. The sediments of the lake mostly consist of detritus, but the western shore is characterized by sandy substrates with a low organic content. The lake has a diverse and abundant fish fauna, and the noble crayfish (*Astacus astacus* [L.]), which is restricted to unpolluted freshwater environments, is abundant in the local streams, including the Saavanjoki River.

2.3. Downcore sediment sequences

Lake Hampträsk (papers II, III, V) is situated in southern Finland (60º17´ N, 25º15´ E) in the municipality of Sipoo (Fig. 5). The surface area of the lake is ca. 3.8 ha and it lies at an altitude of 20.3 m a.s.l. (Table 1). The modern observed mean air $T_{\text{Jul}}$ at the lake is 16.8 °C. The size of the catchment area is 37 ha and it consists of low-lying clay patches east of the lake and elevated rocky areas north and west of it. Forest with occasional paludification covers the elevated land. Cultivated fields and several buildings occur near the lake. One ditch enters the lake from the elevated area, where the paludified areas are heavily ditched. The lake has a single outlet in the southern end. The emergent aquatic vegetation mainly consists of *Phragmites australis* and *Nuphar lutea*. The western shore is paludified and consists of *Sphagnum* mosses. The lake has suffered from nutrient enrichment due to historical and modern cultivation and is currently eutrophic. The lake seems to be experiencing hydroseral development, a plant succession in which the littoral vegetation gradually proceeds towards the open-water areas (cf. Korhola 1990). The present summer epilimnetic total phosphorus (TP) concentration is 58 μg l$^{-1}$ and the summer total nitrogen (TN) concentration is 1123 μg l$^{-1}$ (Nevalainen & Sarmaja-Korjonen 2008). The lake is known to have experienced oxygen
depletion and winter fish kills (Ekholm 2007).

Lake Iso Lehmälampi (papers III, IV) is situated in southern Finland (60°20' N, 24°36' E) in the municipality of Vihti (Fig. 5, Table 1). It covers an area of ca. 5.1 ha in the Nuuksio Upland at an altitude of 91.7 m. The modern observed mean air $T_{Jul}$ at the lake is 16.4 °C. The catchment (ca. 30 ha) is characterized by bedrock outcrops and patches of mire. The lake has one small recently dug outlet, but no inlets. The lake is naturally acidic (Korhola and Tikkanen 1991; Sarmaja-Korjonen & Alhonen 1999; Sarmaja-Korjonen 2001), but experienced repeated major pH decreases in the 1980s leading to a value below 5.0 (Verta et al. 1990). Since then, the lake has recovered and the pH presently ranges between 5.1 and 5.8 (Nevalainen and Sarmaja-Korjonen 2008). Recently, there have been several fish introductions, but only perch (*Perca fluviatilis* L.) is currently known to inhabit the lake (Nevalainen 2008).

The sediment profile in paper VI originates from the same lake as the intralake surface sample dataset (Lake Pieni-Kauro, eastern Finland) described above (Fig. 5, Table 1). The compared tree-ring assemblage used in paper VI originates from eastern Finland (61°–62° N, 29°–28° E) and is based on hundreds of individual tree-ring records (Helama et al. 2005, 2009).

### 3. Material and methods

#### 3.1. Sediment sampling

The surface sediment samples of the 82, 68 and 30 lake datasets (papers I, III, IV) were obtained through the lake ice with a Limnos gravity corer (Kansanen et al. 1991) between February and April 2005. The lakes were chosen to represent a temperature gradient in paper I, a hypolimnetic oxygen gradient in paper III and a water depth gradient in paper IV. The surface sediment sampling of Lake Pieni-Kauro and the Saavanjoki River (paper V) was performed in October 2008 from a boat (M/S Unski), also using a Limnos corer. The retrieved 34 samples were selected to represent different habitat types, with a focus on the effects of depth, stream flow, substrate and vegetation on midge assemblages. The surface sediment samples (topmost 0–1 cm) used in this study represent the recent years of sedimentation. The fossil faunal assemblages in them can be considered as analogues of modern relative abundances (Frey 1960; Nevalainen 2008; Nykänen et al. 2009) and to characterize the lake environment adequately for palaeoenvironmental calibration studies (Bunbury and Gajewski 2008). The samples were stored in plastic bags in a cold room at +4 °C.

Short downcore sediment sequences from
Lake Hampträsk (47 cm) (papers II, III, V) and Lake Iso Lehmälampi (25 cm) (papers III, IV) were cored through the ice in February 2005 and the record from Lake Pieni-Kauro (36 cm) (paper VI) was taken from a boat in October 2008. The corings were performed using the Limnos corer. The water depth at the coring point was 242 cm in Lake Hampträsk, 412 cm in Lake Iso Lehmälampi and 685 cm in Lake Pieni-Kauro. All of the sediment sequences consisted of homogeneous fine-detritus gyttja. The cores were sheared at 1-cm intervals in the field and the sub-samples were placed in plastic bags for storage in a coldroom at +4 °C.

3.2. Limnological, sedimentological and climatological measurements

Limnological measurements were performed as single measurements taken in situ during the collection of the sediment samples (papers I–VI) with an Orion Model 1230 pH/mV/ORP/conductivity/dissolved oxygen/salinity/temperature meter (Thermo Fisher Scientific, Waltham, MA, USA) before sediment sampling to avoid the resulting disturbance of the water column. The oxygen concentration was recorded from the hypolimnion (or below the photic zone/thermocline), ca. 0.5 m from the bottom, and conductivity and pH from the epilimnion. The Orion dissolved oxygen meter calculated the oxygen concentration on the basis of the known relationship between oxygen solubility, temperature and total atmospheric pressure. The oxygen meter has a resolution of 0.01 mg l⁻¹ and an accuracy of ± 0.5% of the measured value ± 1 digit within an ambient temperature range of 5 °C to 30 °C. The Orion MSR™ (Minimum Stir Requirement) DO probe is a stable probe with very low oxygen consumption and zero current at zero oxygen concentration.

Magnetic susceptibility (MS) was measured using a Bartington equipment sensor MS2C (Bartington Instruments Ltd., Witney, Oxon, UK). The measurements for MS were performed from unopened sample bags prior to the other analyses. Loss-on-ignition (LOI) was performed from wet sediment using a sample size of approximately 10 g. The samples were dried at 105 °C for 12 h and ignited in an oven at 550 °C for 2 h (Dean 1974; Heiri et al. 2001) following the standards SFS-EN 12819 and SFS-EN 12880.

The lake depth was measured from the sampling point and is in fact the water depth at the sampling site, which does not mean the same as the maximum lake depth (paper IV). The multilake dataset samples were taken from the sublittoral areas rather than from the deepest point.

The modern mean air $T_{\text{Jul}}$ was estimated for each lake using a geographical information system (GIS)-based method. The temperature data were provided by the Finnish Meteorological Institute and were based on the 1971-2000 climate normals, which take into account all Finnish meteorological data. The temperature data were interpolated from the data of the meteorological stations to a 50 x 50 km grid, taking into account factors such as elevation and lake coverage. If the elevation of the sample point was markedly different from the grid in question, the elevation was reconsidered (Seija Kultti pers. comm.).

3.3. Fossil midge analysis

The sediment samples for fossil midge analysis were prepared applying standard methods described in Hofmann (1986), Walker (2001) and Brooks et al. (2007). Papers V and VI used volumetric (1 cm⁻³) subsamples. The wet sediment was treated with warm 10% KOH for 10-20 minutes in papers I-IV, but not in papers V and VI because it seems to be a generally unnecessary practice. The sediments were sieved through a recommended 100-μm sieve (Larocque et al. 2009)
and the residue was examined using a Bogorov counting chamber (Gannon 1971) or a Petri dish, under a stereomicroscope (25-40 times magnification) for extraction of midge remains with fine forceps. The fossil remains were permanently mounted in Euparal® or Canada balsam (Rennhistol®) on microscope slides and identified to the highest taxonomic resolution possible under a light microscope at 400-times magnification.

In the surface sample datasets, a minimum of 100 midge individuals were identified from each sample to better include rare taxa. In the sediment profiles from Lake Hamptärsk and Lake Iso Lehmalampi, a minimum of 60 individuals were enumerated and in the core from Lake Pienni-Kauro a minimum of 50, which exceeds the minimum count size of 40-50 head capsules recommended for fossil chironomid analysis (Heiri and Lotter, 2001; Larocque, 2001; Quinlan and Smol 2001). In the volumetric samples (papers V, VI), all remains were enumerated, but if a sample had a low number of remains, more sediment was prepared for extra slides to gain the minimum counting sum set for analysis. Two chaoborid mandibles were considered as one individual. The identification was mainly based on the identification guides of Wiederholm (1983) and Brooks et al. (2007). Heiri et al. (2004) was used to identify the Tanytarsini and Rieradevall and Brooks (2001) the Tanypodinae larvae. The identification of Cricotopus pulchripes-type was based on the description of Nyman et al. (2005). The phantom midges (Chaoboridae) and biting midges (Ceratopogonidae) were identified according to descriptions of Finnish specimens by Luoto and Nevalainen (2009) and Luoto (2009). The black fungus gnats (Sciaridae) were identified according to Heiri and Lotter (2007). The remains of the black fly (Simuliidae) Simulium are described in paper VI. The nomenclature follows the above-mentioned literature.

3.4. Numerical analyses
3.4.1. Ordinations

All data analyses, both uni- and multivariate, were performed using relative taxon abundances and square-root transformation of assemblage data with and without taxa deletions (see papers for details). Detrended correspondence analysis (DCA) was applied to explore patterns in distribution of the taxa within spatial and temporal dimensions and to choose between linear- or unimodal-based methods in further numerical analyses by estimating the lengths of compositional gradients (DCA axes 1 and 2). The DCA was run with detrending by segments. DCA is an indirect ordination method that summarizes the variation in species assemblages along the DCA axes (ter Braak 2003).

Canonical correspondence analysis (CCA) was used to explore the relationships between midge assemblages and environmental variables. CCA is a direct gradient technique that can be used to identify environmental variables that are strongly related to the species assemblages (ter Braak 2003). The CCAAs were run with only one environmental variable at a time. The statistical significance of each variable was tested with a Monte Carlo permutation test (499-999 unrestricted permutations), and variables were considered significant if the permutation test value (P) was ≤ 0.05. When only one environmental variable is used, the ratio of the first constrained eigenvalue (λ1) to the second unconstrained eigenvalue (λ2) indicates the relative importance of the specific variable in explaining the cumulative variance in the species data. Explanatory variables that have high λ1:λ2 ratios may be useful for quantitative inference models. In the intralake dataset (paper V), stream flow (lotic index, LI), the proximity of wetland and the presence of Nuphar, Equisetum and Phragmites stands were
entered as nominal variables, using binary codes (value 0 when absent and 1 when present). The stream flow was entered as a ‘dummy’ variable, because discharge can vary greatly among seasons or within and following a precipitation event (Gandoin et al. 2006). The distance from the littoral vegetation (DLV) was measured and determined by examining aerial photographs and field observations. The DCAs, PCAs and CCAs were performed using the program CANOCO, version 4.52 (Plant Research International, Wageningen, the Netherlands) (ter Braak 2003).

Two-way indicator species analysis (TWINSPAN) was used as a divisive technique to classify the 82 lakes from the dataset along the latitudinal gradient in Finland and the 34 samples from the intralake dataset in Lake Pieni-Kauro (in this synopsis). Taxa with less than 2 occurrences were removed from the analyses and pseudospecies cut levels were set to 0, 2, 5, 10 and 20%. TWINSPAN was performed using the program WinTWINS, version 2.3 (Centre for Ecology and Hydrology & University of South Bohemia, Huntingdon & České Budejovicě) (Hill & Šmilauer 2005).

