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**Climate Impacts on Remote Subarctic Lakes in Finnish Lapland:
Limnological and Palaeolimnological Assessment
with a Particular Focus on Diatoms and Lake Saanajärvi**

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Academic dissertation in Hydrobiology

To be presented with the permission of the Faculty of Science of the University of Helsinki, for public criticism in the Lecture Room of the Department of Ecology and Systematics, Pohjoinen Rautatiekatu 13 on June 15, 2001, at 12 o'clock noon.

Helsinki 2001

Cover photo:

Jan Weckström (Lake Saanajärvi)

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ISBN 952-91-3524-6

Yliopistopaino

Helsinki 2001

Abstract

Limnological characteristics and recent environmental history of five remote subarctic lakes in NW Finnish Lapland were investigated using both limnological and palaeolimnological methods with particular attention to diatoms. The studied sites were dilute, oligotrophic, circumneutral clear-water lakes with low productivity. Two different thermal structures were recognised; dimictic lakes with brief spring overturn, a few weeks of stratification, and a relatively long autumn overturn, and isothermal lakes with only one mixing period during the entire open-water season. A single phytoplankton production maximum occurred in the autumn overturn at the main study site, Lake Saanajärvi. The inter-annual variability within the dominant algae groups (chrysophytes and diatoms) was common. Typical benthic habitat preferences were found among diatom communities in Lake Saanajärvi. Epilithic diatoms, such as *Achnanthes*, *Brachysira* and *Denticula* species, were common in the upper littoral zone while epipellic *Fragilaria* and *Navicula* species predominated the deeper littoral zone.

Extremely slow but constant sedimentation rates were characteristic for the studied lakes indicating low allochthonous and autochthonous inputs. Palaeolimnological studies demonstrated a concurrent diatom floristic shift that occurred in all the studied lakes about 100 years ago. The change in diatom assemblages was from benthos to plankton in dimictic lakes, while in isothermal lakes the shift took place among the tychoplanktonic and benthic forms. Multi-proxy analyses from Lake Saanajärvi showed that the change in diatom assemblages was accompanied by synchronous changes in other biological indicators, such as cladocerans, chrysophyte cyst assemblages, and fossil pigments, indicating an overall ecosystem response.

The diatom record was compared to the 200-year long monthly air temperature record, specifically reconstructed for the study region using an European-wide instrumental data and all available proxy data. A significant relationship was found between the reconstructed air temperatures and the diatom species shift in each lake, with spring temperatures explaining most of the variation in the diatom species data. A change in climate represents the only process that is regionally synchronous and can potentially account for the pronounced diatom floristic shift. No other process – such as acidification or catchment disturbance – can explain satisfactorily the diatom assemblage change from benthos to plankton that occurred within the circumneutral taxa. It is suggested that climate affected the diatom flora mainly via the increased spring temperatures, which in turn lengthened the open-water season, and strengthened the thermal structures in dimictic lakes. The changes in the duration of the overturns and summer stratification may have favoured the growth of small *Cyclotella* species through the increased nutrient availability from the hypolimnion during the autumn mixing. The study strongly reinforces the suitability of diatoms for biomonitoring both present and past environmental changes in subarctic aquatic ecosystems.

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List of original papers

The thesis includes a summary and the following papers, which are referred to in the text by their Roman numerals I-V.

- I **Sorvari, S.**, M. Rautio & A. Korhola (2000). Seasonal dynamics of subarctic Lake Saanajärvi in Finnish Lapland. *Verheissungen der Internationale Vereinigung der gesamten Limnologie* 27: 507-512.
- II Rautio, M., **S. Sorvari** & A. Korhola (2000). Diatom and crustacean zooplankton communities, their seasonal variability, and representation in the sediments of subarctic Lake Saanajärvi. *Journal of Limnology* 59 (Suppl. 1): 81-96.
- III **Sorvari, S.** & A. Korhola (1998). Recent diatom assemblage changes in subarctic Lake Saanajärvi, NW-Finnish Lapland, and their paleoenvironmental implications. *Journal of Paleolimnology* 20: 205-215.
- IV Korhola, A., **S. Sorvari**, M. Rautio, P. G. Appleby, J. A Dearing, Y. Hu, N. Rose, A. Lami & N. G. Cameron (2001). A multi-proxy analysis of climate impacts on recent ontogeny of subarctic Lake Saanajärvi in Finnish Lapland. *Journal of Paleolimnology* (in press).
- V **Sorvari, S.**, A. Korhola & R. Thompson (2001). Lake diatom response to recent Arctic warming in Finnish Lapland. (submitted)

