Diatoms as indicators of Holocene climate and environmental change in northern Sweden

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Cover-page: Microscope picture of the diatom *Cyclotella antiqua*

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Abstract
The objective of the thesis was to explore the potential of diatoms (Bacillariophyceae) as indicators of Holocene climate and environmental change in northern Sweden (Abisko region, 68°21'N, 18°49'E). A modern surface-sediment calibration set including 100 lakes was developed and lake-water pH, sedimentary organic content (assessed by loss-on-ignition) and temperature were identified as most powerful environmental variables explaining the variance within the diatom assemblages. Transfer functions based on unimodal species response models (WA-PLS) were developed for lake-water pH and mean July air temperature (July T), yielding coefficients of determination of 0.77 and 0.70, and prediction errors based on leave-one-out cross-validation of 0.19 pH units and 0.96 °C for lake-water pH and July T, respectively. The transfer functions were validated with monitoring data covering two open-water seasons (lake-water pH) and meteorological records covering the 20th century (July T). The good agreement between diatom-based inferences and measured monitoring data confirmed the prediction ability of the developed transfer functions.

Analysing a Holocene sediment core from a lake nearby Abisko (Vuoskkujávri), diatoms infer a linearly decreasing July T trend (1.5 °C) since 6,000 cal. BP, which compares well with inferences based on chironomids and pollen from the same sediment core. The lake-water pH inference shows a pattern of moderate natural acidification (*c.* 0.5 pH units) since the early Holocene, reaching present-day pH values at *c.* 5,000 cal. BP. By fitting fossil diatom samples to the modern calibration set by means of residual distance assessment within canonical correspondence analysis (CCA), the early Holocene (between 10,600 and 6,000 cal. BP) was identified as a problematic time-period for diatom-based inferences and, consequently, reconstructions during this period are tentative. Pollen-based inferences also show ‘poor’ fit between 10,600 and 7,500 cal. BP and chironomids probably provide the most reliable July T reconstruction at Vuoskkujávri, with ‘poor’ fit only during the initial part of the Holocene (between 10,600 and 10,250 cal. BP).

Possible factors confounding diatom-based July T inferences were investigated. Using detrended CCA (DCCA), Holocene sediment sequences from five lakes indicate that during the early Holocene, mainly physical factors such as high minerogenic erosion rates, high temperature and low light availability may have regulated diatom assemblages, favouring *Fragilaria* species. In all five lakes, diatom assemblages developed in a directional manner, but timing and scale of development differed substantially between lakes. The differences are attributed primarily to the geological properties of the lake catchments (with strong effects on lake-water pH), but other factors such as climatic change, vegetation, hydrologic setting and in-lake processes appear to regulate diatom communities in each lake differently. The influence of long-term natural acidification on diatom assemblages progressively declined during the Holocene with corresponding increase of the influence of climatic factors.

Key words
Diatoms, Holocene, paleolimnology, climate change, lake sediments, transfer functions, quantitative environmental reconstructions, northern Sweden, Abisko

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Contents

List of papers

The thesis is based on the following papers, which will be referred to in the text by their respective Roman numerals.

I Bigler, C. & R. I. Hall, *in press*. Diatoms as indicators of climatic and limnological change in Swedish Lapland: A 100-lake calibration set and its validation for paleoecological reconstructions. *Journal of Paleolimnology*

II Bigler, C. & R. I. Hall, *submitted*. Diatoms as quantitative indicators of July temperature: a century-scale validation with meteorological data from northern Sweden. *Palaeogeography, Palaeoclimatology, Palaeoecology*

III Bigler, C., I. Larocque, S. M. Peglar, H. J. B. Birks & R. I. Hall, *accepted for publication*. Quantitative multi-proxy assessment of long-term patterns of Holocene environmental change from a small lake near Abisko, northern Sweden. *The Holocene*

IV Bigler, C., E. Grahn, I. Larocque, A. Jeziorski & R. I. Hall, *submitted*. Effects of Holocene environmental change on diatom assemblages in alpine Lake Njulla (999 m a.s.l.) – a comparison with four small lakes along an altitudinal gradient in northern Sweden. *Journal of Paleolimnology*

Introduction

Knowledge about past climate variability is essential to understand and model current and future climatic trends. Different large-scale forcing mechanisms such as the Milankovitch sun-cycles or tidal forcing build the boundary conditions for current climate (Bradley, 1999; Keeling & Wherf, 2000). Imposed on such large-scale processes, short-term phenomena as the North Atlantic Oscillation (NAO) and stochastic events such as volcano eruptions may affect climatic conditions for shorter periods (Briffa *et al.*, 1998; Luterbacher *et al.*, 1999). In general, the instrumental records are too short and sparse to assess patterns of long-term natural climate variability. As a consequence, there is a need for long-term proxy-data to assess past climatic and environmental conditions, particularly at high latitudes, where greatest effects of potential warming are anticipated (Chapman & Walsh, 1993; Weller & Lange, 1999; Serreze *et al*., 2000).

Paleoecological records allow studying and analysing past climatic and environmental conditions on a regional scale beyond the limited period covered by instrumental measurements (MacDonald *et al.*, 2000). However, paleoecological records contain both information about past climate change and the ecosystem responses to these changes (Alverson *et al.*, 2001). Predicting future ecosystems in the light of climate change involves understanding the interactions between changing climate and non-linear responses of ecosystems. Effects of climate change on ecosystems, particularly in lakes, are complex and remain poorly understood. In addition, over Holocene time scales, development of aquatic communities may be influenced by processes related to primary succession following deglaciation of the landscape (Engstrom *et al.*, 2000).