Taxon-specific optima and tolerances for the environmental variables of interest were calculated using the weighted averaging (WA) technique (complete results presented in the Appendix). The influence of sampling point selection in multilake calibration set studies were assessed by examining Pearson correlations (Pearson product-moment correlation coefficient, ) between the sample-specific and lake-averaged assemblage along the water depth gradient (paper V). Additionally, chironomid-based mean air temperature reconstructions were applied to the intralake samples and to the summary sample containing all the taxa with their average abundances within the lake.

The midge stratigraphy in paper VI was divided into local faunal zones that were identified by major changes in midge assemblages using the program ZONE version 1.2 (Juggins 1991). The zoning was performed using optimal partitioning and the number of zones was determined using the broken stick method (Bennett 1996). Species diversity was assessed using the Shannon (i.e. Shannon-Wiener or Shannon-Wiever) index in paper II and Hill’s N2 (1973) (effective number of occurrences) in papers III, IV and V. The actual number of taxa was expressed as species richness (S) in papers V and VI.

3.4.2. Model development and reconstructions

In the development of palaeoenvironmental inference models, several calibration techniques were used to select the methods that perform best by giving a high squared correlation between jackknife-predicted and observed values ( ), a low prediction error (RMSEP) and low mean and maximum biases in jackknife residuals. The methods used were simple WA with an inverse deshrinking regression, WA with taxon tolerance weighting (WA_tol) and an inverse deshrinking regression, simple WA with a classical deshrinking regression, WA with WA_tol and a classical deshrinking regression, locally weighted WA (LW-WA), partial least squares (PLS), WA-PLS, a Gaussian logit model (i.e. maximum likelihood) and the modern analogue technique (MAT) (Juggins 2007). The optimal number of calibration regression components included in PLS and WA-PLS transfer functions was assessed using leave-one-out cross-validation. Additional components were considered useful if they gave a reduction in the prediction error of at least 5% (ter Braak and Juggins 1993, Birks 1998). MAT was performed by applying average and weighted average (WMAT) values of the 10 closest analogues. The inference models were run and developed with the program C2, version 1.5.0 (University
of Newcastle, UK) (Juggins 2007).

The palaeoenvironmental reconstructions were implemented with C2. The reconstructions were evaluated using four different approaches (Birks et al. 1990; Birks 1998; Bigler et al. 2002; Velle et al. 2005; Sarmaja-Korjonen et al. 2006): 1) by calculating the proportion of taxa from each fossil assemblage that was represented in the modern calibration set (cutoff for samples with poorly represented assemblages < 90–95%); 2) by examining the squared residual distance (square residual length, SqRL) of the modern and fossil passive samples in a CCA with the environmental variable of interest as the sole constraining variable (lack-of-fit > 10% of the extreme values in the modern calibration set); 3) by testing whether the samples have good modern analogues (MAT) (threshold for good assemblage > 5% chord distance); and 4) by comparing whether the modern measured values exceeded the topmost inferred values by more than the model’s RMSEP.

In paper VI, the relationship between the reconstructions was examined by calculating the Pearson product-moment correlation between the reconstructed environmental variables.

4. Results and discussion

4.1. Distribution and diversity of midges at regional, local and site-specific scales

The distribution of midge taxa in the dataset along the latitudinal gradient in Finland (paper I) corresponded with general faunal observations made in the Palaearctic region (Brooks et al. 2007) and with the previous data from Finland (Nyman et al. 2005; Paasivirta 2007). Of the individual taxa, *Micropsectra radialis*-type, *Heterotrissocladius maeaeeri*-type, *Corynocera oliveri*-type, *Psectrocladius* (*Monopsectrocladi-
ative of low oxygen levels in accordance with previous studies (e.g. Wiederholm & Eriksson 1979, Kansanen 1985, Meriläinen et al. 2000).

The taxon most indicative of high water levels in the dataset of 68 pristine lakes (Paper IV) was *Heterotrissocladius marcidus*-type, and the other *Heterotrissocladius* species also had high optima. This corresponds well with the results from previous studies in the Holarctic (Walker & MacDonald 1995; Korhola et al. 2000; Barley et al. 2006). Other common taxa of deeper waters in the present dataset included *Tanytarsus lugens*-type and *T. pallidicornis*-type. Together with *Heterotrissocladius* species, *T. lugens* is well known from cold and deep waters (Brundin 1949) and *T. pallidicornis*-type is also restricted to the deepest parts of lake basins in shallow lakes in Norway (Heiri 2004), fitting well with the present results. Of the shallow-water taxa of this study, *Polypedilum nubeculosum*-type indicated very shallow lakes. Korhola et al. (2000) also found that *Polypedilum* was indicative of shallow lakes, and another feature common with their dataset was the association of *Psectrocladius* (*Monopsectrocladius*) with shallow lakes. This was also indicated by the results of Nyman and Korhola (2005) and Mousavi (2002). Additionally, the shallow-water indicators in this study, such as *Glyptotendipes, Cladotanytarsus, Cladopelma* and *Zalutschia* species, also indicated shallow-water habitats in Canadian datasets (Walker & MacDonald 1995; Barley et al. 2006). Thus, it appears that the present results represent a pattern consistent with that of previous studies on midge distributions along depth gradients in the Holarctic region. The broad distribution of the tanytopods *Procladius* and *Ablabesmyia monilis*-type may be due to the fact that they are free-living and not sessile, as the tube-building midges are.

The taxon richness in the surface sediments of Lake Pieni-Kauro and the Saavanjoki River (Paper V) was very high, since over 100 midge taxa were identified. This was most likely due to the great diversity of habitats available for midges, including lentic and lotic environments with different exposures, substrata and vegetation types. The midge assemblages showed significant heterogeneity between the samples, and the highest taxon richness and absolute midge abundance was found at intermediate sample depths (Fig. 7). The deepwater samples may be expected to have lower diversity, because the profundal provides a more uniform habitat without the shelter of vegetation or rocks. Most of the midge taxa apparently prefer intermediate depths, because the results showed that the midge diversity of the shallow waters was high only in the riverine samples.

Among the most common midge taxa in Lake Pieni-Kauro, *Heterotrissocladius marcidus*-type prefers deep waters with well-oxygenized hypolimnia while *Ablabesmyia monilis*-type and *Procladius* are frequently found in all lake types in Finland (Nyman et al. 2005; Paasivirta 2007, papers I, III, IV). The profundal zone in Lake Pieni-Kauro was dominated by cold-indicating *H. maeaeeri*-type, while it was absent from other parts of the lake. Many other cold water taxa, such as *Sergentia coracina*-type, *Protanypus, Micropsectra radialis*-type and *Tanytarsus lugens*-type were also restricted to the profundal zone. The littoral areas of Lake Pieni-Kauro were characterized by taxa such as *Psectrocladius* (*P. sordidellus*)-type, while the riverine samples were dominated by the *Thienemannimyia pseudocarnea*-type. The lotic environments were characterized by the presence of *Simulium, Rheotanytarsus, Nanocladius* (*P.*) *branchicolus*-type, *Rheocricotopus chalybeatus*-type and *T. clavicornis*-type, fitting well with previous data on their ecology (Wiederholm 1983; Currie & Walker 1992; Gandoin et al. 2006; Brooks et al. 2007).

The occurrence of *Zalutschia mucronata*-type in Lake Pieni-Kauro seemed to be con-
trolled by the proximity of paludification and thus humic substances, while sphagnum mosses seemed to provide part of its habitat. *Psectrocladius (P.)* sordidellus-type, *Cladopelma viridulum, Parakiefferiella bathophila*-type, *Nanocladius rectinervis*-type and *B.*-type ceratopogonids were strongly associated with *Phragmites australis* stands. Previous data confirm that

*Psectrocladius (P.)* sordidellus and *Cladopelma* are common taxa in vegetated lake shores (Tołonen et al. 2001) and ceratopogonids are often associated with submerged vegetation (Brooks et al. 2007).

**4.2. Mystery of the midges: what forcing factors are communities responding to?**

Previous studies based on surface sediment samples have shown that in north-eastern Finnish Lapland, chironomid distribution and abundance are mainly controlled by the substrate type (sediment organic content measured as LOI), air/surface water temperature and lake depth (Olander et al. 1997, 1999; Nyman et al. 2005). Because of the pronounced effect of temperature on midge distributions, many chironomid-based temperature inference models have been developed, such as those for northern Europe by Olander et al. (1999), Brooks and Birks (2001, 2004), Larocque et al. (2001) and Seppä et al. (2002). However, it has remained unclear whether chironomids respond to temperature directly through physiological temperature tolerances or indirectly through changes in the lake habitat and other intralake processes (Anderson et al. 2008; Brodersen et al. 2008). Furthermore, limnological factors, such as lake trophic status, can have an overwhelming influence in warmer climatic conditions or within short climatic gradients (Brodersen & Lindegaard 1999; Brooks et al. 2001).

The results from the present dataset of 82 lakes in a transect across Finland (1080 km) demonstrated that the mean air $T_{\text{Jul}}$ is a major factor affecting chironomid distribution and abundance, together with sampling depth and dissolved oxygen (paper I). The DCA sample plot showed a fanlike shape from the coldest lakes towards the warmest (Fig. 8), and it thus seems that temperature is clearly the most important
factor influencing chironomid distributions in the entire dataset, whereas in southern regions other factors also become significant. The results suggest that many of the taxa succeeding in particular limnological conditions, such as an elevated trophic status, may also favor warm lakes. It has been shown that in northern and alpine areas, nutrient conditions are related to summer temperatures, with cool lakes often having reduced nutrient conditions, while lowland areas at lower latitudes are more often subject to anthropogenic nutrient enrichment (Brodersen & Anderson 2002; Heiri & Lotter 2005). This is also probably the reason for the variation found in the current DCA plot, as the southern parts of Finland are extensively utilized by man, whereas the environment in northern Finland is more close to its natural state.

Temperature, metabolism and respiratory requirements are directly linked to each other, and respiration physiology is thus among the indirect causal responses and mechanisms making midges useful as climate indicators (Brodersen et al. 2004, 2008). The oxygen conditions can definitely change under stable climate conditions, but climate hardly ever changes without affecting the oxygen status. Under significant temperature changes, oxygen, productivity and climate in combination are probably the forcing factors determining midge distribution.

Many of the deepwater taxa in this study, such as Micropsectra radialis-type, Heterotritsoscladius maeaei-type, Corynocera oliveri-type and Tanytarsus lugens-type, appear to also be those indicating cold temperatures. This is most likely because deepwater environments are characterized by colder water temperatures during the summer. There is also the discrepancy over whether some cold-indicating midges are responding to changes in temperature or in hypolimnetic oxygen or depth, since well-oxygenated profundal environments provide refugia for cold stenothermic taxa (Brodersen et al. 2004, 2008). However, some cold-indicating taxa, such as Corynocera ambigua and Zalutschia mucronata-type, which also tolerate moderate hypolimnetic oxygen deficiency, indicate shallow water in the present dataset and show that not all cold-indicating midge taxa are restricted to deep and well oxygenated waters. In addition, Chaoborus flavicans, a species that is absent from the coldest parts in Finland (Luoto & Nevalainen 2009), was found solely in the deepwater samples in this study.

Since multiple environmental factors influence midge assemblages, it may also be possible to use these assemblages to infer multiple environmental variables. The best means for isolating the effects of temperature in lake-level reconstructions is to look for synchronous changes within a region (Dearing & Foster 1986). The ultimate environmental forcing factors evidently vary among different taxa, but apparently it is also a matter of spatial and environmental scaling (Fig. 9). Along the latitudinal gradient of

Figure 8. Detrended Correspondence Analysis (DCA) plot of samples based on the midge assemblages in the 82 study sites along the latitudinal gradient in Finland (redrawn from paper I). The gradient lengths for the axis are 2.9 (axis 1) and 3.2 (axis 2) standard deviation units.
over 1000 km in Finland, summer air temperature was the most important factor controlling midge distribution (paper I), but when deep and anthropogenically disturbed lakes were excluded, the influence of water depth became more predominant (paper IV). Furthermore, the dataset restricted to southern Finland, with a temperature gradient of only 1.1 °C, revealed that a major forcing factor on midge assemblages was the late-winter hypolimnetic oxygen content (paper III), while summer air temperature was still statistically significant, but the water depth lost its significance. The hydrological variables of stream flow and water depth were the most important factors controlling midge distribution when the study was scaled to a single lake, while the submerged vegetation patterns and catchment characteristics also contributed as significant explanatory variables (paper V). In addition, the TWINSPLAN grouping of samples identified indicator taxa representative for different parts of the climatic gradient in the 82 lake dataset (Fig. 10), whereas the taxa were divided into indicator groups based on their habitat preferences in the intralake dataset (Fig. 11). Therefore, if large-scale regional datasets are divided into smaller local datasets or screened to reduce background variance (cf. Hausmann & Kienast 2006), inference models can be developed for multiple environmental variables, and lake-specific datasets can moreover provide inference models of factors affecting species assemblages within a lake basin (i.e. habitats).