The author's contribution

- I Sanna Sorvari was responsible for the project rationale, fieldwork, physicochemical data processing and statistical treatments together with Milla Rautio. All the authors took part in the interpretation of results and writing.
- II Sanna Sorvari organised and carried out the fieldwork 1996-1998 together with Milla Rautio. Sanna Sorvari collected, prepared and analysed the diatom samples, and contributed to the statistical and graphical data processing. Milla Rautio and Sanna Sorvari wrote the paper under the supervision of Atte Korhola. All the authors took part in the interpretation and discussion of results.
- III Sanna Sorvari planned and carried out the fieldwork, prepared and analysed diatom samples, including statistical and graphical data processing. Both authors participated in the interpretation of results and writing.
- IV Sanna Sorvari planned and performed the fieldwork, and was responsible for preparation and logistics of samples to special analyses. Sanna Sorvari analysed loss-on-ignition, dry weight and diatoms from the sediment. Milla Rautio was responsible for cladocera analysis, Peter Appleby for dating results, John Dearing and Y. Hu for mineral magnetics, Neil Rose for counting spheroidal carbonaceous particles, Andrea Lami for measuring fossil pigments and Nigel Cameron for counting chrysophyte cysts. John-Arvid Grytnes and John Birks contributed to the statistical analyses. The first three authors participated actively in interpretation of results and all the authors wrote their own area of expertise. Atte Korhola was responsible for the data synthesis.
- V Sanna Sorvari planned and carried out all the fieldwork during 1996-2000 and prepared and analysed the diatom samples. Sanna Sorvari performed statistical analyses of the diatom data and produced all the graphics for the paper. Roy Thompson provided the meteorological data. All the authors took part in the interpretation of the results and wrote their own area of expertise.

1. Introduction

1.1. Limnology and palaeolimnology

In response to increasing concerns about the effect of human activities on aquatic ecosystems (e.g. acidification, eutrophication, climate warming), an increasing number of limnological monitoring programs are being established to determine the environmental condition of lakes and ponds. However, temporal scales of limnological monitoring studies normally stretch back 1 to 3 years in time, and rarely more than 10 years. Lakes, however, are usually at least 10 000 years old in most parts of the world, and they have faced several substantial changes through time (Whitehead *et al.* 1989, Renberg 1990, Korhola & Tikkanen 1991, Engstrom *et al.* 2000). In addition, human impacts have often dramatically altered the aquatic ecosystem before monitoring has started. To track these recent changes and to understand more precisely the present-day state of the lakes, it is essential to relate recent changes to the long-term trends in lake ontogeny. Palaeolimnological techniques, (palaeolimnology, a multidisciplinary science that uses physical, chemical, and biological information in sediment profiles to reconstruct past environmental conditions in aquatic systems) can be used as a supplementary approach to limnological monitoring studies to answer many questions posed by scientists as well as public and policy makers concerning threats to the environment (Smol 1992).

Nowadays, limnological and palaeolimnological approaches often tend to be used together (e.g. Bradbury 1988, Cameron 1995, Anderson *et al.* 1997, Lotter & Bigler 2000, II). This collaboration offers several advantages; limnological monitoring can be placed in an historical context and palaeolimnology can give valuable knowledge of organism and ecosystem responses to environmental change and

possible recovery of the populations and ecosystems. Limnologists can extract information from high-resolution palaeo-data for example, of long-term biological variability and time scales of sexual reproduction. For palaeolimnologists interaction and collaboration between neo- and palaeolimnology can be as valuable as it is for limnologists. Palaeolimnologists seldom spend their time examining recent abiotic and biotic interactions from the lakes where they have taken and analysed sediment cores. Furthermore, short sampling visits certainly do not reveal the ecosystem dynamics of the study site. The successful interpretation of past environmental conditions is particularly dependent on a good knowledge of short scale processes and ecosystem interactions (Smol & Cumming 2000). In this study both contemporary limnological and palaeolimnological approaches are used to examine the specific questions and concerns associated with subarctic lake ecosystems.

1.2. Temporal scales in palaeolimnology

The variability of temporal processes within lakes is a continuum (Harris 1980). Seasonal and inter-annual variability in populations is closely related to biological and physico-chemical processes. Same interactions incorporate longer-term variability resulting from lake ontogeny, stochastic processes and anthropogenic disturbances (Engstrom *et al.* 2000). Figure 1 illustrates different temporal scales in limnology and palaeolimnology. It is critical to internalise the nature of processes and phenomena which are expressed differently over different time scales (Anderson 1995). For example, it is commonly known that total phosphorus (TP) values can greatly vary within one year but over the course of 10 years, one year's seasonal variability can be less than total inter-annual variability. When working on even longer time scales, time itself averages the data through reduced sampling resolution and sediment mixing, and by smoothing the