Numerous lakes in northern Sweden were formed after deglaciation and their sediments often provide a continuous record of deposited remains of aquatic and terrestrial organisms (e.g., diatoms, chironomids, beetles, pollen, plant macrofossils) throughout the Holocene. Sedimentary and fossil remains of most of these organisms have been widely used to quantify and assess past climatic shifts in northern Sweden (e.g., Lemdahl 1997; Barnekow 1999a; Kullman & Kjällgren 2000; Rosén *et al.*, 2001). However, compared to other organism groups, the potential of diatoms as climatic indicators is poorly investigated. Until a few years ago, sedimentary remains of diatoms have been mostly used as indicators for reconstructing past acidification or eutrophication patterns in northern Sweden (Birks *et al.*, 1990; Renberg *et al.*, 1993; Anderson *et al.*, 1995), but not as climatic indicators. However, particularly in arctic regions, diatoms have shown to be a valuable proxy for past climatic shifts (Smol, 1988; Douglas *et al.*, 1994). Recently, these findings have stimulated increasing interest as well in northern Fennoscandia to use diatoms as indicators for past climatic shifts using quantitative approaches (e.g., Korhola *et al.*, 2000; Rosén *et al.*, 2001; Sorvari *et al.*, in press).

Objectives

The objective of my research was to explore the potential of diatoms as paleoclimatic indicators. The study was part of the research program of the Climate Impacts Research Centre (CIRC) which has a research focus on northernmost Sweden. The thesis builds upon three steps that are closely related. First, a large calibration set had to be developed for northernmost Sweden to collect information about present-day distribution of diatoms and to empirically model the species-environment relationships (Paper I, Bigler *et al.*, 2000). Second, the developed quantitative inference models for temperature and lake-water pH were validated and verified with monitoring data for lake-water pH (Paper I) and instrumental meteorological records (Paper II). The third step involved the application of the quantitative inference models on a Holocene time-scale in order to reconstruct past environmental conditions in northernmost Sweden and assess the responses of ecosystems to climate change. One study involved a multi-proxy approach in the subarctic lake Vuoskkujávri within the birch forest using pollen, chironomids and diatoms to provide a comprehensive assessment of climatic and environmental changes near Abisko (Paper III). The last contribution focuses on diatom-inferred Holocene lake development patterns using data from five different lakes along an elevation gradient near Abisko to assess the main factors regulating long-term changes in diatom communities (Paper IV).

Study sites and previous local paleoecological evidence

The mountainous region surrounding the village of Abisko, 200 km north of the Arctic Circle, offers an ideal setting for paleoecological research. First, lakes are relatively easily accessible, and the well-developed research station in Abisko (http://www.ans.kiruna.se) provides an ideal base for field activity. Second, the lakes around Abisko are located within broad climatic and ecological gradients, covering lakes within coniferous forest (*Pinus sylvestris*, *Picea abies*), mountain birch forest (*Betula pubescens* ssp. *tortuosa*) and lakes above the tree-limit that is formed by mountain birch at an elevation of *c.* 600-700 m a.s.l. Finally, Abisko lies in a region sensitive to climate change due to shifting influences of air masses with Atlantic or Arctic origin that lead to contrasting temperature and precipitation regimes over time (Shemesh *et al.*, 2001).

The natural ideal setting has stimulated many previous paleoecological studies and compared with other arctic and subarctic regions, Abisko probably offers the highest density of different methodological approaches to reconstruct past climate and environments. First, extensive pollen-based investigations were initiated by Sonesson (1974), continued by Küttel (1984) and later extended and refined with a comprehensive investigation along an altitudinal transect by Berglund *et al.* (1996) and Barnekow (1999a). Pine trees in the Torneträsk area were recovered and used for reconstructing short-term patterns of past summer temperature from tree-rings (Briffa *et al.*, 1988; Briffa *et al.*, 1992; Briffa *et al.*, 2001). Tree megafossil remains from high altitudes have also been collected and dated to assess past elevation of tree-limit and indirectly as a proxy for past climate (Karlén, 1976; Kullman, 1999). Sedimentological studies of pro-glacial lakes sediments have been used by Karlén (1976; 1988) and investigations involving mineral magnetic susceptibility have been made in the Kårsa Valley adjacent to the main Abisko valley to infer past changes in glacial activity of the Kårsa glacier (Snowball, 1996). Attempts to reconstruct past precipitation patterns have been made using oxygen isotope analysis of lake sediments (Berglund *et al.*, 1996; Hammarlund *et al.*, in press) as well as of subfossil diatoms (Shemesh *et al.*, 2001). Past precipitation conditions have also been studied using pollen (Seppä & Hammarlund 2000; Hammarlund *et al.*, in press). However, to date, aquatic organisms such as diatoms or chironomids have never been used or evaluated in detail to reconstruct past climatic shifts in the well-investigated Abisko surroundings. All the listed, previous studies provide important baseline information upon which diatom-based inferences can be evaluated. Furthermore, several lakes were investigated within the EU-project CHILL-10,000 in northern Finland and in the Sarek region south of Abisko using similar methodological approaches and providing valuable possibilities for comparison on a regional scale in northern Fennoscandia (Korhola *et al.*, 2000; Seppä & Birks, 2001; Sorvari, 2001; Weckström, 2001; Rosén, 2001).

Modern calibration set based on surface sediment samples

A powerful tool for quantitative environmental reconstructions is the use of modern calibration sets and transfer functions (Birks, 1995; 1998). Present-day ecological parameters (i.e., optimum, tolerance) of each diatom taxon for particular environmental variables are estimated and then applied to fossil assemblages. Under the assumption that the taxon's environmental requirements have remained unchanged during the time-period of interest (Birks *et al.*, 1990), it allows to reconstruct quantitatively past environmental conditions. It is advantageous to use a relatively large set of modern calibration samples and to include the whole biological assemblage instead of indicator species (Birks, 1981). The predictive power of a developed model can be assessed by leave-one-out (jack-knifing) cross-validation (Birks, 1995). Applying this approach, one lake in the calibration set is left out of the model iteratively and the diatom assemblages of the remaining lakes are used to predict the environmental variable of interest of the lake that has been excluded.