4.3. Potential and problems of midge-based palaeoenvironmental inference models

4.3.1. Training set design

The development of training sets for palaeolimnological purposes has focused on sampling the most recent fossil fauna from the surface sediments of multiple lakes (Smol 2008). The supposed advantage of this approach is that the surface sediments in profundal areas are considered to integrate organisms with respect to spatial and temporal dimensions, including all seasons and habitats (Frey 1988). However, this may not always be the case, as the fossil fauna in the surface sediments sometimes represent fauna living in close proximity to the sampling site (Heiri et al. 2003; Heiri 2004; Kurek & Cwynar 2009). Therefore, alternative methods, such as those based on contemporary pupal exuviae (chironomid pupal exuvial technique, CPET, Wilson & Ruse 2005, Ruse 2010), are promising perspectives in developing better training sets through a more accurate species assemblage description (Luoto & Raunio subm.). The greatest advantage of the CPET method is that it usually provides a more representative sample of midges from all depths and aquatic microhabitats (e.g. Raunio et al. 2007, 2010) compared to the traditional single-point training set sampling of fossil specimens. However, this method only considers recently emerged species, whereas surface sediment sampling for fossil specimens integrates fauna during a longer temporal dimension, in-
Excluding all seasons (Frey 1988).

The surface sediment sampling in papers I, III and IV was performed from the sublittoral areas of the lakes and not from the profundal, as usually in training sets. The study in paper I used all the sampled 82 lakes, except for the exclusion of five outliers from the temperature inference model. These outlier lakes were the only large lakes in the dataset and had extreme pH conditions. The study in paper IV focused on pristine shallow lakes with sampling depths < 7 m (Table 1), because short environmental gradients may assist in estimating environmental optima that are more realistic for the taxa involved (Velle et al. 2005). In addition to deeper lakes, disturbed lakes that are mostly located in urban or cultivated areas were excluded to reduce the effects of nutrients and hypolimnetic oxygen on midge assemblages. This exclusion aimed to create a consistent dataset (shallow lakes without major anthropogenic influence) on which the new inference model for water level was based. There is, however, a concern that even though editing of a dataset may improve the model performance statistics, it may not eliminate the true inference error, leading to the requirement of incorporating longer environmental gradients (Walker & Cwynar 2006).

The water depth model was based on measurements of the sampling depth, which does not mean the same as the maximum lake depth, because the samples in this study have been taken from the sublittoral. Nevertheless, the midge assemblages of the sampling points seemed to represent the water level (i.e. sampling depth) very well. Cores taken from the deepest point are generally insensitive to small changes in water depth (Hofmann 1998; Battarbee 2000), and the present methods therefore probably provide more sensitive cues of lake-level changes. Thus, the results in paper IV indicate that lake-level transfer functions can also be developed by using intralake datasets (cf. Kurek & Cwynar 2009), as midge assemblages of a particular sampling point are representative of certain depths. This was supported by the results from paper V, which showed significant shifts in midge assemblages within Lake Pieni-Kauro. Because the death assemblages represent fauna that lived in close proximity to the sampling point, the examination of intralake gradients using surface sediment samples can be rewarding. However, in lakes

Figure 10. TWINSPLAN grouping of lakes and the assigned indicator taxa (see Appendix for codes) based on the midge assemblages in the 82 study sites along the latitudinal gradient in Finland.
with only a few habitat types, such as most of the lakes in arctic and subarctic regions, the fossil lake fauna is likely to be more uniform (e.g. Holmes et al. 2009). In addition, arctic and subarctic lakes are more exposed to wind created currents, which cause within-lake transportation of fossil remains. Intralake models may also suffer from many potential limitations, such as lower applicability, shorter environmental gradients and lake-specific discrepancies in the modern distribution (Kurek & Cwynar 2009). However, because the present results showed a close relationship in taxon-specific water depth preferences between the examined dataset types (papers IV, V), it is possible to combine these training sets to provide better estimates of the taxon optima and to enhance the transfer function (Luoto subm. a).

Environmental perturbations operating in lacustrine or riparian systems may be dampened or irrelevant at regional or even local scales. Thus, one potential approach in training set design could be to increase the number of samples, but not necessarily the environmental gradient or the size of the geographical area. It is clear from the present results that the selection of the sampling point in training set development and in downcore studies is crucial in order to be able to detect the environmental signal of interest. However, the selection of the study lakes is also important, because environmental changes, such as those related to climate, can appear very differently in different lake types, and the actual changes may remain undetected or become falsely interpreted. Alternative midge communities can exist under similar trophic or climate conditions, but changes in communities may occur over thresholds and these ecosystem switches can be detected using palaeoecological proxies, such as midges (Langdon et al. 2006).

4.3.2. On the search for the perfect sampling point

The influence of basin morphometry, windiness and currents on the taphonomic processes of midges, such as selective offshore transport, mixing and resuspension, are relatively poorly understood, but apparently there is wide taphonomic variability among lakes (Walker et al. 1984; Frey 1988; Schmäh 1993; Hofmann 1998; Heiri 2004; Holmes et al. 2009; Kurek and Cwynar 2009). In paper V, the high level of heterogeneity in the fossil surface sediment midge assemblages clearly indicated that the assemblages predominantly incorporate the locally dwelling fauna, instead of integrating remains from a larger area around the lake. This is proven by the fact that the surface sediments of different parts of Lake Pieni-Kauro were dominated by different taxa. This is essential information for all midge-based studies dealing with surface sediment datasets that are based on a single sample per lake; the selection of the sampling point may profoundly affect the results when aiming to develop training sets, e.g. for temperature. However, midge-based downcore studies that are based on a single sample may not be as severely affected, because
the downcore samples always represent the same spot in the lake, and the possible resulting error would thus be systematic (under- or overestimation of the environmental variable studied) (Heiri et al. 2003).

According to the present results, the samples taken from a water depth of approximately 3 m had the highest midge abundance, taxon richness and strongest correlation with the whole-lake species assemblage (Fig. 7). However, most of the samples showed strong correlations with the average species assemblage, and only if a sediment sample had been taken from the location of a few of the sampling points would the assemblages have been significantly different from the lake system average. The test of the effect of sampling point on chironomid-based temperature reconstructions indicated that there is a potential risk of underestimating the temperatures when the sample is taken from the deepest point (Fig. 12). However, if there are randomly occurring errors in the temperature estimates of calibration models, these are likely to be detected as outliers in earlier statistical analyses. One possibility in the development of a chironomid-temperature training set could be to amalgamate more than one sample from each lake (modification from Olander et al. 1999).

A major advantage in coring the deepest points are that they also integrate some littoral taxa while the littoral samples lack profundal organisms. In addition, the sedimentation processes are usually more continuous in the lake centre, with a reduced risk of running into hiatuses or sediment mixing (cf. Iovino 1975, Walker et al. 1984). However, in the present dataset, the lake-specific summary sample (average depth of 3.1 m) showed an estimated value identical to that of the modern observed temperature (Fig. 12). This indicates that the sublittoral is probably the best coring point in single-sample midge-based studies in shallow boreal lakes. Consistently with the present midge-based results, Kattel et al. (2007) showed that fossil cladoceran samples in lake sediment gave a biased reflection of the communities from which they were derived in a small lake in Scotland, and suggested that the best coring point would be in the sublittoral. In the case of diatoms, the best coring point in shallow boreal lakes seems to be at depths > 6 m (Kauppila 2002), most likely because the light diatom frustules are more easily transported towards the primary accumulation zones than the considerably larger and heavier midge and cladoceran remains. However, to be representative, the location of core samples should always match that of the training set samples.

Another point worth mentioning from the results of Lake Pieni-Kauro is that the stream flow of the Saavanjoki River had little influence on the midge-inferred temperatures, as they showed only slight overestimation, which was within the model’s error estimate. This observation is in accordance with a previous study by Engels et al. (2008), which also indicated that the river contribution has no major effect on chironomid-based temperature estimations.

In principle, the best coring point to detect stream flow events would be in the lake basin as close to the river mouth as possible, where continuous sedimentation occurs. However, the close proximity of a stream would obviously affect water depth reconstructions, as the samples would be enriched with stream taxa, which may not have a preference for a particular depth. Careful selection of the sampling point is also crucial when littoral vegetation shifts are reconstructed. Estimation of the changes that have occurred in the water level and thus in the location of the littoral vegetation is important, but the best sampling point would probably be in the sublittoral, between the vegetation and profundal. In water depth reconstructions it is important that the sampling point is in the range of the mod-
4.3.3. Environmental intercorrelation and spatial autocorrelation

There are intercorrelations among the examined variables in the present intralake dataset (paper V), as depth and DLV are positively correlated. However, there appears to be no significant relationship between temperature and water depth (paper IV), temperature and DO (paper III, Fig. 6) or water depth and DO (paper III, Fig. 6) in the datasets used. Model intercorrelations complicate isolation of the effects of the different environmental variables and may cause ambiguity in the reconstructions. In addition, the use of midges to infer multiple parameters in the same lake may sometimes increase the ambiguity, because the factors that most strongly impacted the midges at a given time may remain unsolved. However, the combined use of midge-based inference models may help in interpreting midge responses to environmental changes (Quinlan et al. 1998). In lakes with a high number of species, such as those in the present study, it may be possible to infer multiple environmental factors based on midges, because of the community response and the high number of indicator taxa. Midge communities are unique in a given spatiotemporal environment and the presence and abundance of taxa thus mirrors a particular environment, which consists of multiple forcing factors. Therefore, there is no reason why multiple variables could not be reconstructed using fossil midge assemblages from a single lake, but effort should be given to estimating the reliability of the reconstructions using various numerical methods.

In addition to model intercorrelations, there are inevitable taphonomy-related model autocorrelations involved with intralake calibration sets, as fossil remains can be transported (postmortem) downstream or downslope, but probably not in the opposite directions. Spatial autocorrelation, the tendency of closely located sites to resemble one another, is not solely a problem in intralake models, but a common factor in other training set types and in ecological data in general as well (Legendre 1993), and may lead to inappropriate model choice and misleading and

4.3.4. Development of transfer functions

The best chironomid-based WA-PLS temperature inference model using one WA-PLS component (assessed by leave-one-out cross-validation) performed well, with an RMSEP of 0.721 °C, an $r^2$ of 0.78 and a maximum bias of 0.794 °C (paper I, Table 2, Fig. 13a). A one-component WA-PLS model is the statistical equivalent of WA with inverse deshrinking, having only a minor difference in the $r^2$ and RMSEP values. The favourable model performance of the present training set may be due to the relatively long geographic distance included in the transect of the study lakes, together with the high number of lakes, head capsule-counting sum and taxonomic resolution (cf. Brooks and Birks 2001). In a previously produced chironomid-based dataset from northwestern Finnish Lapland by Seppä et al. (2002), which is a taxonomically improved training set based on 63 lakes examined by Olander et al. (1999) and Vasko et al. (2000), the RMSEP for mean air $T_{Jul}$ was 0.73 °C and $r^2$ was 0.76 (reported by Sarmaja-Korjonen et al. 2006). Since both Finnish datasets show favourable model performance statistics, it seems that midge distribution in Finland is particularly strongly linked to mean $T_{Jul}$. Short environmental gradients can sometimes provide more realistic estimates of taxon optima, but training sets with lakes over a large geographic transect, such as in the present study, may contribute to a better understanding of the ecology and biogeography of midges (Larocque et al. 2006).