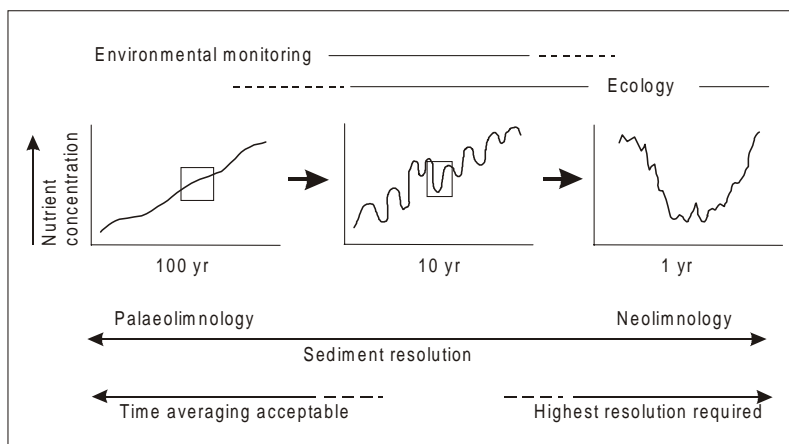


Figure 1. A schematic representation of how temporal scales affect the conception of limnological processes (Anderson 1995).

data long-term trends may become more apparent (e.g. in TP concentrations) (Anderson 1995).

The challenge for the palaeolimnologist is to interpret operating processes from the observed physical, chemical or biological changes which have occurred at specific times (Birks & Birks 1980). Several theoretical tools can be used to perceive the concept of change, its intensity, magnitude and the relationships between forcing, response and ecosystem equilibrium (Birks & Birks 1980, Roberts 1994). Figure 2 illustrates schematically a range of different (eco)system responses to linear forcing of environmental change (Roberts 1994).

A gradual external forcing can lead to a concurrent system response (Fig. 2a) or a system response can lag behind the forcing (Fig. 2b). Often an environmental system and forcing itself is more complex, and response is more likely to be c and d type (Fig. 2). In the instances where a system responds to forcing with a time lag (2c), it may have to cross certain thresholds (2d) before it can shift to a new equilibrium (Roberts 1994). A non-linear response can also result from the interaction of different processes (forcing

factors) that include both slow and fast components. In environmental sciences research is often concentrated on human activity and its impacts on environment. For this reason it is vital to separate how forcing affect the system and what type of response(s) is expected. These conceptual schemes can hopefully help researchers to interpret complex causal processes, which have been operating in the past.

The reports of International Panel of Climate Change (IPCC, Houghton *et al.* 1996, Watson *et al.* 1996, Bruce *et al.* 1996) have emphasised the importance of global warming as one of the major issues with which mankind is likely to be confronted in the near future. A warming of the Earth's surface is likely to have vital ecological, economic and political consequences, not only because of its effect on terrestrial environments, but also because of its effect on aquatic ecosystems, water supplies and fisheries. However, it is widely known that climate has varied naturally (pre-anthropogenic) in the past. There are documentary data and sedimentary proxy-data about the so-called 'Little Ice Age' (LIA) (Grove 1988), 'Medieval climate anomaly' (MCA) (Hughes & Diaz 1994), the early Holocene warm period and subsequent

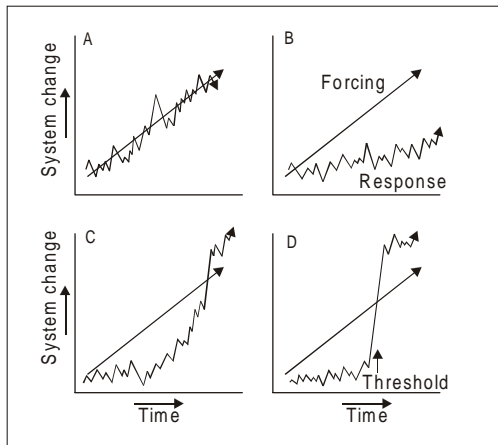


Figure 2. Several alternative system responses to the external forcing (Roberts 1994).

Neoglacial cooling (COHMAP members 1988, Huntley & Prentice 1993, Bradley 1999, Korhola *et al.* 2000). In order to build reliable future climate warming scenarios, it is necessary to understand how and why climate has naturally varied in the past and what role humans have played in the recent climate warming. In the temporal interface of the last 150 years, instrumental and sediment proxy records can be calibrated and tested against each other. The focus of this study is to operate within such a time window (the last 150 years) where both instrumental and sediment proxy-data can be used optimally.

1.3. Climatic trends during the last centuries

Northern Hemisphere temperature fluctuations during the last 400-600 years are well documented on the basis of various proxy archives, such as tree-rings, glaciers, and lacustrine and marine sediments (Overpeck *et al.* 1997, Mann *et al.* 1998, Mann *et al.* 1999). In NW Europe, the proxy evidence from glacier fluctuations suggests cool summer conditions for most of the last 600 years (Bradley & Jones 1993). These observations are supported by tree-ring data from the northern Scandinavia (Briffa *et al.*