The occurrence of subfossil diatoms in surface sediments of subarctic lakes in northernmost Sweden was explored and related to a set of environmental variables collected at each site. The initial calibration set, including 42 lakes sampled during summer 1997 (Bigler *et al.*, 2000), was expanded up to 100 lakes during summer 1998 (Paper I). Of 19 environmental variables determined for each site, lake-water pH, the organic content of lake sediment as assessed by loss-on-ignition (LOI) and estimated mean July air temperature (July T) explained the greatest amounts of variance in the distribution of diatom taxa (8.0, 5.9 and 4.8%, respectively). For the variables of paleoecological interest (i.e., lake-water pH, July T) transfer functions using a unimodal regression and calibration technique (WA-PLS) were developed (Birks, 1995; ter Braak, 1995) and yielded prediction errors based on leave-one-out cross-validation of 0.19 pH units and 0.96 °C, respectively (Paper I). Temperature and lake-water pH optima were calculated for diatom species occurring in at least ten out of 100 calibration lakes (Paper 1, Table 4). Interestingly, the dissolved organic carbon (DOC) concentration in lakes explained only a small amount of variance in the diatom distribution (2.9%), which was not statistically independent of the variance explained by July T, and, as consequence, no transfer functions could be developed to estimate past changes in DOC. Variation within the measurements of nutrient concentrations (e.g., nitrogen, phosphorus) from individual lakes exceeded the gradient of the entire calibration lake-set and, therefore, these variables had to be excluded in the statistical analysis. However, even though nutrients seem to be less important in regulating diatom assemblage composition in this present-day calibration set, that does not imply that they were unimportant in the past (Engstrom *et al.*, 2000).

Similar calibration approaches were simultaneously performed in other parts of northern Fennoscandia using diatoms and covering comparable environmental gradients. In northern Sweden, an additional calibration set located 100-500 km further south of the calibration set area included in this thesis (Paper I) was established and transfer functions were developed for lake-water pH and July T based on about 50 lakes, yielding prediction errors of 0.30 pH units and 0.86 °C, respectively (Rosén *et al.*, 2000). In northern Finland, transfer functions for lake-water pH and July T were established yielding a prediction error of 0.39 units (Weckström *et al.*, 1997) and 0.89 °C (Korhola *et al.*, 2000), respectively, both using calibration sets including about 40 lakes. The similar results between different subarctic regions in northern Fennoscandia established by different research groups illustrate that transfer functions with similar prediction ability are reproducible.

Validation of diatom transfer functions

Besides statistical validation by leave-one-out cross-validation and bootstrapping approaches, comparison of paleolimnological inferences with historical measurements is probably the most appropriate way to assess the performance of transfer functions. Validations of diatom transfer functions with monitoring data have been carried out for example for total phosphorus (TP) in Austrian Alps (Bennion *et al.*, 1995) or in the Swiss Plateau (Lotter, 1998) and for lake-water pH in Sweden (Renberg & Hultberg, 1992). However, to my knowledge, diatom-temperature transfer functions have not previously been validated with meteorological temperature records.

The predictive ability of lake-water pH transfer functions was assessed using an independent cross-validation approach. To do this, the 100-lake calibration set was divided in two subsets. An 85-lake calibration set was used to develop transfer functions and an independent 15-lake test-set with monthly monitoring data of lake-water over two growing seasons was used to test the prediction accuracy of the developed transfer functions (Paper I). The results of this intra-set cross-validation exercise demonstrated that errors associated with the diatom lake-water pH predictions are usually within the range of seasonal and inter-annual variability of measured lake-water pH values (Paper I). The comparison of diatom-based predictions with measured lake-water pH data covering several visits during two years illustrates the power of numerical transfer functions and justifies an application over longer time-scales.

The predictive ability of diatom-July T transfer functions was assessed by directly comparing diatom-based inferences with measured values of century-long meteorological records (Paper II). The comparison includes sediment cores from three lakes dated by radiometric methods (^{210}Pb, ^{137}Cs) and records from two meteorological stations in Kiruna and Abisko. Over the past century, the diatom-based quantitative July T inferences correspond in general closely with the meteorological records and particularly in Lake Alanen Laanijärvi, the proportion of planktonic diatoms in the stratigraphy reflects the meteorological record very well. Interestingly, periods of relatively weak correspondence between measured and inferred July T (at Lake 850 from 1910-1940, at Lake Njulla from 1955-1990) correspond with periods when diatom-inferred lake-water pH shows distinct trends of pH change. Because lake-water pH is a stronger factor influencing diatom community composition than July T (Paper I), accuracy of diatom-inferred July T appears to be reduced during periods when lake-water pH fluctuates. Overall, diatoms provide reliable estimates of July T over the past century from sediment samples in northern Sweden and the reliability of the inferences further increases when lake-water pH remains constant.