The best late-winter hypolimnetic oxygen model was also developed with WA-PLS regression using one component (paper III, Table 2). The RMSEP of the model was 2.35 mg l$^{-1}$, the $r^2_{jack}$ 0.72 and the maximum bias 4.23 mg l$^{-1}$. The model appeared to predict late-winter hypolimnetic oxygen levels reasonably well and quite evenly within the observed oxygen gradient (Fig. 13b). The Canadian inference models for end-of-summer hypolimnetic oxygen produced by Quinlan and Smol (2001a) showed an $r^2_{jack}$ of 0.56 and an RMSEP of 2.15 mg l$^{-1}$, while the best models of Little and Smol (2001) had an

Table 2. General information and performance statistics for the midge-based palaeoenvironmental inference models developed in this thesis.

<table>
<thead>
<tr>
<th>Dataset type</th>
<th>Mean air $T_{Jul}$</th>
<th>Hypolimnetic oxygen</th>
<th>Water depth</th>
<th>Water depth</th>
<th>Littoral veget. shift (DLV)</th>
<th>Stream flow</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude</td>
<td>60-70 °N</td>
<td>60-63 °N</td>
<td>60-70 °N</td>
<td>64 °N</td>
<td>64 °N</td>
<td>64 °N</td>
</tr>
<tr>
<td>Technique</td>
<td>WA-PLS</td>
<td>WA-PLS</td>
<td>WA-PLS</td>
<td>WA-PLS</td>
<td>WA$_{classical}$</td>
<td>WA$_{classical}$</td>
</tr>
<tr>
<td>No. samples</td>
<td>77</td>
<td>30</td>
<td>68</td>
<td>34</td>
<td>34</td>
<td>34</td>
</tr>
<tr>
<td>No. taxa</td>
<td>72</td>
<td>63</td>
<td>84</td>
<td>107</td>
<td>107</td>
<td>107</td>
</tr>
<tr>
<td>Gradient</td>
<td>11.3-17.0 °C</td>
<td>0.5-18.1 mg l$^{-1}$</td>
<td>0.7-7.0 m</td>
<td>0.5-7.3 m</td>
<td>0-270 m</td>
<td>0-1 LI</td>
</tr>
<tr>
<td>RMSEP</td>
<td>0.72 °C</td>
<td>2.35 mg l$^{-1}$</td>
<td>0.78 m</td>
<td>0.94 m</td>
<td>41.81 m</td>
<td>0.17 LI</td>
</tr>
<tr>
<td>$r^2_{jack}$</td>
<td>0.78</td>
<td>0.72</td>
<td>0.68</td>
<td>0.76</td>
<td>0.71</td>
<td>0.77</td>
</tr>
<tr>
<td>Max. bias</td>
<td>0.79 °C</td>
<td>4.23 mg l$^{-1}$</td>
<td>2.02 m</td>
<td>1.95 m</td>
<td>67.28 m</td>
<td>0.25 LI</td>
</tr>
</tbody>
</table>
The better correlation in the present study is most likely due to the fact that the largest gradient in the parameters that were measured was in DO, not in temperature. In the present dataset the temperature gradient was only 1.1 °C, while in the other datasets for DO the temperature gradient was more than 5 °C.

In the 68 lake dataset, the best of the water depth models was developed with WA-PLS regression using three WA-PLS components (pa-
The model yielded an RMSEP of 0.78 m, an $r^2_{\text{jack}}$ of 0.68 and maximum bias of 2.02 m. The best chironomid-based linear PLS maximum lake depth model with two components produced by Korhola et al. (2000) from northwestern Finnish Lapland also provided favourable performance statistics, since the RMSEP was 0.49 m and $r^2_{\text{jack}}$ was 0.70. A similar trend in the inference values and residuals was observed in this study as in the calibration model of Korhola et al. (2000), since the inferred values led to overestimation of the depth in shallow lakes and underestimation in deeper lakes. However, the trend was more pronounced in the present study. The minimum water depth at the sampling site in the present dataset was 0.7 m and the maximum depth 7.0 m, while the range in the dataset of Korhola et al. (2000) was 0.9–27.0 m. In both studies, the mean depth was at the shallow end of the gradient, i.e. 2.7 m in the present dataset and 6.4 m in the dataset by Korhola et al. (2000). This bias could possibly be weakened if the number of samples representing the deeper end of the depth gradient would be increased without increasing the depth gradient itself. However, the nonlinear distortions at the ends of the gradients are an inherent problem in all unimodal-based calibration methods that use weighted averaging (ter Braak & Juggins, 1993), and the so-called edge effect may possibly only be reduced by using shorter gradients and linear-based methods (Birks 1998, Brooks & Birks 2001).

Larocque et al. (2006) developed a chironomid-based inference model based on PLS for lake depth in northwestern Quebec, Canada, but because the lake depth model suffered from a low coefficient of determination they speculated that the model would not be reliable. Barley et al. (2006) also developed a midge-based model based on WA-PLS for lake depth in northwestern North America and the model yielded an $r^2_{\text{boot}}$ of 0.38 and RMSEP of 0.58 log transformed depth units (ln (x+1)). Later, Kurek and Cwynar (2009) presented site-specific (based on one lake, 29 samples) and local (based on three lakes, 87 samples) PLS inference models for water depth in Alaska, USA, and compared them with the regional model of Barley et al. (2006). The results of Kurek and Cwynar (2009) showed that the site-specific ($r^2_{\text{boot}} = 0.90$, RMSEP = 1.76 m) and local ($r^2_{\text{boot}} = 0.68$, RMSEP = 4.36 m) inference models had better performance statistics than the regional model. In comparison to these previous chironomid-based lake depth models, the present multilake model shows relatively favourable performance statistics. However, because the measured water levels in this study do not refer to maximum lake depths, the results are not directly comparable to some of the prior studies.

The best of the intralake water depth inference models from Lake Pieni-Kauro was developed with the WA-PLS technique, using two WA-PLS components (paper V, Table 2). The model’s $r^2_{\text{jack}}$ of 0.76, RMSEP of 0.94 m and maximum bias of 1.95 m imply that the model is able to perform quantitative estimates on past lake levels. The site-specific depth-inference model by Kurek and Cwynar (2009) showed better statistics than the local and regional models they compared their results with (see above). The higher prediction error in their study, when compared with the present results, is most likely explained by the greater depth gradient in their study. The cross-validated $r^2$ value of the present intralake model is higher than that of both Finnish regional models. This may be due to a more detailed representation of the habitat, which in a broad sense is probably the most important factor enabling the use of midges as a proxy for water depth. The present results indicate similar trends in the models’ inferred values and in the residuals as were found in the multilake depth
model (paper I) and by Korhola et al. (2000): The inferred values overestimated the depth of shallower samples and underestimated the deeper samples (i.e. the edge effect) (Fig. 13d). This may have again resulted from fewer samples at the deeper end of the depth gradient. Therefore, more even sample distances could make this bias weaker. Currently, both of the present water depth models tone down the extreme values and thus underestimate the magnitude of changes in water depth.

The best of the DLV models use WA with classical deshrinking without tolerance weighting (Table 2). The statistics of the best model imply that the model produces reliable reconstructions, because the $r^2\text{jack}$ was 0.71, RMSEP 41.8 m and the maximum bias 67.2 m. The use of the DLV model is based on the idea that when changes in lake level occur, this results in horizontal shifts in littoral vegetation. Thus, changes in the species assemblages around the sampling area are expected, because the littoral vegetation has moved and likewise the midge taxa associated with it. Thus, if a lake level were to rise, the sediment fossil assemblage would become poor in taxa that have low optima for DLV. In contrast, when lake level decreases, the fossil assemblage is expected to become abundant in these vegetation-associated taxa, because the littoral vegetation is then closer to the sampling point. Apparently, the DLV model suffers from a problem similar to that of the water depth models in its predictions (the inherent edge effect) (Fig. 13e). This is most likely due to a similar reason: there are more samples representing the near-vegetation habitats than those taken from offshore. In addition, the edge effect may reflect the fact that the environment-assemblage descriptions are most accurate at intermediate water depths, where the model also produces the most reliable reconstructions (e.g. Fig. 7).

Similarly to the DLV models, the best of the stream flow inference models use WA techniques with classical deshrinking and without tolerance weighting (Table 2). The $r^2\text{jack}$ of the best model was 0.77, RMSEP 0.17 LI and the maximum bias 0.25 LI. The stream flow model and thus the LI optima for the different midge taxa are based on binary codes ($0 = \text{lacustrine, } 1 = \text{riverine}$) (Fig. 13f), because discharge can vary enormously within or among seasons and following a precipitation event. Furthermore, the model is more applicable when it is not restricted to a particular stream flow gradient. The model is designed to be used in lake basins that have experienced past fluctuations in their river contribution or in internal turbulence, rather than in the stream environments themselves. The output of the model significantly depends on the sampling point selection, as samples taken closer to a stream would infer higher values.

4.4. Midge-based palaeoenvironmental reconstructions

4.4.1 Lake Hampräsk

The palaeoenvironmental records from Lake Hampräsk showed some clear natural and anthropogenic changes over the past 700 years (papers II, III, V, Table 3). Cultivation is known to have begun in the Sipoo area during the Iron Age (Sarmaja-Korjonen 1992), and the trophic status of Lake Hampräsk was already elevated by the 14th century, representing mesotrophic conditions at the base of the core (Figs. 14, 15). Reconstruction of the hypolimnetic oxygen levels revealed that the 14th century was also characterized by poor oxygen conditions (Fig. 15), probably resulting from the elevated trophic status. The reconstructed water levels indicated that the lake was quite deep (approx. 10 m) during that time (Fig. 16). However, there are serious uncertainties in lake-level reconstructions when the recon-
constructed values are higher than the depth gradient of the models. Thus, the lake level before the decrease may be overestimated, as the present model provides a reliable prediction up to ca. 7 m. Nevertheless, evidence for the elevated lake level is provided by the dominant midge taxon in Lake Hamprésk at the time, *Chaoborus flavi-cans* (Luoto et al. 2008), which cannot survive in shallow lakes in Finland (Luoto and Nevalainen 2009), and the species also has a high depth optimum in the applied transfer function (paper V).

During the 15th century the lake level dropped...
dramatically, as shown by the reconstructed water depth at the sampling point, which decreased by over 6 m. This lake level lowering may very well have been due to human activities, since lakes have traditionally been drained in Finland for cultivation purposes, and there was evidence of hemp (Cannabis sativa L.) cultivation in the catchment of Lake Hampträsk since ca. 1050 AD (Sarmaja-Korjonen 1992, 2003). Although the inferred massive lake drainage at the time implies human activity, there is no direct evidence that the lake was drained by humans and the lake-level lowering may also have been caused by natural factors. Furthermore, the changes in species assemblages might have been driven by changes in food web structures as speculated by Nevalainen and Luoto (subm.), and thus the reconstructed water depth values for the base of the core would be overestimated. However, the reconstruction trend is apparent even with uncertainties in its magnitude, and it is likely that the lake level was indeed higher at the beginning of the stratigraphy. From 1500 AD to the present, the inferred water depth has remained relatively low.

The DLV reconstruction showed an increasing trend during the 14th century (Fig. 16). The high DLV value during that time was most likely caused by the elevated lake level shown in the water depth reconstruction. When the inferred lake level rapidly dropped during the 15th century, the littoral vegetation also approached the sampling point. The reconstructed stream flows indicated two increased surface runoff/turbulence events, the first around 1400-1500 AD and the second more recently (Fig. 16). The reconstructed changes in Lake Hampträsk were more likely caused by anthropogenic manipulation of the local hydrology than by climate change. The first minor increase in the stream flow (approx. 0.1 LI) occurred soon after the reconstructed decrease in the water level, possibly resulting from the anthropogenic activities.