1988, Briffa *et al.* 1990). Moreover, historical evidence of changes in European climate over the past few centuries is abundant. In particular, there are many paintings of alpine glaciers, which show clearly that the glaciers have previously been far in advance of their current positions thus indicating severe climate conditions (Grove 1988). Evidence from high mountain areas and end moraines caused by glacier advances led Matthes (1940) to introduce the term ‘Little Ice Age’ (LIA) to describe this cool period of time that ended approximately 150 years ago. Unfortunately, the term LIA is often used without clarity; some authors consider the LIA to began in the fourteenth or fifteenth centuries, while others date it as starting in the 1600s (Bradley 1999). In reality, the LIA was likely one of the several late Holocene cool episodes and it probably was not continuously cold, nor was it uniformly cold in all regions simultaneously. Nowadays most of the researchers use the term LIA to describe the last and the most dramatic episode of neoglaciation, which occurred between ~1500 and ~1850. In NW Europe, the coldest climate conditions were probably between AD 1570 and 1730, and in the 19th century, especially in 1830-1860 (Bradley & Jones 1993). After mid-19th century mean annual temperatures has warmed 1-2°C, with a clear peak in the 1930s (Alexandersson & Eriksson 1989). The long-term mean annual temperatures in Fennoscandia follow the behaviour of Northern Hemisphere temperature variations (Tuomenvirta & Heino 1996, V). LIA ended in Fennoscandia around the 1870s and this cold period was followed by a relatively linear temperature increase for the next 60 years, which culminated at the 1930s (Koutaniemi 1990, V). The warming trend observed during the first three decades of the 20th century reversed to cooling from the 1950s. During the 1980s and 1990s, Northern Hemisphere temperatures have risen to the level never before reached in the entire 400-years record (Mann *et al.* 1998). In contrast, temperatures over the same period in Finland have not passed the maximum of the 1930s (Tuomenvirta & Heino 1996).

1.4. Global warming and the Arctic waters

General circulation models (GCMs), which simulate future climates, have consistently indicated that the increase in greenhouse gas emissions is likely to have its greatest impacts on northern high latitudes (Kattenberg *et al.* 1996). The reasons for amplified effects in the Arctic region are due to a complex series of interactions and several positive feedback mechanisms among the region's oceanic and atmospheric circulation patterns, temperature regime, hydrologic cycle, and sea ice formation (AMAP 1998). For example, sea ice and snow reflect a much higher fraction of incident sunlight than water and soil, so that reduction of sea ice and snow cover decreases surface albedo, amplifying warming in the Arctic. In addition to decreasing albedo, atmospheric stability and cloud dynamics are suggested to change in the future (Overpeck *et al.* 1997, Rouse *et al.* 1997). Broad-scale effects of climatic warming in the Arctic are numerous and may include a decrease in the area of permafrost, a decrease in ice extent and ice-cover period on both inland waters and on sea ice, and changes in hydrological conditions (Rouse *et al.* 1997). It has been suggested that in permafrost areas where the annual temperature is higher than -6°C or where the annual mean ground temperature is near 0°C , permafrost could disappear completely (Rouse *et al.* 1997). The long-term warming scenarios produced by the various GCMs include the poleward movement of the permafrost boundaries by about 500 km. This would reduce the area of continuous permafrost to less than 80% of its present coverage (Woo *et al.* 1992). Spatial changes in the permafrost area can lead to dramatic changes in hydrological conditions and thus affect aquatic ecosystems. In addition, areas of discontinuous permafrost would also face severe changes in hydrological conditions. In general, evaporation and transpiration are predicted to increase together with increased summer temperatures in northern high latitudinal areas. There is evidence to contradict this

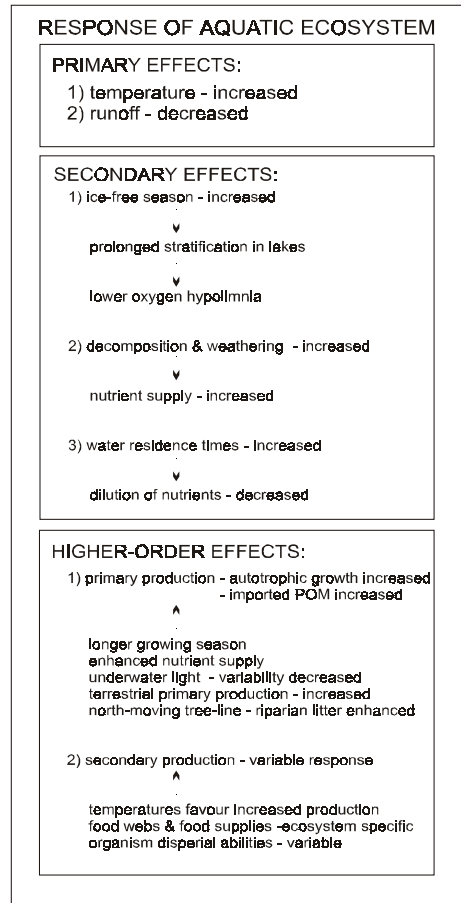


Figure 3. Potential responses of aquatic ecosystems to increased temperature and decreased runoff (Rouse *et al.* 1997).