Holocene climate and environmental reconstructions

The multi-proxy Holocene record from Vuoskkujávri

The developed and validated diatom transfer functions (Paper I, II) were applied in a multi-proxy framework to reconstruct past Holocene climate and environmental change in northern Sweden (Paper III). At the first study site, Vuoskkujávri, a lake located 10 km east of Abisko, a quantitative Holocene reconstruction of mean July air temperature (using pollen, chironomids and diatoms), mean January temperature (pollen), mean annual precipitation (pollen) and lake-water pH (diatoms) was attempted. All mean July air temperature (July T) inferences based on the three proxy indicators reveal a general trend of decreasing temperature since 6,000 calibrated radiocarbon years before present (henceforth abbreviated as cal. BP), with a magnitude of 1.5 °C (diatoms), 1.1 °C (pollen) and 0.8 °C (chironomids), respectively (Paper III). Considering the prediction error associated with each model (~1 °C), these results are consistent and strengthen confidence in the quantitative multi-proxy approach for paleoenvironmental and paleoclimatic assessment. However, prior to 6,000 cal. BP the reconstructions between the three proxy indicators disagree substantially. Diatoms infer an increasing July T between 10,600 and 7,000 cal. BP and a subsequent cooling between 7,000 and 6,000 cal. BP, while pollen infer a moderate warming trend and chironomids a moderate cooling trend between 10,600 and 6,000 cal. BP. The obvious disagreement prior to 6,000 cal. BP can partly be assigned to the 'poor' fit of the fossil pollen and diatom samples to the calibration set. The fit of fossil samples to the modern calibration set is assessed by the residual distance to the first CCA axis in a CCA ordination with the variable of interest as the sole explanatory variable (Birks *et al.*, 1990). This assessment suggests that chironomids provide the most reliable July T reconstruction with a linear July T decrease of 1.2 °C since 10,600 cal. BP.

Pollen-inferred mean January air temperature indicates that the winters may have been warmer by 3.0 °C during the early Holocene, followed by a gradual cooling until 8,500 cal. BP (1.0 °C warmer than today) and a subsequent warming until 7,000 cal. BP (2.0 °C warmer than today). Since 7,000 cal. BP, a gradual cooling towards the present-day values is inferred. According to the pollen, annual precipitation may have been considerably higher during the early Holocene than today (+150 mm) and increased until *c.* 7,000 cal. BP (+320 mm). Since 7,000 cal. BP, annual precipitation decreased continuously towards present-day values. Both reconstructions are rather tentative during the early Holocene, as the fossil samples show 'poor' fit to the modern calibration set. However, the inferred precipitation patterns are largely consistent with independent oxygen isotope data from lake sediments in the Abisko region (Shemesh *et al.*, 2001; Hammarlund *et al.*, in press).

Diatom-inferred pH trends show that natural acidification of *c.* 0.5 pH units occurred since deglaciation, with present-day values being reached at 5,000 cal. BP. Even though the diatom assemblage shows 'poor' fit to the modern calibration set, the inferred pattern is consistent with the general pattern of natural acidification taking place in Sweden since deglaciation (Renberg *et al.*, 1993; Korsman & Segerström, 1998).

Holocene diatom records from five subarctic lakes nearby Abisko

To assess whether the patterns of Holocene diatom assemblage development are similar among subarctic lakes, Holocene diatom stratigraphies from sediment cores of five lakes nearby Abisko were compared (Paper IV). It is assumed that all lakes experienced a similar pattern of climate changes due to their close geographic proximity, but that lake-catchment conditions differ because they are situated within different bedrock and terrestrial vegetation zones. The comparison of lakes with a similar underlying climate but different catchment conditions provides a method to identify the environmental factors that play important roles in regulating Holocene patterns of diatom community development in subarctic lakes.

Diatom communities from all five lakes were dominated by *Fragilaria* species after deglaciation, suggesting that the initial environmental conditions may have been quite comparable for all lakes during early stages of primary succession. Often, small *Fragilaria* species (e.g., *F. pseudoconstruens*, *F. pinnata*, *F. construens* var. *venter* and *F. brevistriata*) dominate postglacial and early Holocene sediments of lakes throughout glaciated regions (Smol, 1983; 1988). These species favour relatively high alkalinity (Battarbee, 1986), tolerate relatively poor light conditions (Anderson, 2000) and are characterised as adaptable and competitive (Lotter *et al.*, 1999). However, the *Fragilaria* assemblages were, with exception of Lake Njulla, replaced within a few hundred years, indicating that clear-water conditions were established relatively quickly after lake-formation. It seems that early Holocene diatom assemblages were most strongly regulated by physical factors, such as the influence of high rates of minerogenic erosion and abundant supply of epipsammic habitats and corresponding low light availability (Paper IV).

After the early Holocene, diatom assemblages show certain differences between the five lakes. It appears that different mechanisms regulated development of diatom communities in these five lakes depending on bedrock and terrestrial vegetation in the catchment, climate, and in-lake processes such as thermal stratification. In general, patterns of Holocene lake-water pH changes exerted a major influence on diatom assemblages. In three lakes (Lake Njulla, Lake 850, Vuoskkujávri; for map see Paper IV, Fig. 1) there is evidence that natural acidification played a strong role in diatom community development during the first few millennia of the Holocene (Paper IV). In contrast, the other two lakes (Lake Tibetanus, Vuolep Njakajaure) are subjected to exceptional geological catchment properties with strong buffering capacity that originates from weathering of calcite marble in the drainage area and enters the lakes through groundwater inputs (Hammarlund *et al.*, in press). As consequence, these properties may have led to relatively constant lake-water pH during the entire Holocene.

Temperature might have influenced the diatoms mainly indirectly via alteration of ice-cover duration and thermal stratification. The changes in life-form (benthic vs. planktonic diatoms) likely reflect changes in length of ice-cover and prevailing water-column mixing regimes and strength of thermal stratification (Lotter & Bigler 2000; Sorvari *et al.*, in press). In order to grow and reproduce, planktonic diatoms are dependent on turbulent mixing in the water column and benefit from a prolonged ice-free season. In Vuoskkujávri and Vuolep Njakajaure, there is indirect evidence for prolonged ice-free season between 10,600 and 6,000 cal. BP and between 10,000 and 4,000 cal. BP, respectively, as the ratio of planktonic to benthic diatoms was highest during these periods.