The effects of enhanced nutrient input were accompanied by deteriorating climatic conditions, and the aquatic ecosystem was severely disturbed ca. 1700 AD (Luoto et al. 2008, paper II), when chironomid-inferred temperatures also dramatically decreased, coinciding with the timing of the LIA (Jones et al. 2009). The results of Luoto et al. (subm.) from another lake in southern Finland, Lake Hirvijärvi, indicate a temperature change that was similar in magnitude to the present results. The temperature drop of 3.5-4 °C reconstructed at Lake Hirvijärvi indicates a coherent reconstruction of the LIA and reproducibility of midge-based results. The cladoceran, diatom and midge assemblages changed in Lake Hampträsk and the diversity and pro-
portion of planktonic diatom species decreased. In addition, oribatids (Arachnida: Acari: Oribatida) disappeared from the sediment record during the coldest period. The cold phase was also well represented by changes in the physical properties of the sediment, as the LOI and MS decreased (paper II), possibly due to increased erosion from the catchment and decreased biological productivity. The LIA seems to be reflected as an increase in chironomid-inferred hypolimnetic oxygen levels, which peaked twice, during the 16th and 17th centuries. Tiljander et al. (2003) noted from annually laminated lake sediments from southern Finland that during two phases, ca. 1580-1630 and 1650-1710 AD, a colder climate prevailed. The study of Luoto et al. (2008) also suggested that the LIA was not uniformly cold, as cold-indicating chironomids peaked at separate depths and chydorid ephippia had two maxima, which was consistent with the results of Tiljander et al. (2003).

The dominating midges in Lake Hampträsk during the LIA were Tanytarsus lugens-type, Micropsectra insignilobus-type and Corynocera ambigua (Luoto et al. 2008), which indicate cold climatic conditions (Appendix, paper I). Tanytarsus lugens-type and M. insignilobus-type are missing from the present calibration set for DO, and they do not therefore contribute to the oxygen reconstruction. This is because they have northern distributions (paper I) and they only occur at a very low abundance in the DO calibration dataset (southern Finland). However, if these taxa contributed to the oxygen recon-

![Figure 16. Midge-inferred water depth, distance to littoral vegetation (DLV) and stream flow (i.e. turbulence) for Lake Hampträsk, southern Finland, during the past 700 years (redrawn from paper V). The age estimations are based on the radiocarbon dating results and time-depth model applied by Luoto et al. (2008).]
construction they would probably increase the reconstructed values, since they are known to prefer deep and cold lakes with good hypolimnetic oxygen conditions. The cold climate episode of ca. 1700 AD is also reported in historical documents, as around 25% of the local population of Sipoo died in a famine (Rantanen and Kuvaja 1994).

The chironomid-inferred DO was elevated during the cooling of the LIA between ca. 1550 and 1850 AD (Fig. 15). Interestingly, diatom-inferred TP reconstruction from Lake Hampträsk showed a major increase during the LIA (Fig. 14). It is generally expected that lake productivity decreases during cold climate events, although Kirilova et al. (2009) showed that during the extreme Younger Dryas (YD) cold event the productivity truly increased in a lake in Central Europe. However, evidence for decreased productivity in Lake Hampträsk was also provided by the strongly decreased organic content during the LIA (Luoto et al. 2008). The diatom assemblages were dominated by a single taxon (*Fragilariula pinnata*) during the LIA, and this most likely caused the overestimation, since the TP inference is based on its temperature optimum, which may be biased in the training set (see discussion in paper II).

The increase in the DLV at ca. 1700 AD coincided with the coldest period of the LIA in the area. Although the LIA was characterized by wetter climate conditions (Tiljander et al. 2003), the water depth reconstruction showed no marked changes in Lake Hampträsk (Fig. 16). Therefore, the reconstructed change in the DLV was most likely due to diminished littoral vegetation caused by the harsh and cold climate and the resulting reduction in vegetation-associated midges. After the LIA, the DLV began to decrease. This decrease was probably associated with the hydroseral development that can currently be observed on the lake shores.

Clear changes in the stream flow occurred from ca. 1900 AD onwards, represented by three separate reconstructed peaks, the last one (ca. 0.2 LI) representing the present situation (Fig. 16). The first two peaks, with LI values over 0.3, can be considered to indicate relatively large changes in the lake’s environmental conditions. These recent changes in the reconstruction are probably the results of large-scaled ditching, which has increased the surface runoff in the catchment, thus creating streams and water turbulence in the lake. The dominant midge taxa during the stream flow events were *Chironomus anthracinus*-type, *Dicrotendipes nervosus*-type, *Cladotanytarsus mancus*-type and *Procladius*, which thus seem to be quite tolerant of limnological perturbation. The absence of true lotic taxa from the entire sediment sequence and the occasional presence of turbulence-tolerant taxa indicate that there has not been a permanent stream in the lake.

The reconstructed oxygen conditions deteriorated especially from the 19th century onwards (Fig. 15), most likely as a consequence of climate warming and induced nutrient enrichment in the lake, as cultivation in the catchment increased. Some diatom species that thrive in eutrophic conditions increased in abundance from the end of the 18th century onwards, but in contrast the diatom-based TP reconstruction showed decreasing values (Fig. 14). However, the representativeness of these diatom samples in the calibration set was not good. The reason behind this may be other environmental changes unrelated to TP, such as hydroseral development, as the shoreline vegetation (e.g. *Phragmites australis* and *Spagnum* mosses) would have spread and reduced the lake surface area. Thus, the result would have been an increase in the proportion of littoral area at the expense of the pelagic area, which would have led to an increased proportion of littoral habitats for periphytic diatoms. The high number of periphytic taxa in the sam-
samples may result in lower predicted TP concentrations, as shown by Kauppila et al. (2002b). The present diatom-based TP reconstruction provided a value for the surface sample that is clearly lower than the observed one (underestimation of $38.0 \mu g l^{-1}$). A similar type of underestimation in diatom-inferred and measured TP values occurred in a reconstruction from a small lake in southern Finland (Kauppila & Valpola 2003), and the higher proportion of periphytic taxa in the samples is likely to be a major factor behind the underestimation of the recent TP values also found in the present reconstruction. In the most recent sample (0 cm), the reconstructed DLV reached its minimum (32 m) (Fig. 16), providing evidence for the development of plant succession towards the sampling point.

The inferred values showed a distinct and rapid change in temperature in the surface samples as they increased by 1.3 °C at the top (Fig. 13). These recent inferred changes correspond well with the general changes in observed mean $T_{Jul}$ values (data provided by the Finnish Meteorological Institute). However, the surface sediments have not been accurately dated and the 1-cm sample resolution restricts more detailed tracking. The inferred mean $T_{Jul}$ for the surface sample showed only a slight underestimation (0.3 °C) that is within the error limits of the model (RMSEP = 0.72 °C). In the hypolimnetic oxygen reconstruction, the taxa in the fossil samples were relatively poorly represented in the training set, and only seven of the samples were well represented in the training set (see paper II for details). The main reason for this is that the studied time period was mostly affected by the cold LIA, and cold-associated chironomids that are not included in the calibration dataset (warm lakes) were therefore common (e.g. Tanytarsus lugens-type, Micropsectra insignilobus-type and Constempeplina brevicosta) (Luoto et al. 2008). When considering all the analogue statistics, only three of the samples (0, 5 and 9 cm) showed good reliability. However, the ‘poor’ fit/analogue samples may also provide accurate estimations and the ‘good’ fit/analogue samples may provide erroneous estimations (Bigler et al. 2002). The DO reconstruction showed underestimation (3.7 mg l$^{-1}$) in the topmost sample when compared to the modern measured value. Nevertheless, the lower estimations appears to be logical, because Lake Hamprüsk is known to have experienced oxygen depletion during late winter (Ekholm 2007), and the measured value thus seems to overestimate the oxygen conditions.

The reconstructed water depth for the surface sample showed that the inferred value was very close to the actual value and clearly within the depth model’s error limits. The slight overestimation was also expected in the light of the model’s tendency to overestimate shallow depths (Fig. 13c). The estimated (field observation and map interpretations) DLV showed a slight underestimation that was, however, close to the model’s prediction error. In addition, a minor stream flow influence may be expected, based on the lake’s inlet and the observed ditches, and this is also indicated by the reconstructed turbulence. The reliability estimations for the reconstructions provided by using the intralake models showed ‘good’ reliability for all of the reconstructions based on the SqRLs and MATs, but six of the samples failed to contain 90% of the taxa present in the training set. Interestingly, the sample at 0 cm, which showed poor taxon representativeness, had the minimum DLV value and the poorly represented sample at 6 cm had the minimum water depth and maximum stream flow values. The missing taxa that contributed to the poor taxon representativeness were Chironomus plumosus-type and Einfeldia pagana-type. Chironomus plumosus-type is a taxon that mostly occurs in profundal zones, whereas E. pagana-type occurs in littoral zones (Brooks et al. 2007).
Both taxa are rarely found in purely lotic habitats (Pinder and Reiss 1983). Thus, the absence of these taxa from the reconstructions may result in overestimation of the stream flow reconstruction, but the joint effect on water depth and DLV reconstruction may be insignificant. Therefore, since the poorly represented samples with relatively abundant appearance of C. plumosus-type and E. pagana-type represent the maximal stream flow peaks in the reconstruction, the actual changes may have been less pronounced.

4.4.2. Lake Iso Lehmälampi

The water level, which is considered to reflect the effective moisture in Lake Iso Lehmälampi (cf. Mason et al. 1994), showed a decreasing trend from ca. 300 AD to ca. 1000 AD, when it attained minimal levels (Fig. 17, paper IV). The lowest reconstructed water levels occurred during the timing of the MCA (Esper et al. 2002), with the minimum at ca. 1100 AD. Helama et al. (2009) showed that the MCA was characterized by a multienvironmental megadrought in northern Europe and linked it with a coinciding global El Niño–Southern Oscillation drought pattern. In accordance with their results, the water depth reconstruction from Lake Iso Lehmälampi indicates reduced lake levels (i.e. effective moisture) during the MCA, providing further evidence for these large-scale patterns. From ca. 1200 AD onwards, both cladocerans and chironomids indi-

Figure 17. Midge-inferred water depth and Cladocera-based planktonic:littoral ratio (P:L) for Lake Iso Lehmälampi, southern Finland, during the past 2000 years (redrawn from paper IV). The age estimations are based on the radiocarbon dating results and time-depth model applied by Nevalainen et al. (2008).
cate an increased water level, which fits well with the general trends found by Luoto et al. (subm.) in southern Finland and Hyvärinen and Alhonen (1994), Seppä and Birks (2001) and Korhola et al. (2005) in Finnish Lapland, indicating an elevated water level during the Late Holocene in both northern and southern Finland. The cladoceran- and chironomid-based reconstructions showed relatively close correlation ($r = 0.5$) (Fig. 17, Nevalainen et al. subm. b), indicating that the reconstruction trend is reliable and reproducible.

The reconstruction of hypolimnetic oxygen revealed that good DO conditions ($> 11 \text{ mg l}^{-1}$) prevailed in the late Holocene (Fig. 18). From ca. 1100 AD, the inferred hypolimnetic oxygen levels increased, possibly due to an elevation of the water level and consequent change in late-winter oxygen conditions as a result of the enlarged volume of the lake. However, this interpretation is in contrast to the results of Ilyashuk et al. (2005), who speculated that the lowering of lake level weakened the thermal stratification and led to improved hypolimnetic oxygen conditions in a lake in the Kola Peninsula, Russia.