hypothesis, though. Precipitation has actually increased in high latitudes by up to 15% over the last 100 years (Groisman 1991, Karl *et al.* 1993, Hanssen-Bauer & Førland 1994), and thus the critical equation with respect to the effects of climate warming on the water balance must involve both the magnitude of the warming effect and the responses of the precipitation regime. The potential responses of aquatic ecosystems to climate change, in particular to increased temperature and decreased runoff, are summarised in Figure 3. The main response to increased temperature will be a longer ice-free period for lakes,

which will in turn increase the length of the thermal stratification and create more stable thermal structure and underwater light climate conditions during the open-water season (Rouse *et al.* 1997). The prolonged thermal stratification may lead to lower oxygen concentrations and resulting in increased phosphorus concentrations in the hypolimnion. Primary production should benefit from this situation because aquatic autotrophs tend to be limited by nutrients, while benthic fauna is supposed to suffer most from the reduced oxygen content in the hypolimnion. The observed and suggested aquatic responses to climate warming will be discussed later in Section 4.

1.5. Arctic versus subarctic

There are several definitions to the term 'Arctic', which can sometimes be confusing. A common geographical definition of the Arctic is the area north of the Arctic Circle (N 66°32'), which marks the northernmost point at which the sun can be seen at the winter solstice and the southernmost point of the northern polar regions at which the midnight sun is visible. From the environmental point of view, defining the Arctic solely on the

basis of the Arctic Circle makes little sense. The most commonly used definitions of the Arctic in the framework of ecology refer to climatological and phytogeographical definitions. Climatologically, the Arctic is commonly defined as the area north of the July 10°C isotherm, i.e. the region where mean July temperature is below 10°C. According to this definition, the whole northern part of Scandinavian Lapland falls out of the determination of the arctic area because of the warming effect of the Gulf Stream. Phytogeographically, the northern tree-line, i.e. the boundary between two global biomes, namely the boreal coniferous forest and the arctic tundra is used to determine the Arctic. The tree-line is a simple, visual criterion for the Arctic. The term 'subarctic' is commonly used for the transitional area, which lies between the tree-line and the dense boreal coniferous forest. In Finnish Lapland, where the tree-line is more of oroarctic nature (i.e. it is affected by both latitude and altitude, Kalliola 1973), researchers use the term 'subarctic' to cover the whole of Finnish Lapland. Therefore, in papers I-V the term 'subarctic lakes' is used to describe the study lakes although they are situated in a treeless area in more extreme, arctic-like environmental conditions.

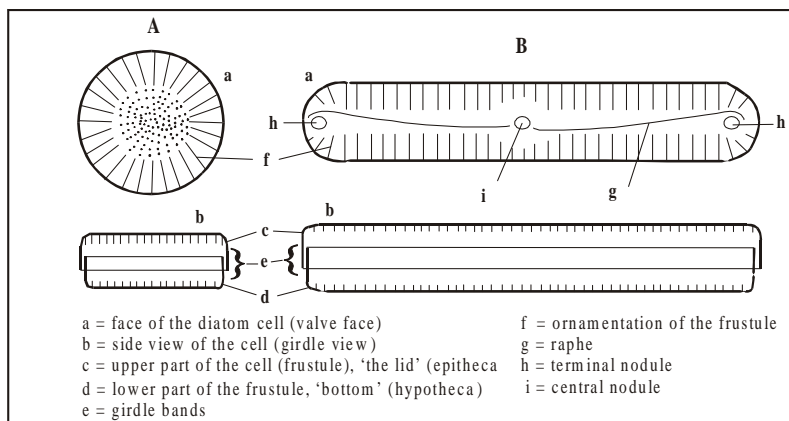


Figure 4. The structure of a diatom cell. Schematic representation of typical shapes of centric (A) and pennate (B) diatoms (modified after Tikkanen 1986).

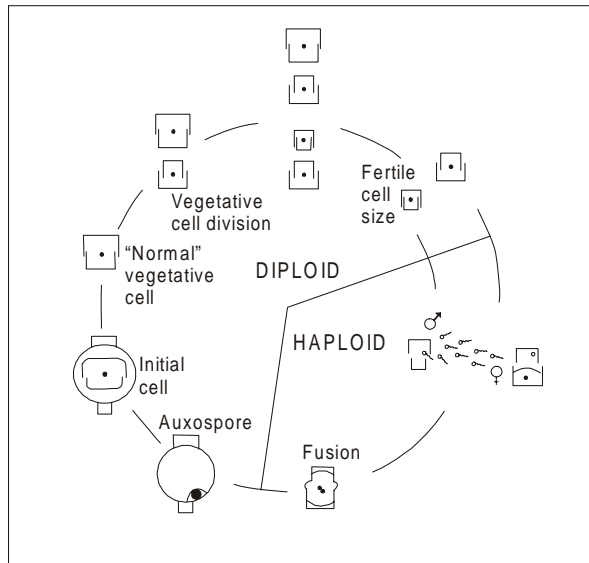


Figure 5. Life cycle of a centric diatom (modified after Hasle & Syvertsen 1997).