In Lake Njulla, the disappearance of trees in the catchment at *c.* 4,700 cal. BP (Barnekow 1999b) coincided with increasing abundances of *Aulacoseria* species (Paper IV). The increased relative abundance of *Aulacoseira* taxa has been interpreted as response to increased wind-induced mixing in Elk Lake, Minnesota (Bradbury & Dieterich-Rurup, 1993), and similar processes could apply for Lake Njulla, where the loss of trees lead to increased windiness and water-column turbulence that favours *Aulacoseria* species. This illustrates that diatoms, even though having relatively short generation times, appear to respond to long-term (centuries to millennia) vegetational changes in the catchment (MacDonald *et al.*, 1993).

The influence of changing nutrient concentrations during the Holocene on diatom community development remains speculative. In the calibration set, concentrations of nutrients are in general low, and they do not explain a significant part of variance in the diatom communities that is independent from variance explained by organic content of the sediment (assessed as LOI) or July T (Paper I). However, modest abundance of *Stephanodiscus alpinus* and *Asterionella formosa*, which are planktonic taxa indicative of meso- to eutrophic conditions, were identified during the early Holocene in Vuoskkujávri, and suggest changes in nutrient availability exerted, at least on occasion, important influences on diatom communities (Paper III). In Vuoskkujávri, these changes coincided with the expansion of *Alnus*, which could have led to an increased nitrogen supply due to contributions from endosymbiotic nitrogen fixers (Engstrom *et al.*, 2000).

To summarise, it appears that development of diatom assemblages during the early Holocene was similar in all lakes and most strongly controlled by environmental conditions of a mainly physical character (i.e., warm temperature, high erosion rates and mineral turbidity). Subsequently, diatom assemblages seemed to be regulated by many factors, such as changes in catchment acidification and lake-water pH, succession of vegetation, climate, in-lake processes and differences in the hydrologic setting, leading to variability in rate and scale of diatom community development among lakes. However, over Holocene time-scales the influence of lake-water pH on diatoms probably tends to decrease and other factors such as temperature may play an increasingly important role (Paper IV). Probably, diatom assemblages were not as strongly regulated by temperature during the entire Holocene as in the recent past.

Limitations associated with diatoms as climate indicators in subarctic lakes

Strictly, a quantitative inference model works when the variable to be reconstructed reveals significant changes and other environmental variables have a minor or negligible influence on assemblage composition (Birks, 1995). Even though temperature is an important variable regulating the diatom communities in subarctic lakes, several additional factors that are related or not related to temperature may confound the established relationships between temperature and diatoms, such as changes in lake-water pH or nutrient concentrations (Paper II; Anderson, 2000). Furthermore, important variables might be correlated within the calibration set, as for example nutrient concentrations and temperature (Lotter *et al.*, 1997) and, as consequence, it is impossible to disentangle the driving influence of such variables during the Holocene. Besides the combined influence of several variables, Holocene climate changes have not been great compared with major climatic and environmental shifts such as the Younger Dryas (Johnson *et al.*, 1995). Furthermore, stratigraphic sequences often record short-term, abrupt changes and drastic responses instead of gradual changes. In geology, the concept of gradual change was replaced by 'incremental catastrophism' or short-term changes that often occur rapidly and represent significant deviations from earlier environmental modes (Bradbury, 1999). That concept can be fully adapted as well for the Holocene, even though the Holocene is, in geological terms, a relatively short time-scale. Single events associated with erosion or avalanches might affect a lake ecosystem more severely and over a longer time-scale than the gradual increase or decrease in temperature, lake-water pH, precipitation or other factors. As consequence, it is difficult to reconstruct subtle changes when biota is under control of many variables and their complex interactions.

Overall, the results presented in this thesis illustrate that the early Holocene is likely a problematic period for estimating July T from diatoms, because natural processes such as soil and catchment development resulted in marked natural declines in lake-water pH. Similarly, short-term stochastic events, such as sediment in-wash due to single erosional events, forest clearance and forest fires, also may lead to inaccurate diatom-temperature inferences through changes in lake-water pH and nutrient supply (Renberg *et al.*, 1993; Korsman *et al.*, 1998). In order to identify periods that may affect the accuracy of diatom-based July T inferences, diatoms should be combined with other paleoecological proxy indicators.

A limiting factor associated with the calibration set method used in this study is that mean July air temperatures were estimated for each site, rather than measured directly. In fact, estimates of present-day temperature optima and tolerance of diatom species were based on mean July air temperatures derived from Climate Normals (1961-1990) of the closest meteorological station. Recently, this approach has been questioned (Seppälä, 2001). However, the data based on Climate Normals extrapolated for each lake probably provides a good approximation of the 'true' average temperature by reducing the influence of interannual variability and extreme weather years. Furthermore, studies from Switzerland have shown that surface water temperature is closely correlated with air temperature (Livingstone & Lotter, 1998; Livingstone *et al.*, 1999). Nevertheless, long-term monitoring of relationships between air and water temperatures in lakes over a gradient of temperature and topographic factors might greatly improve future paleolimnological reconstructions.

A further limitation of diatoms as environmental and climatic indicators may arise when the preservation of diatoms is poor and the concentration in the sediment core does not allow an enumeration of sufficient numbers of diatom valves. In northern Sweden, mainly lakes with high lake-water pH values are potentially affected. One of the initially selected study lakes, Alanen Laanijärvi, with an exceptional high lake-water pH (8.1), did not have well preserved diatoms except for in the uppermost 25 cm of the sediment core. Preservation problems occur under a complex set of lacustrine conditions that remain poorly understood (Flower, 1993) and experiments have shown that species-specific dissolution differences may occur (Ryves *et al.*, 2001).