The maximal inferred water depth value occurred in Lake Iso Lehmälampi ca. 1700 AD, which is consistent with the results of Tiljander et al. (2003), who suggested wetter climatic conditions at that time. The coolest time period of the LIA occurred ca. 1700 AD in southern Finland (Tiljander et al. 2005; Fig. 14), but the reconstructed $T_{\text{hal}}$ levels from Lake Iso Lehmälampi do not show clear signs of this cooling (paper IV). This may be simply due to the fact that even though the sediment was sampled and studied in papers II and IV using similar 1-cm intervals, the sedimentation rate in Lake Hamträsk was higher, thus providing better chronological resolution. This may have resulted in the signal of the climatic episode being missed in Lake Iso Lehmälampi. However, this does not explain why the signal of increased effective moisture (precipitation - evapotranspiration) appeared at ca. 1700 AD, while a decreased air temperature was not shown, given that the LIA was characterized by a long lasting change to colder conditions. It may also be simply that the chironomid taxa did not respond to temperature variations at that time, and the present temperature reconstruction may not therefore give reliable results.

There is also a problem with the reconstructed water level at that time, because the sample at 4 cm showed a ‘poor’ fit with the water level. However, since the previous sample also indicated an elevated water level, it may be that the ‘poor’ fit value is representative of the actual environmental conditions.

![Figure 18. Midge-inferred hypolimnetic oxygen for Lake Iso Lehmälampi, southern, Finland during the past 2000 years (redrawn from paper III). The age estimations are based on the radiocarbon dating results and time-depth model applied by Nevalainen et al. (2008).](image-url)
The oxygen levels in lake Iso Lehmälampi experienced a major increase around 1700 AD (Fig. 18), occurring simultaneously with the coldest period of the LIA in southern Finland (Tiljander et al. 2003; paper II). The elevated oxygen conditions were represented by an increased abundance of *Heterotanytarsus apicalis*-type and *Psectrocladius (M.) septentrionalis*-type, which have the highest hypolimnetic oxygen optima in the present dataset (paper III). After a short reduction ca. 1800 AD, which was probably caused by the warming climate, the inferred hypolimnetic oxygen levels increased during the 20th century and have remained high until the present (Fig. 18). This could reflect a reduction in the biological production of the lake caused by anthropogenic acidification (Verta et al. 1990). Although the lake has always been acidic and oligotrophic (Korhola & Tikkanen 1991), the additional reduction in biological production could have led to improved winter oxygen conditions because oxygen consumption under the ice decreased. The recent success of *C. anthracinus*-type may be due to the reduced pH in the lake, since the taxon is known to be tolerant of very acidic conditions (Mousavi 2002). However, even though *C. anthracinus* can be common in oligotrophic lakes, it is also known to tolerate organic pollution and hypoxia (Sæther 1979, Moller-Pillot 2009), implying the potential problems in its value as an indicator species. The CCA results (SqRL < 10%) showed a ‘good’ fit for the DO in all of the samples, but the taxa in the fossil samples were poorly represented in 12 of the samples. The MAT results showed a ‘poor’ fit for hypolimnetic oxygen in four of the samples and the inferred DO in the surface sample showed an underestimation of 3.2 mg l⁻¹ when compared to the measured value. Nevertheless, the lower estimation in the surface sample appears to be logical, because the measured value in Lake Iso Lehmälampi is anomalously high.

The inferred water level and mean $T_{30}$ values increased in the recent sediments, the temperature reconstruction showing trends similar to those observed in measured values during the past two centuries in southern Finland (data provided by the Finnish Meteorological Institute). A slight underestimation, as found from the present results (-0.2 m), is expected in the water-level reconstruction results at depths around 4 m based on the model’s performance as assessed by the training set samples (Fig. 13c). However, the error in estimation for the mean $T_{30}$ of -1.0 °C seems high, since the RMSEP of the air temperature model is 0.7 °C. However, because of the relatively slow sedimentation rate in Lake Iso Lehmälampi, the surface sediment sample of 1-cm thickness most likely represents midge assemblages from multiple decades, and the sample’s assemblages may not therefore be able to reflect the recent increase in temperature. The other estimates of the reliability of the reconstructions, the proportion of taxa from each fossil assemblage represented in the modern calibration set and the SqRL of the modern and fossil samples, showed a ‘good’ fit for both environmental variables in the topmost samples. Using statistical techniques, Nevalainen et al. (2008) demonstrated that prominent changes occurred in the recent cladoceran and chironomid species assemblages in Lake Iso Lehmälampi. They speculated that the forcing factors for these changes were water chemistry variables caused by the anthropogenic loading of pollutants. The most distinct increases in chironomid proportions occurred in the tanypodines (*Procladius* and *Ablabesmyia monilis*-type) and *Chironomus anthracinus*-type (Nevalainen et al. 2008), which are known to be more tolerant of contamination processes (Ilyashuk et al. 2003), while taxa such as the *Paratanytarsus penicillatus*-type and *P. austriacus*-type disappeared. Therefore, it is likely that not only changes in water level and air temperature, but
also in the water chemistry of Lake Iso Lehmälampi occurred during recent decades, which led to these changed species assemblages.

4.4.3. Lake Pieni-Kauro

The chironomid-based mean air $T_{\text{Jul}}$ reconstruction from Lake Pieni-Kauro (paper VI) indicates elevated temperatures between ca. 600 and 1300 AD, with two distinct periods (Fig. 19). The first occurs between ca. 600 and 700 AD and the second, coinciding with the general timing of the MCA (Esper et al. 2002), between ca. 800 and 1300 AD. The MCA was characterized by a multicentennial megadrought in northern Europe, including eastern Finland (Helama et al. 2009, Fig. 19). These results are well-matched with those found from the reconstructed effective moisture in Lake Iso Lehmälampi (Fig. 17). The sediment MS showed two distinct decreases during the MCA, around 900 AD and 1000 AD (paper VI). Changes in sediment MS can be used as indications of forest fires (Rummery 1983), and it is therefore possible that these MS anomalies resulted from extensive fires during the MCA megadrought. There are also major char layers in the podsol soils of the catchment that could represent these fires, but they have not been dated.

Even though there are clear signs of the MCA drought, the stream flow reconstruction shows elevated values. The reason for the controversy between the increased stream flow and the precipitation record based on tree-rings is probably that the stream flow model apparently indicates values that represent the magnitude of spring floods, which led to subsequent increased deposition of stream taxa at the sampling point. The increased spring floods, resulting from snowmelt, could therefore imply that the winters were characterized by elevated precipitation during the MCA (Fig. 19). However, it is also possible that early spring warming could have caused more rapid ice breakup and occasionally changed the hydrology. Despite the increased winter precipitation, the evidence points to reduced summer precipitation during the MCA in the catchment of Lake Pieni-Kauro in eastern Finland, in close
agreement with the present results from Lake Iso Lehmälampi in southern Finland (Fig. 17).

The inferred summer air temperatures markedly decreased around 1300 AD, indicating the onset of the LIA (Fig. 19). The decreased temperature event continued for 600 years in Lake Pieni-Kauro, showing that the LIA was a long lasting event in eastern Finland. Similarly, according to the results of Helama et al. (2008), a generally cool climate period prevailed in southeast Finland between 1300 and 1850 AD. The LIA continued from ca. 1500 AD until 1850 AD, with the coldest period around 1700 AD in southern Finland (Fig. 14), but the temperature reconstruction from Lake Pieni-Kauro indicates that the cold climate prevailed until ca. 1900 AD in eastern Finland (Fig. 19). In addition, historical records show that the climate in the region remained cold for relatively long and, for instance there was a serious famine in Kuhmo after the cold summers in the 1860s (Wilmi 2003). Fitting well with the present results, Weckström et al. (2006) showed from northern Finland that the LIA continued until the early 20th century.

The reconstructed precipitation, based on the tree-ring data of Helama et al. (2009) in a relatively closely located area (south-east Finland, approx. 300 km from Lake Pieni-Kauro), shows increased values during the LIA (Fig. 19). This agrees with the results of Tiljander et al. (2003) from the central part of the country, which indicate that the LIA was a wetter climatic episode in Finland. In addition, there is evidence that lake levels were elevated during and after the LIA in southern Finland (Fig. 17) and also in mid-Europe (Magny 2004). However, the present stream flow reconstruction shows greatly reduced values during the LIA, possibly implying decreased snowmelt during the spring and thus reduced winter precipitation in eastern Finland.

In the present results, the clearest evidence for historical human activity in the catchment of Lake Pieni-Kauro is the increased organic content of the sediment. The changes in the organic content correspond well with the known human history, as it begins to slightly increase during the 16th century (when the first people arrived and began slash-and-burn agriculture), followed by a more extensive increase during the 17th century. The organic content remained elevated between 1700 and 1800 AD and began to decrease before 1900 AD. It most likely increased due to the ash fallout from the slash-and-burn agriculture and tar burning, beginning in the 16th century (paper VI). The decreasing trend in the MS results between 1500 and 1900 AD may reflect the anthropogenic ash fallout, and the decrease in the organic content from 1800 AD onwards most likely reflects the reduction in slash-and-burn agriculture and tar burning (Wilmi 2003).

At ca. 1900 AD the regional precipitation shows an elevated trend (Fig. 19), but the stream flow reconstruction indicates generally decreased values, possibly implying reduced spring floods and winter precipitation. The inferred mean air \( T_{\text{Jul}} \) values from ca. 1900 AD onwards indicate increasing temperatures, corresponding with previous multiproxy evidence from southern Finland (Holopainen et al. 2009). The inferred increase is also similar to the trend of the present global warming, showing the ‘so-called’ hockey stick shape since the time of the LIA (cf. ICCP 2007). However, there is some overestimation in the inferred temperature values compared to the modern measured values. In addition, the inferred temperature for the surface sample indicates values that are close to the MCA temperatures. This is in contrast with previous chironomid-based studies from other regions (e.g. Rolland et al. 2009).

The overestimation in the temperature reconstruction (0.81 °C) is, however, close to the models’ error estimates. In the stream flow reconstruction, the fossil taxa have good coverage
in the dataset used. However, many of the lotic taxa occurring in the present sediment profile are missing from the temperature inference model. This is because the temperature calibration dataset was developed using enclosed basins without major inlets (papers I, III). The absence of lotic taxa from the temperature calibration model probably increases the reliability of the reconstruction, because the lotic taxa obviously respond more strongly to changes in stream flow than to changes in temperature. Therefore, the samples in the temperature reconstruction that have poor representativeness in the training set (see paper VI for details) may nevertheless represent reliable inference values, despite some of the taxa being missing from the calibration datasets. The MAT indicated some ‘poor’ analogue samples. However, the earliest of these samples predates the time period of interest in this study, as it is located at the bottom of the sediment profile. The sample at 7 cm shows no major change compared to the neighbouring samples, and the low temperature value at 2 cm is supported by the historical evidence (Wilmi 2003). In addition, statistical edge effects in the calibration models (paper VI; Fig. 13) have most likely influenced the quantitative results. Nevertheless, the reconstruction trends are axiomatic, even with the potential problems in the reliability of the numerical results. Correlations between midge and tree-ring based records were probably underestimated due to differences in chronological control between the sedimentary and incremental records.

The proximity of the North Atlantic to the study region enables the interpretation of the present palaeoclimatic results in the context of the NAO. The region-specific correlations between the temperature and precipitation and the NAO showed, consistently with the preceding studies (Hurrell 1995; Hurrell & van Loon 1997; Dickson et al. 2000; Hurrell et al. 2001; Trigo et al. 2002; Uvo & Berndtsson 2002), that the temperatures in winter and summer could be positively related to the NAO index (paper VI). Furthermore, the precipitation during winter and summer appeared to be positively and negatively related to the NAO index, respectively, indicating warm and moist winter conditions and warm and dry summer conditions during the positive NAO phase. The results from Lake Pieni-Kauro also agreed with the previous results regarding the late-Holocene climate variations in southern Finland (e.g. Helama et al. 2008, 2009; Luoto et al. 2008; Nevalainen et al. 2008; papers II, III, IV), indicating the reliability of the results and also their reproducibility. A large-scale long-term phase of positive NAO seems to have prevailed during the MCA, and weaker NAO conditions during the LIA (Trouet et al. 2009). This is consistent with the present interpretation of the long-term climatic variations in the study region during the MCA and LIA, which could have been triggered, at least partly, by changes in the energy output of the Sun (Helama et al. 2009) and some reinforcing mechanism.