1.6. Diatoms, bioindicators of past environmental change

The main information source in this thesis comes from diatoms (*Bacillariophyceae*), which are microscopic siliceous unicellular algae, common everywhere if water and light are available for photosynthesis. There is no accurate estimate of the number of diatom species globally but often estimates of the order of 10^4 are given (Stoermer & Smol 1999). Most of the diatom species are cosmopolitan. They constitute a significant fraction (~25%) of Earth's biomass (Stoermer & Smol 1999) and therefore have an important role in primary production and food web dynamics in aquatic ecosystems.

The diatom cell (frustule) is composed of two separate valves (*epitheca* and *hypotheca*) and a number of girdle bands holding the valves together (Fig. 4). Identification of the diatoms is based on the shape and species-specific pores and ornamentations on the siliceous cell wall (valves). Fairly distinct, siliceous cell walls of diatoms are abundant and well preserved in the sediments (Battarbee 1986).

Diatoms reproduce vegetatively by binary fission, and two new individuals are formed within the parent cell frustule (Fig. 5). Each daughter cell received one parent valva as epitheca, and the cell division is terminated by the formation of a new hypotheca for each daughter cell. In favourable conditions vegetative cell division can occur as often as every 4–8 hours (Round *et al.* 1990). Gradually, due to successive division, cell size decreases. When the minimum cell size is reached (60–80 % of the maximum size) diatoms reproduce sexually to obtain favourable size by developing auxospores (Round *et al.* 1990). In auxospore formation, a large sphere surrounded by an organic membrane allows a new diatom frustule of maximum size to develop. The first cell formed inside the auxospore is called 'initial cell'. Below the size limit diatoms are unable to rejuvenate themselves and the tiniest diatoms continue to divide vegetatively until they die (Hasle & Syvertsen 1997). If environmental conditions are unfavourable for diatom growth, diatoms may produce resting spores.

Diatoms can be classified into different 'life-forms'; *planktonic* species float freely in the water column while *benthic* diatoms live near the bottom of a lake or are attached to the bottom substrate (Stevenson 1996). Benthic diatoms can be motile or non-motile and have a great morphological diversity with unicellular, colonial, and filamentous forms (Stevenson 1996). Non-motile adnate diatoms (e.g. *Achnanthes*, *Cocconeis*) grow firmly and flat on substrata and are well sheltered from strong currents and grazing. Adnate diatoms are usually the first to colonise the substrata after disturbance, followed by apically attached diatoms (e.g. *Synedra*). Slowly growing stalked (e.g. *Cymbella* and *Gomphonema*) and motile (e.g. some *Nitzschia* and *Aulacoseira* species) diatoms overgrow adnate and apically attached diatoms and form more complex communities by exploiting light and nutrients from adnate and apically attached diatoms (Lowe 1996). Furthermore, attached diatoms can be classified by the substrate on which they live. *Epiphytic* diatoms live on the surface of a plant or larger algae, *epilithic* diatoms are attached to stones and rocks, and *epipsammic* diatoms grow attached on small sand grains. *Epipelagic* diatoms grow freely on fine, inorganic or organic sediment. Some of the diatom species inhabit different habitats at different stages of their life cycles (i.e. *tychoplankton* species).

Like all the algae, abundance and productivity of the diatoms are controlled by many abiotic and biotic factors. The most important environmental factors for diatoms are water salinity, pH, nutrients, temperature, and zooplankton grazing (Battarbee 1986). Salinity and pH mainly determine the spatial distribution of diatom species (Battarbee 1986). Temperature also has multiple effects on diatom growth and distribution patterns (Patrick 1971, Round *et al.* 1990), while inorganic phosphorus, nitrogen and silica are the most important nutrients for growth (Reynolds 1984). On the other hand, diatoms can also affect the water quality, for example by causing water colour and odour problems

during massive diatom blooms in spring.

Abiotic factors are joined with biotic factors such as zooplankton grazing by e.g. rotifers, cladocerans and copepods, having distinct effects on diatom abundance and species composition because of the selective feeding of the predators (Reynolds 1984, Sommer 1991). The effect of grazing is usually greatest in the mid-summer in temperate lakes, when zooplankton productivity is at its highest (Wetzel 1983).