Future perspectives

Initiatives to use diatoms as climatic indicators have been made not only in northern Fennoscandia, but as well in other arctic and subarctic regions around the world (Lotter *et al.*, 1999). A future worthwhile task is to merge and cross-validate developed diatom calibration sets within Scandinavia, and even more broadly including the circumpolar north. Such an initiative will need a tremendous effort in harmonising and comparing taxonomical concepts between different research groups, but would lead to a common, valuable calibration data set covering broad geographical and environmental gradients with more 'environmental relevance' than local or regional calibration sets. The number of lakes should be increased mainly through expanding the temperature gradient at the 'colder' end of the gradient, for example with lakes from Svalbard. The 'warmer' end of the gradient is more problematic, as one is faced with confounding problems (e.g., nutrients, human impact).

To improve the calibration data sets and transfer functions, the limiting factor is often the quality of the environmental data. Ecologically, it is more useful to calibrate requirements of aquatic organisms with water temperature data measured in lakes than with air temperature data interpolated from meteorological stations. However, the collection of long-term water temperature data is time- and cost-intensive and logistically challenging. But the use of long-term limnological data will inevitably improve the empirically developed relationship between diatom species and temperature.

To obtain reproducible quantitative reconstructions, a careful site selection is even more crucial for 'reconstruction' lakes than calibration set lakes. There is a need to identify representative ecosystems close to ecotonal boundaries such as the tree-limit that have similar properties as the calibration set lakes. Moreover, by assembling evidence from several lakes to reconstruct climate, and assessing at each site possible confounding factors as pre-historical human impact, in-lake processes, influence of geomorphology and stochastic events, future studies will lead to a more generally valid picture than traditional single lake studies. Future emphasis should be put also on a shorter time-scale than the entire Holocene (e.g., the past 2000 years), as the density of independent paleoclimate information is much higher and allows a better validation of diatom-based inferences. Finally, analysis of contiguous sedimentary intervals with high temporal resolution is needed to improve the understanding of effects of short-term climate changes on aquatic ecosystems. Annually laminated sediments provide undoubtedly the best sediment archive to assess the length of the environmental memory and response time of aquatic ecosystems to known environmental extreme events. Unfortunately, annually laminated sediments appear to be rare in the mountain region of northern Sweden.

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References

Alverson, K., R. Bradley & T. Pedersen, 2001. Environmental variability and climate change. Bern, IGBP Pages, IGBP Science report Nr. 3, 31 pp.

Anderson, N. J., 2000. Diatoms, temperature and climatic change. *European Journal of Phycology* 35: 307-314.

Anderson, N. J., I. Renberg & U. Segerström, 1995. Diatom production responses to the development of early agriculture in a boreal forest lake-catchment (Kassjön, northern Sweden). *Journal of Ecology* 83: 809-822.

Barnekow, L., 1999a. Holocene vegetation dynamics and climate changes in the Torneträsk area, northern Sweden. Lund, Lund University, Ph.D. Dissertation, 30 pp.

Barnekow, L., 1999b. Holocene tree-line dynamics and inferred climatic changes in the Abisko area, northern Sweden, based on macrofossil and pollen records. *The Holocene* 9: 253-265.

Battarbee, R. W., 1986. Diatom analysis. In: Berglund, B. E. (ed.) Handbook of Holocene Palaeoecology and Palaeohydrology. London, John Wiley & Sons Ltd., 527-570.

Bennion, H., S. Wunsam & R. Schmidt, 1995. The validation of diatom-phosphorus transfer functions: an example from Mondsee, Austria. *Freshwater Biology* 34: 271-283.

Berglund, B. E., L. Barnekow, D. Hammarlund, P. Sandgren & I. F. Snowball, 1996. Holocene forest dynamics and climate changes in the Abisko area, northern Sweden - the Sonesson model of vegetation history reconsidered and confirmed. *Ecological Bulletins* 45: 15-30.

Bigler, C., R. I. Hall & I. Renberg, 2000. A diatom-training set for paleoclimatic inferences from lakes in northern Sweden. *International Association of Theoretical and Applied Limnology* 27: 1174-1182.

Birks, H. J. B., 1981. The use of pollen analysis in the reconstruction of past climates: a review. In: Wigley, T. M. L., M. J. Ingram & G. Farmer (eds) Climate History: Studies in Past Climates and Their Impact on Man. Cambridge, Cambridge University Press, 111-138.

Birks, H. J. B., 1995. Quantitative palaeoenvironmental reconstructions. In: Maddy, D. & J. S. Brew (eds). Statistical Modelling of Quaternary Science Data. Cambridge, Cambridge: Quaternary Research Association XII: 161-254.

Birks, H. J. B., 1998. Numerical tools in paleolimnology - progress, potentialities, and problems. *Journal of Paleolimnology* 20: 307-332.

Birks, H. J. B., J. M. Line, S. Juggins, A. C. Stevenson & C. J. F. ter Braak, 1990. Diatoms and pH reconstruction. *Philosophical Transactions of the Royal Society of London* B327: 263-278.

Bradbury, J. P., 1999. Continental diatoms as indicators of long-term environmental change. In: Stoermer, E. F. & J. P. Smol (eds). The diatoms: applications for the environmental and earth sciences. Cambridge, Cambridge University Press: 169-182.