There was a negative correlation in the present results between the stream flow reconstruction, mostly reflecting the spring floods resulting from snowmelt, and the other precipitation-related reconstructions that are indicative of summer conditions (paper V). The negative correlation is consistent with the observed NAO-climate associations, which showed divergent correlation directions for winter and summer precipitation. In addition, the seasonal and annual stream flow of Finnish rivers has been shown to be positively correlated with prevailing temperatures and the NAO index (Korhonen 2007). In the context of European stream flow data, the study region exhibits the most significant positive correlation with the NAO index during winters (Shorthouse & Arnell 1997, 1999).
5. Concluding remarks

5.1. Environmental factors affecting midge distribution

The present results indicated that the most important environmental forcing factor behind midge distribution along the latitudinal gradient in Finland was mean air \( T_{jul} \), but when the dataset was environmentally screened to include only undisturbed, close to pristine lakes, water depth at the sampling sites became more important. Geographical scaling to southern Finland revealed that the influence of hypolimnetic oxygen conditions became the dominant environmental factor, because the lakes were situated in warmer climate conditions and within a shorter climatic gradient, and the lakes were also considerably more stressed by human activities when compared to those in northern Finland. The results from the intralake dataset from Lake Pi- eni-Kauro, eastern Finland showed that the most important environmental factors controlling the distributions on a site-specific scale were river contribution, water depth and submerged vegetation patterns.

These findings show that the distribution and abundance of midge taxa are scale-dependent: on the regional scale the forcing factors are climate and morphometry, on more local scales they are related to water quality and on site-specific scales the habitat determines the species assemblages. The intralake processes are externally forced by climate and anthropogenic influence through the catchment. The complex internal processes within a lake basin have direct and indirect influences on the macrobenthic fauna. Of these forcing variables (Fig. 20), the food web structure, including phytoplankton, zooplankton and fish, is not included in the variables that were examined in this thesis. However, many of the midge taxa are sensitive to fish predation (Olander 1992; Liljendahl-Nurminen 2006; Luoto & Nevalainen 2009) and the predatory midges are known to control zooplankton communities (Einarsson et al. 2002), and it would therefore most likely be possible to develop quantitative palaeoecological reconstruction methods for the past food web structure based on midge assemblages. This is particularly intriguing in the case of fish, for which postmortem remains are rarely preserved in lake sediments, and indirect midge-based reconstructions of fish populations as carried out by Uutala (1990) in North America have not yet been possible in Palaearctic lakes. However, a cladoceran-based transfer function has already been developed in Denmark (Amsinck et al. 2005), and a corresponding model can probably also be constructed from midge remains (Brodersen 1998). In fact, the potential for invertebrate-based (insects, crustaceans and arachnids) reconstruction of the past presence of fish also exists in Finland, as their distribution can locally be determined by predation pressure (Nevalainen & Luoto subm.).

5.2. Model applicability

The results of numerical analysis of the developed temperature and hypolimnetic oxygen inference models showed that they performed well
and thus can be used for the purpose for which they were created. The palaeotemperature inference model can be used to reconstruct past climate conditions, which is crucial background knowledge for understanding the present climatic change and for reliable assessment of future changes and their effects on organisms. The hypolimnetic oxygen model can provide valuable information on past water quality conditions, and may serve as a tool for lake management when setting guidelines for preserving or restoring lakes. The combined use of temperature and water quality inference models can provide useful insights into the long-term relationship between climate and water quality, which can be used for assessing the effects of the present climatic change on freshwater lakes. However, when examining the temperature-trophic interactions, a multiproxy approach is required.

When using multiple midge-based inference models on the same downcore assemblage, it is important to assess the suitability of the different models to the particular study site. Especially in lakes with a low number of taxa, it is often difficult to assess which environmental variables that the taxa are responding to. In addition, if the training sets used have environmental intercorrelation between the variables to be reconstructed, the output would have serious uncertainties. In the case of the present multilake inference models for temperature, hypolimnetic oxygen and water depth, no variable intercorrelations were found, but among the intralake models, water depth and DLV were strongly correlated in the dataset. Thus, the use of these models on the same downcore assemblage may be problematic. Nevertheless, the results from the applying the models in Lake Hamträsk showed that the DLV model reflected the changes in the position of littoral vegetation following the apparent hydroseral development, whereas the water depth model indicated a major lake level change at the beginning of the sediment profile, thus confirming that the reconstructions were independent and without correlation.

During many climatic episodes, such as the MCA and LIA, the balance of evaporation vs. precipitation of the climate fluctuated, resulting in changes in lake levels. Therefore, it is important not only to interpret temperature reconstructions per se, but to understand the influence of depth, which is often a crucial secondary factor in explaining the midge distributions. The use of water level and temperature models together may provide important information on the variability of both climate-related variables, but it is also necessary to understand the ecology of the specific taxa behind the variations in the reconstructions. Kurek and Cwynar (2009) showed that intralake models may suffer from lower applicability, shorter environmental gradients and lake-specific discrepancies in modern distribution. Nevertheless, since many of the indicator taxa have geographically rather uniform responses to water depth, the present intralake model can possibly provide reliable reconstructions whenever the taxa that occur in the fossil assemblages are similar to those of the intralake dataset. However, in general, water depth models based on intralake datasets are probably best suited for studying past changes in the dataset lake itself.

The LI model can be used to track increased stream flow events, using downcore sediment samples in lakes that have permanent river contribution or at least occasional, such as possibly in an oxbow lake. In addition, smaller-scale changes in water turbulence, such as those resulting from catchment ditching or forest clearcutting, may be detected using the stream flow model. The vegetation shift model can be useful in studies involved with hydroseral succession or with past water volume fluctuations in large shallow lakes with level catchments, where
depth models are likely to have problems because the increased water volume would not markedly change the lake depth. Since the present intralake paleohydrological models are best suited to particular lake types, it should be carefully considered which of the models are appropriate for each study in future applications.

In all reconstructions it is important that the changes in the reconstructed variable remain within the range of the model’s environmental gradient. Otherwise, the magnitude of change would become underestimated under extreme conditions. Furthermore, interpretations should not be based solely on the reconstructed variables, because other environmental factors, such as pollution or changes in ecological interactions, may interfere with the reconstruction results. Multiproxy studies provide the most reliable picture of past environmental changes, and it is also beneficial to have background knowledge on recent anthropogenic environmental changes in the area to ease the interpretation process of the results. In addition, it is important to assess the reliability of the inferred values (Birks et al. 1990; Birks 1998). However, the methods used to assess reliability may not always provide correct information, as the ‘poor’ fit/analogue samples may provide reliable reconstructions while ‘good’ fit/analogue samples may provide erroneous reconstructions (Bigler et al. 2002). Lakes having a low number of taxa may more easily provide erroneous reconstruction results than those with high taxon richness, due to the lower number of indicator taxa.

5.3. Synthesis of the palaeoenvironmental reconstructions

The midge-based palaeoclimatic reconstructions from Lake Pieni-Kauro indicate that summer air temperatures in eastern Finland followed the general patterns of the known late Holocene climate events in northern Europe. The inferred mean air $T_{\text{ Jul}}$ increased markedly during the MCA, which was also characterized by decreased precipitation. In addition, the MS results indicated forest fires in eastern Finland during the multicentennial MCA megadrought. The MCA drought was also clearly represented in the reconstructed water levels from Lake Iso Lehmälampi in southern Finland, with minimum values at ca. 1100 AD. The water-level reconstruction of Lake Iso Lehmälampi over the past 2000 years agreed with previous results from the lake (Sarmaja-Korjonen & Alhonen 1999; Sarmaja-Korjonen 2001; Nevalainen et al. 2008, subm. b) and showed clear resemblance to the changes in the proportion of planktonic cladocerans (P:L ratio).

The calculated correlations between climate and the NAO in eastern Finland fit well with the tree-ring records and midge-based reconstructions from Lake Pieni-Kauro. The results thus seem to indicate a relatively warm climate with rainless summers but snowy winters during the MCA and a cool climate with rainy summers and dry winters during the LIA. In the record of Lake Pieni-Kauro, the inferred air temperature decreased during the LIA, which seems to have been a long lasting episode in the region beginning at ca. 1300 AD and ending at ca. 1900 AD. However, the cooling during the LIA appears to have been shorter in southern Finland (ca. 1550-1850 AD), but more severe according to the temperature reconstruction and magnitude of ecosystem change in Lake Hampträsk.

DO reconstructions from Lake Hampträsk and Lake Iso Lehmälampi indicated that during the LIA, late-winter hypolimnetic oxygen conditions improved. This could indicate the effect of decreased biological production in the lakes during cold climate periods, which led to reduced oxygen consumption and consequently enhanced oxygen conditions. The low produc-
tivity in the lakes and thus well-oxygenated conditions therefore have an overwhelming effect, countering the lengthened ice-cover period (cold climate), which is known to cause oxygen depletion when wind exposure and turbulence are inhibited. The long winters are also illustrated in the biostratigraphy of Lake Hampträsk during the LIA as an increase in chydorid ephippia (Luoto et al. 2008), which are sensitive indicators of the length of the open-water season (Sarmaja-Korjonen 2003). In agreement with the present results, Quinlan and Smol (2002) reported that most of the lakes they examined in Ontario, Canada, have recorded some decline in the hypolimnetic oxygen content as a possible consequence of recent climatic warming. However, in all of the present hypolimnetic oxygen reconstructions the samples showed mostly ‘poor’ reliability during the LIA. This may be because the magnitude of the temperature change overrode the effect of hypolimnetic oxygen on chironomid assemblages. This is suggested by the fact that taxa that are seldom observed even from the most oxidized shallow lakes in southern Finland, but are common in cold northern lakes, dominated in Lake Hampträsk during the LIA (Luoto et al. 2008).

Historical anthropogenic activities were detected in the sediment physical properties as changes in LOI and MS values in Lake Hampträsk, where historical cultivation occurred, and in Lake Pieni-Kauro, which was also influenced by slash-and-burn agriculture and additionally by tar burning. The recent changes in all the study lakes include the present climate warming, which is reflected in the temperature reconstructions. Similar increases have also been found from other midge-inferred results in Finland, including those by Luoto (2006) from subarctic northern Finnish Lapland (Lake Várdnojárvri in Utsjoki) and Luoto et al. (subm.) from southern Finland (Lake Hirvijärvi in Kärkölä/Orimattila). The inferred increases in temperatures closely follow the observed changes and thus give evidence for the reliability and reproducibility of the midge-based reconstructions.

The midge assemblages of the sediment sequences from Lake Pieni-Kauro, Lake Iso Lehmälampi and Lake Hampräsk showed results that can be reasonably associated with anthropogenic and natural changes. The inferred changes in Lake Hampräsk using the intralake dataset from Lake Pieni-Kauro were larger than the models’ prediction errors. Thus, since the training set lake and the test lake are limnologically very different and geographically remote but the reconstructed results were nevertheless reasonable, it appears that the models may be used whenever the down-core species assemblages are relatively close to those of the training set, because the taxon responses to water depth, aquatic vegetation and streamflow are geographically rather uniform. In the present study, no distinct evidence for systematically incorrect reconstructions was found considering all the inferred parameters, and all the reconstructions showed logical results with regard to previous data and general expectations.