Diatoms are ecologically a diverse algal group and thanks to their short life cycles, changes in the environment are reflected rapidly in the diatom species composition. Therefore by establishing modern relationships between diatoms and environmental factors it is possible to infer past environmental conditions by following the changes in the fossil species composition. Ecological optima and tolerances of the diatom species have been quantified for several environmental parameters, including total phosphorus (Hall & Smol 1992, 1996, Anderson *et al.* 1993, Wunsam *et al.* 1995, Bennion 1994, 1995, Bennion *et al.* 1995, 1996, Lotter *et al.* 1998), pH (Stevenson *et al.* 1991, Birks *et al.* 1990, Dixit *et al.* 1993, Korsman & Birks 1996, Weckström *et al.* 1997a,b, Korhola *et al.* 1999, Cameron *et al.* 1999), dissolved inorganic carbon (DIC) and dissolved organic carbon (DOC) (Birks *et al.* 1990, Pienitz & Smol 1993, Pienitz *et al.* 1999, Fallu *et al.* 1999), epilimnetic water temperature (Pienitz *et al.* 1995, Weckström *et al.* 1997a), air temperature (Lotter *et al.* 1997, Korhola *et al.* 2000, Rosén *et al.* 2000), water colour (Seppä & Weckström 1999), and specific conductivity (Gregory-Eaves *et al.* 1999). The sensitivity of diatoms to track past environmental conditions have made them one of the most studied fossil organism groups in palaeolimnology (Douglas *et al.* 1994, Moser *et al.* 1996, Stoermer & Smol 1999).

1.7. Objectives of the study

The overall objective of this thesis was to obtain a temporal and spatial view of climate impacts on subarctic lakes, particularly on diatom communities, in NW-Finnish Lapland. The specific aims of the papers were:

- a) to understand limnology and ecosystem dynamics of poorly studied subarctic lakes;
- b) to examine the sedimentation rates and representation of diatom species in the fossil material;
- c) to study recent environmental history of subarctic lakes (the last 200 years);
- d) to examine which environmental factors are responsible for the observed changes in the diatom communities;
- e) to study the response of aquatic organisms to environmental change and evaluate underlying mechanisms.

2. Study area

2.1. The Kilpisjärvi region

Five subarctic lakes representing different limnological characteristics and environmental conditions were selected for the study. The study lakes are situated in NW Finnish Lapland (N 69°, E 21°), in the commune of Enontekiö, in the Kilpisjärvi region (Fig. 6). The research area lies close to the Norwegian and Swedish borders, only 50 km from the Arctic ocean and 450 km north of the Arctic Circle.

Climatically, the study area lies between the North Atlantic oceanic climate and the Eurasian continental climate. Mean annual temperature is -2.6°C , mean January temperature is -14.1°C and mean July temperature is 10.6°C (Fig. 7) (Järvinen 1987). Meteorological data from the automatic weather station of the main study

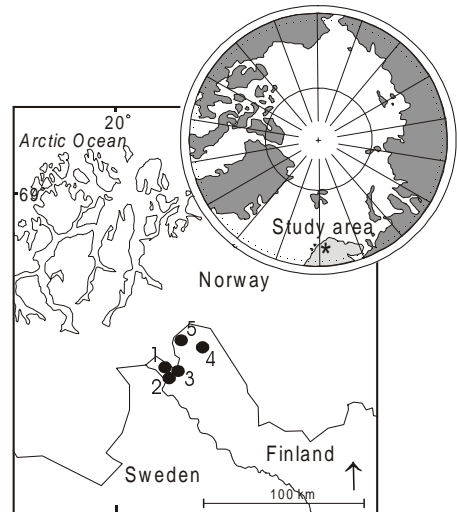


Figure 6. Location of the study sites in the NW Finnish Lapland. The study sites are indicated by solid dots (1, Saanajärvi; 2, Tsahkaljavri; 3, Masehjavri; 4, Toskaljärvi; and 5, Stuuramohkki).

site, Lake Saanajärvi, in 1996-1998 clearly shows the high latitude location; daily mean air temperatures varied from -22.6°C to $+18.0^{\circ}\text{C}$, and monthly temperatures between -11.0°C and $+11.4^{\circ}\text{C}$ (Sorvari *et al.*, in prep.). Daily mean air temperatures were below 0°C from October to May in 1996-1998. The length of the growing season is *ca.* 100 days in the Kilpisjärvi region (Järvinen 1987).

Kilpisjärvi lies in the rain-shadow of the Norwegian mountains. Therefore precipitation is low in this region (annual mean *ca.* 420 mm). Most of the rain falls in summer, the maximum precipitation being in July (60 mm). Heavy rainfall events (over 10 mm) are unusual, which is also demonstrated by the meteorological data from Lake Saanajärvi (Sorvari *et al.*, in prep.). Consequently, surface water runoff is minimal, except during the spring snow melt period when heavy floods can be common.

The special feature of the study area is the large annual variation in solar radiation. Between Nov 25 – Jan 18, the sun is below

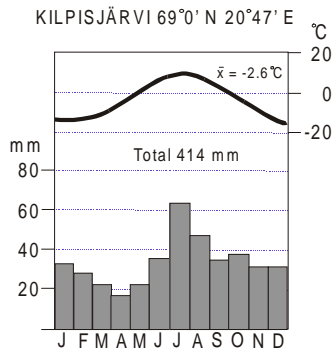


Figure 7. Long-term means of temperature and precipitation (1961-1990) for the Kilpisjärvi region (data adapted from the Finnish Meteorological Institute 1991).

the horizon, resulting in 55 days of darkness, which is called the polar night. In contrast, in the summer the sun does not set for 62 days between May 22 – Jul 22. In summer the total solar irradiance reaches its highest values, which match total irradiance levels in the equatorial region (Kirk 1983).