Bradbury, J. P. & K. V. Dieterich-Rurup, 1993. Holocene diatom paleolimnology of Elk Lake, Minnesota. In: Bradbury, J. P. & W. E. Dean (eds). Elk Lake, Minnesota: Evidence for rapid climate change in the north-central United States. Boulder, The Geological Society of America. Special Paper 276: 215-237.

Bradley, R. S., 1999. Paleoclimatology - reconstructing climates of the Quaternary. San Diego, Academic Press. 613pp.

Briffa, K. R., P. D. Jones, T. S. Bartholin, D. Eckstein, F. H. Schweingruber, W. Karlén, P. Zetterberg & M. Eronen, 1992. Fennoscandian summers from AD 500: temperature changes on short and long timescales. *Climate Dynamics* 7: 111-119.

Briffa, K. R., P. D. Jones, J. R. Pilcher & M. K. Hughes, 1988. Reconstructing summer temperatures in northern Fennoscandinavia back to A.D. 1700 using tree-ring data from Scots pine. *Arctic & Alpine Research* 20: 385-394.

Briffa, K. R., P. D. Jones, F. H. Schweingruber & T. J. Osborn, 1998. Influence of volcanic eruptions on Northern Hemisphere summer temperature over the past 600 years. *Nature* 393: 450-455.

Briffa, K. R., T. J. Osborn, F. H. Schweingruber, I. C. Harris, P. D. Jones, S. G. Shiyator & E. A. Vaganov, 2001. Low-frequency temperature variations from a northern tree ring density network. *Journal of Geophysical Research-Atmospheres* 106: 2929-2941.

Chapman, W. L. & J. E. Walsh, 1993. Recent variations of sea ice and air temperatures in high latitudes. *Bulletin of the American Meteorological. Society* 74: 33-47.

Douglas, M. S. V., J. P. Smol & W. Blake, 1994. Marked Post-18th Century Environmental Change in High-Arctic Ecosystems. *Science 2*66: 416-419.

Engstrom, D. R., S. C. Fritz, J. E. Almendinger & S. Juggins, 2000. Chemical and biological trends during lake evolution in recently deglaciated terrain. *Nature* 408: 161-166.

Flower, R. J., 1993. Diatom preservation: experiments and observations on dissolution and breakage in modern and fossil samples. *Hydrobiologia* 269/270: 473-484.

Hammarlund, D., L. Barnekow, H. J. B. Birks, B. Buchardt & T. W. D. Edwards, in press. Holocene changes in atmospheric circulation recorded in the oxygen-isotope stratigraphy of lacustrine carbonates from northern Sweden. *The Holocene*.

Johnson, S. J., D. Dahl-Jensen, W. Dansgaard & N. S. Gundestrup, 1995. Greenland temperatures derived from GRIP borehole temperature and ice core isotope profiles. *Tellus* 47: 624-629.

Karlén, W., 1976. Lacustrine sediments and tree-limit variations as indicators of Holocene climatic fluctuations in Lappland, northern Sweden. *Geografiska Annaler* 3A: 1-36.

Karlén, W., 1988. Scandinavian glacial and climatic fluctuations during the Holocene. *Quaternary Science Reviews* 7: 199-209.

Keeling, C. D. & T. P. Wherf, 2000. The 1,800-year oceanic tidal cycle. a possible cause of rapid climate change. *Proceedings of the National Academy of Sciences of the United States of America* 97: 3814-3819.

Korhola, A., J. Weckström, L. Holmström & P. Erästö, 2000. A quantitative Holocene climatic record from diatoms in northern Fennoscandia. *Quaternary Research* 54: 284-294.

Korsman, T. & U. Segerström, 1998. Forest fire and lake-water acidity in a northern Swedish boreal area: Holocene changes in lake-water quality at Makkassjön. *Journal of Ecology* 86: 113-124.

Kullman, L., 1999. Early Holocene tree growth at a high elevation site in the northernmost Scandes of Sweden (Lapland): a palaeobiogeographical case study based on megafossil evidence. *Geografiska Annaler* 81A: 63-74.

Kullman, L. & L. Kjällgren, 2000. A coherent postglacial tree-limit chronology (Pinus sylvestris L.) for the Swedish Scandes: aspects of paleoclimate and "Recent Warming", based on megafossil evidence. *Arctic, Antarctic and Alpine Research* 32: 419-428.

Küttel, M., 1984. Vuolep Allakasjaure - eine pollenanalytische Studie zur Vegetationsgeschichte der Tundra in Nordschweden. Festschrift Welten. *Dissertationes Botanicae*. 72: 191-212.

Lemdahl, G., 1997. Early Weichselian insect faunas from northern Sweden: climatic and environmental implications. *Arctic & Alpine Research* 29: 63-74.

Livingstone, D. M. & A. F. Lotter, 1998. The relationship between air and water temperatures in lakes of the Swiss Plateau: a case study with palaeolimnological implications. *Journal of Paleolimnology* 19: 181-198.

Livingstone, D. M., A. F. Lotter & I. R. Walker, 1999. The decrease in summer surface water temperature with altitude in Swiss alpine lakes: a comparison with air temperature lapse rates. *Arctic, Antarctic and Alpine Research* 31: 341-352.

Lotter, A. F., 1998. The recent eutrophication of Baldeggersee (Switzerland) as assessed by fossil diatom assemblages. *The Holocene* 8: 395-405.

Lotter, A. F. & C. Bigler, 2000. Do diatoms in the Swiss Alps reflect the length of ice-cover? *Aquatic Sciences* 62: 125-141.

Lotter, A. F., H. J. B. Birks, W. Hofmann & A. Marchetto, 1997. Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. I. Climate. *Journal of Paleolimnology* 18: 395-420.