### 5.4. Implications for environmental change assessments

Lake sediment research is necessary in modern lake management (Valpola 2006), and palaeolimnological studies can be used in defining reference conditions and the goals and tools for conservation and restoration acts (Valpola & Salonen 2006; Buczkó et al. 2009). Eutrophication is a serious lake management problem and can be considered as the single greatest threat to global freshwater resources (UNEP 1999; Smol 2008). Palaeolimnological proxies can be used as an informative and cost-effective monitoring and assessment tool for the implementation of the WFD of the EU (Buczkó et al. 2009), and chironomid midges have been shown to be an ex-
cellent means for this (Nyman & Korhola 2005). Besides inferences of past TP conditions (Brooks et al. 2001), the midge-based estimation of hypolimnetic oxygen changes provides a useful tool when assessing anthropogenic effects, because lakes under anthropogenic nutrient stress record decreases in DO (Quinlan & Smol 2002). Resulting from eutrophication, long-lasting hypolimnetic oxygen depletion causes the elimination of fish and other biota from the deep water, and the potential release of orthophosphate from the sediments causes internal loading with phosphorus, which is the ultimate limiting nutrient for algal growth in freshwaters in Finland.

It is also evident from the present results that in addition to the direct anthropogenic influence on water quality, natural and human-induced climate change can strongly affect the lake trophic status, and the recent climate change thus presents major concerns in lake management. The combined uses of midge-based water quality and temperature inference models may help in interpreting past environmental changes and increase the knowledge of the relationship between temperature and water quality. Temperature can have an overwhelming direct influence on midges through metabolism, but it is also a driving factor of lake trophic and hypolimnetic oxygen conditions, thus affecting them indirectly. Biological productivity in lakes and in their catchments most often decreases under cold climate conditions. The winter hypolimnetic oxygen conditions are closely related to temperature changes through the length of the open-water period and summer biological productivity, which results in elevated oxygen consumption under ice due to the increased amount of decaying organic matter. Furthermore, lake-level changes are a potential factor in determining phosphorus and oxygen availability through, for instance, the establishment of stratification. Therefore, changes in long-term precipitation, such as those following the prevailing NAO index phase, probably influence the general water quality of lakes. The close relationship between climatic factors and water quality entail that the projected increase in temperature and precipitation, driven by the current climate change, will cause increased nutrient and decreased hypolimnetic oxygen conditions in lakes, thus affecting whole lake ecosystems.

In the future, the palaeoenvironmental reconstruction methods developed in this thesis could be enhanced by increasing the number of study sites in the training sets, and the general trends in long-term environmental dynamics could be tested using a multiproxy approach and an increased number of sediment profiles from various lakes types. Thus, the most promising approach towards the consistent site-specific, local and regional establishment of past environmental conditions is to ensure the reproducibility of results.

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Appendix. Weighted averaging (WA) optima and tolerances for mean air $T_{Jul}$, water depth, late-winter hypolimnetic oxygen, autumnal epilimnetic total phosphorus (TP) and stream flow (lotic index, LI) of the most common midge taxa in the surface sediment samples in Finland. The TP optima are derived from Luoto (subm. b), whereas the other optima are derived from the studies in this thesis. The taxon coding system mostly follows Schnell et al. (1999).

<table>
<thead>
<tr>
<th>Code</th>
<th>Mean $T_{Jul}$ (°C)</th>
<th>Depth (m)</th>
<th>Oxygen (mg l⁻¹)</th>
<th>TP (μg l⁻¹)</th>
<th>Lotic index (LI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bezzia-type</td>
<td>Bezzind</td>
<td>15.3 ± 1.4</td>
<td>2.3 ± 1.4</td>
<td>6.5 ± 4.3</td>
<td>20.5 ± 18.0</td>
</tr>
<tr>
<td>Dasyhelea-undif</td>
<td>Dasyind</td>
<td>14.4 ± 1.3</td>
<td>2.3 ± 1.2</td>
<td>3.3 ± 3.7</td>
<td>10.7 ± 11.1</td>
</tr>
</tbody>
</table>

**CERATOPOGONIDAE**

**CHAOBORIDAE**

Chao fia | 16.4 ± 0.6 | 3.7 ± 1.5 | 2.6 ± 2.1 | 24.9 ± 23.3 | 0.0 ± 0.4 |

**SIMULIDAE**

Simulium | Simuind | * | 2.5 ± 2.1 | 10.9 ± 3.5 | * | 0.6 ± 0.5 |

**CHIRONOMIDAE**

**TANYPODINAE**

Abalabesmia longistyra-type | Abla lon | 15.3 ± 0.9 | 2.7 ± 1.8 | 5.0 ± 3.1 | 14.8 ± 9.7 | 0.3 ± 0.5 |
| Abalabesmia monilis-type | Abla mon | 14.8 ± 1.5 | 2.9 ± 1.6 | 5.6 ± 4.9 | 15.6 ± 15.6 | 0.1 ± 0.2 |

**DIAMESIANAE**

Protanypus | Protind | 13.3 ± 1.3 | 4.0 ± 2.0 | 5.5 ± 3.4 | 7.9 ± 3.9 | 0.0 ± 0.4 |

**PRODIAMESIANAE**

Monodiamesa | Monind | 13.5 ± 1.2 | 2.8 ± 0.8 | * | 7.0 ± 17.5 | * |

**ORTHOCLADINAE**

Acamptocladius | Acamind | 15.5 ± 0.2 | 3.7 ± 1.5 | 10.9 ± 3.5 | * | 0.0 ± 0.4 |
| Brilla | Brilind | 15.7 ± 1.0 | 3.1 ± 1.4 | 4.3 ± 2.9 | 24.7 ± 14.7 | 0.8 ± 0.7 |
| Chaetocladius | Chaelind | 16.1 ± 0.8 | 1.0 ± 1.4 | 1.0 ± 3.4 | 40.0 ± 25.1 | 1.0 ± 0.4 |
| Corynoneura coronata-type | Cory cor | 14.7 ± 1.2 | 2.8 ± 1.1 | 9.4 ± 3.4 | 19.0 ± 17.5 | * |
| Corynoneura lacustris-type | Cory lac | 15.4 ± 0.2 | 3.4 ± 1.4 | * | 7.0 ± 17.5 | * |

**PSEUDOCERANEAE**

Thienemannimyia pseudocarnea-type | Thy pse | 14.7 ± 1.7 | 2.3 ± 1.8 | 4.2 ± 3.9 | 11.5 ± 7.7 | 0.4 ± 0.5 |

<table>
<thead>
<tr>
<th>Code</th>
<th>Mean $T_{Jul}$ (°C)</th>
<th>Depth (m)</th>
<th>Oxygen (mg l⁻¹)</th>
<th>TP (μg l⁻¹)</th>
<th>Lotic index (LI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>14.3 ± 1.7</td>
<td>2.3 ± 1.8</td>
<td>4.2 ± 3.9</td>
<td>11.5 ± 7.7</td>
<td>0.4 ± 0.5</td>
<td></td>
</tr>
</tbody>
</table>

<p>| Gradient | 11.3−17.1 | 0.5−7.3 | 0.5−18.1 | 2−105 | 0/1 |</p>
<table>
<thead>
<tr>
<th>Code</th>
<th>Mean $T_{Jul}$</th>
<th>Depth (m)</th>
<th>Oxygen (mg l$^{-1}$)</th>
<th>TP (μg l$^{-1}$)</th>
<th>Lotic index (LI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Psesind</td>
<td>16.1 ± 1.2</td>
<td>4.3 ± 1.7</td>
<td>3.2 ± 3.4</td>
<td>56.0 ± 17.5</td>
<td>0.0 ± 0.4</td>
</tr>
<tr>
<td>Rheoind</td>
<td>15.8 ± 1.2</td>
<td>1.3 ± 0.8</td>
<td>10.9 ± 3.5</td>
<td>*</td>
<td>0.8 ± 0.4</td>
</tr>
<tr>
<td>Smit fol</td>
<td>16.0 ± 0.8</td>
<td>3.4 ± 1.6</td>
<td>4.2 ± 3.0</td>
<td>22.0 ± 18.5</td>
<td></td>
</tr>
<tr>
<td>Syno sem</td>
<td>13.9 ± 1.2</td>
<td>3.3 ± 2.2</td>
<td>10.9 ± 3.5</td>
<td>7.0 ± 17.5</td>
<td>0.4 ± 0.5</td>
</tr>
<tr>
<td>Thie cla</td>
<td>15.5 ± 0.2</td>
<td>2.3 ± 1.0</td>
<td>10.9 ± 3.5</td>
<td>*</td>
<td>0.6 ± 0.6</td>
</tr>
<tr>
<td>Tris bre</td>
<td>15.4 ± 1.2</td>
<td>2.0 ± 1.4</td>
<td>*</td>
<td>9.0 ± 17.6</td>
<td></td>
</tr>
<tr>
<td>Zalu muc</td>
<td>14.0 ± 1.1</td>
<td>2.5 ± 1.5</td>
<td>4.9 ± 3.2</td>
<td>9.6 ± 7.5</td>
<td>0.0 ± 0.4</td>
</tr>
<tr>
<td>Zalu zal</td>
<td>15.5 ± 1.1</td>
<td>2.5 ± 1.2</td>
<td>5.2 ± 4.5</td>
<td>23.9 ± 18.6</td>
<td>0.0 ± 0.4</td>
</tr>
</tbody>
</table>

### CHIRONOMIINA

#### CHIRONOMINI

- **Chironomus antiquus**-type
- **Chironomus plumosus**-type
- **Cladopelma viridulum**
- **Cryptochironomus**
- **Cryptotendipes**
- **Demicyprorrhynchus**-type
- **Dicrotendipes nervous**-type
- **Einfellid pagana**
- **Endochironomus albipennis**-type
- **Endochironomus impar**-type
- **Microtendipes rydalen**-type
- **Microtendipes syneuroides**-type
- **Microtendipes rydalen**-type
- **Omis callicereus**
- **Pagasiella orophila**
- **Parachironomus varus**-type
- **Paracalocelpa**
- **Paratendipes alburnus**-type
- **Paratendipes nudiargus**-type
- **Phaenopsectra flavipes**-type
- **Polypedilum nubeculosum**-type
- **Polyphemus pedipalpus**-type
- **Polypedilum pugio**
- **Polypedilum sericeum**
- **Polypedilum sordens**-type
- **Sergentia coracina**-type
- **Sericobrornus**
- **Stefichironomus**
- **Tribelos intuctus**-type
- **Tribolium sericeum**
- **Pseudechinomus prasina**-type

### TANYTARSINI

- **Cladotanytarsus mandibuts**-type
- **Contstempellina brevicosta**
- **Corynocera ambigua**
- **Corynocera oliveri**-type
- **Micropsectra insignilobus**-type
- **Micropsectra paludalis**-type
- **Micropsectra radialis**-type
- **Paratanytarsus australicus**-type
- **Paratanytarsus penicillatus**-type
- **Paratanytarsus undif.**
- **Rheotanytarsus**
- **Stemellina**
- **Stemellinella**
- **Tanytarsus chinensis**-type
- **Tanytarsus glabrescens**-type
- **Tanytarsus lactescens**-type
- **Tanytarsus lugens**-type
- **Tanytarsus mendax**-type
- **Tanytarsus pallicornis**-type
- **Tanytarsus undif.**

#### DEPARTMENT OF GEOSCIENCES AND GEOGRAPHY

### Appendix (Continued)
Paper I

Paper II

A 700 year record of temperature and nutrient changes in a small eutrophied lake in southern Finland.
Paper III

Fossil midge larvae (Diptera: Chironomidae) as quantitative indicators of late-winter hypolimnetic oxygen in southern Finland – A calibration model, case studies and potentialities.
Boreal Environment Research 15: 1–18.
Paper IV

A Finnish chironomid- and chaoborid-based inference model for reconstructing past lake levels.
Quaternary Science Reviews 28: 1481–1489.
Paper V

Luoto, T.P. 2010.
Hydrological change in lakes inferred from midge assemblages through use of an intralake calibration set.
Paper VI

Luoto, T.P. & Helama, S.
Palaeoclimatological and palaeolimnological records from fossil midges and tree rings: the role of the North Atlantic Oscillation in eastern Finland through the Medieval Climate Anomaly and Little Ice Age.
Submitted to Quaternary Science Reviews.