Lotter, A. F., R. Pienitz & R. Schmidt, 1999. Diatoms as indicators of environmental change near arctic and alpine treeline. In: Stoermer, E. F. & J. P. Smol (eds) The diatoms: application to the environmental and earth sciences. Cambridge, Cambridge University Press: 205-226.

Luterbacher, J., C. Schmutz, D. Gyalistras, E. Xoplaki & H. Wanner, 1999. Reconstruction of monthly NAO and EU indices back to AD 1675. *Geophysical Research Letters* 26: 2745-2748.

MacDonald, G. M., T. W. D. Edwards, K. A. Moser, R. Pienitz & J. P. Smol, 1993. Rapid response of treeline vegetation and lakes to past climate warming. *Nature* 361: 243-246.

MacDonald, G. M., B. Felzer, B. P. Finney & S. L. Forman, 2000. Holocene lake sediment records of Arctic hydrology. *Journal of Paleolimnology* 24: 1-14.

Renberg, I. & H. Hultberg, 1992. A paleolimnological assessment of acidification and liming effects on diatom assemblages in a Swedish lake. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 65-72.

Renberg, I., T. Korsman & N. J. Anderson, 1993. A temporal perspective of lake acidification in Sweden. *Ambio* 22: 264-271.

Renberg, I., T. Korsman & H. J. B. Birks, 1993. Prehistoric increases in the pH of acid-sensitive Swedish lakes caused by land-use changes. *Nature* 362: 824-826.

Rosén, P., 2001. Holocene climate history in northern Sweden reconstructed from diatom, chironomid and pollen records and near-infrared spectroscopy of lake sediments. Umeå, Umeå University, Ph.D. Dissertation, 24pp.

Rosén, P., R. I. Hall, T. Korsman & I. Renberg, 2000. Diatom transfer-functions for quantifying past air temperature, pH and total organic carbon concentration from lakes in northern Sweden. *Journal of Paleolimnology* 24: 109-123.

Rosén, P., U. Segerström, L. Eriksson, I. Renberg & H. J. B. Birks, 2001. Holocene climatic change reconstructed from diatoms, chironomids, pollen and near-infrared spectroscopy (NIRS) at an alpine lake (Sjuodjijaure) in northern Sweden. *The Holocene* 11: 551-562.

Ryves, D. B., S. Juggins, S. C. Fritz & R. W. Battarbee, 2001. Experimental diatom dissolution and the quantification of microfossil preservation in sediments. *Palaeogeography, Palaeoclimatology, Palaeoecology* 172: 99-113.

Seppä, H. & H. J. B. Birks, 2001. July mean temperature and annual precipitation trends during the Holocene in the Fennoscandian tree-line area: pollen-based climate reconstructions. *The Holocene* 11: 527-539.

Seppä, H. & D. Hammarlund, 2000. Pollen-stratigraphical evidence of Holocene hydrological change in northern Fennoscandia supported by independent isotopic data. *Journal of Paleolimnology* 24: 69-79.

Seppälä, M., 2001. Unsatisfactory field data in a calibration model for inferring past temperature from chironomid assemblages in northern Fennoscandia: a comment on Olander, Birks, Korhola and Blom. *The Holocene* 11: 613-622.

Serreze, M. C., J. E. Walsh, F. S. Chapin, T. Osterkamp, M. Dyurgerov, V. Romanovsky, W. C. Oechel, J. Morison, T. Zhang, R. G. Barry, 2000: Observational evidence of recent change in the northern high-latitude environment. *Climatic Change* 46: 159-207.

Shemesh, A., G. Rosqvist, M. Rietti-Shati, L. Rubensdotter, C. Bigler, R. Yam & W. Karlén, 2001. Holocene climatic change in Swedish Lapland inferred from an oxygen-isotope record of lacustrine biogenic silica. *The Holocene* 11: 447-454.

Smol, J. P., 1983. Paleophycology of a high arctic lake near Cape Herschel, Ellesmere Island. *Canadian Journal of Botany* 61: 2195-2204.

Smol, J. P., 1988. Paleoclimate proxy data from freshwater arctic diatoms. *International Association of Theoretical and Applied Limnology* 23: 837-844.

Snowball, I. F., 1996. Holocene environmental change in the Abisko region of northern Sweden recorded by the mineral magnetic stratigraphy of lake sediments. *Transactions of the Geological Society in Stockholm (GFF)* 118: 9-17.

Sonesson, M., 1974. Late Quaternary forest development of the Torneträsk area, North Sweden 2. Pollen analytical evidence. *Oikos* 25: 288-307.

Sorvari, S., 2001. Climate impacts on remote subarctic lakes in Finnish Lapland: limnological and paleolimnological assessment with a particular focus on diatoms and lake Saanajärvi. Helsinki, *Kilpisjärvi Notes* 16*,* Ph.D. Dissertation, 50pp.

Sorvari, S., A. Korhola & R. Thompson, in press. Lake diatom response to recent Arctic warming in Finnish Lapland. *Global Change Biology*.

ter Braak, C. J. F., 1995. Non-linear methods for multivariate statistical calibration and their use in palaeoecology: a comparison of inverse (k-nearest neighbours, partial least squares and weighted averaging partial least squares) and classical approaches. *Chemometrics and Intelligent Laboratory Systems* 28: 165-180.

Weckström, J., 2001. Assessment of diatoms as markers of environmental change in northern Fennoscandia. Helsinki, University of Helsinki, Ph.D. Dissertation, 67pp.

Weckström, J., A. Korhola & T. Blom, 1997. Diatoms as quantitative indicators of pH and water temperature in subarctic Fennoscandian lakes. *Hydrobiologia* 347: 171-184.

Weller, G. & M. Lange, 1999. Impacts of Global Climate Change in the Arctic Regions. Tromsø, IASC-report, 59pp.