The bedrock of the research area consists of two different elements: Precambrian bedrock, which is typical for most of Finland, and Paleozoic Caledonian schist and gneiss (Hirvas 1991). Caledonian nappe, which is relatively young (400 million yr.) and belongs to the Scandinavian mountain range, is underlain by sedimentary rocks and dolomitic limestones. The relative difference in altitude is often more than 300-500 m, while the highest fells exceed 1 000 m above the sea level (a.s.l.). Due to the harsh climate, soils are poorly developed and catchment areas mainly consist of thin humus underlain by quarternary deposits, bare rock surfaces and boulder fields. The predominant soil-forming process in treeless areas is podzolisation of mineral soils (Kähkönen 1996).

Extreme climate conditions, the high altitude and the alkaline-rich bedrock greatly affects the vegetation of the research area. The Kilpisjärvi region has a rich diversity of various arctic and alpine plants. Most of the species are rare and some are protected (e.g.

Ranunculus glacialis, *Saxifraga oppositifolia*, *S. foliolosa*, *Cassiope tetragona*, *Silene wahlbergella*, *Veronica fruticans*). Vegetation in the region can be divided into different zones according to the altitude, exposure and nutrient conditions (Kyllönen & Laine 1980). Generally, field vegetation above the tree-line, in nutrient poor areas consists of low dwarf shrubs and lichens (e.g. *Betula nana*, *Empetrum nigrum*, *Loiseleuria procumbens*, *Vaccinium myrtillus*) and in more nutrient rich (alkaline) areas mosses, grasses and sedges are common. At the lower altitude (600 m to 950 m a.s.l.) vegetation is relatively continuous and rich in species, which is in contrast to higher altitudes (up to 1 200 m a.s.l.), where bare rocks, snow patches and few plants (e.g. *Cassiope tetragona* and *Ranunculus glacialis*) colonise the landscape.

In terms of atmospheric pollution, the research area is one of the most cleanest areas in Europe (Rühling 1992). This is mostly due to the remoteness of the area and the fact that the prevailing winds are from north (56%) and west (20 %) (Sorvari *et al.* in prep.), i.e. from less polluted areas of Greenland and the North Pole. There is no industrial or other extensive human activity in the vicinity of the study area. All the five study sites are remote from settlements and roads.

2.2. Study sites

The main study site, Lake Saanajärvi (Fig. 6, site 1), is situated in the treeless tundra at 679 m a.s.l. between two fells, Saana (1024 m a.s.l.) and Iso-Jeahkas (960 m a.s.l.). The northern slope of fell Saana, which faces the lake, is steep and consists mainly of bare rocks and boulder fields. Other parts of the catchment area are covered by meadow-type, subalpine vegetation. The catchment area is 461 ha and the area of the lake itself is 70 ha; the catchment:lake ratio is 6.6. Lake margins are steep, and there is a relatively large, even-bottomed deeper central area in the lake, which is 24 m deep. The shorelines are rocky

Table 1. Selected morphometric and hydrographic characteristics of the study lakes.

Parameter	Lake Saanajärvi	Lake Tsahkaljavri	Lake Masehjavri	Lake Toskaljärvi	Lake Stuoramohkki
Latitude (°N)	69°05'	69°01'	69°05'	69°19'	69°14'
Longitude (°E)	20°87'	20°55'	20°59'	21°27'	21°04'
Altitude (m a.l.s.)	679	559	687	704	1024
Area (ha)	70	113	17	100	18
Catchment area (ha)	461	3396	173	1433	98
Catchment/area (ratio)	6.6	30	10.2	14.3	5.4
Maximum depth (m)	24	18	11	22	27
Thermal structure	dimictic	dimictic	isothermal	dimictic	isothermal
Epilimnetic temp. (°C)*	9.8	12.5	12.6	10.6	5.4
pH (units)*	6.8	6.6	6.6	7.2	6.4
Conductivity ($\mu\text{S cm}^{-1}$)*	27.7	23.5	18.2	39.0	7.1
DOC (mg l^{-1})*	1.6	3.4	2.5	0.9	L 0.5
Colour (PT mg l^{-1})*	5.0	10.0	5.0	2.5	2.5
TP ($\mu\text{g l}^{-1}$)*	3.0	5.0	6.0	5.0	4.0
TN ($\mu\text{g l}^{-1}$)*	97	140	130	79	58
Ca (mg l^{-1})	3.4	3.0	1.5	4.2	0.6

* Measured in the end of July 1998, L = Less than detection limit

and macrophytes are absent from the lake littoral. The lake is ice-free between late June and mid-October. Lake Saanajärvi is a dimictic, ultra-oligotrophic clear-water lake. There is no cultivated land or summer cottages in the catchment area. Only occasional hiking tourists pass the lake.

Lake Tsahkaljavri is situated at a lower elevation than Lake Saanajärvi, at 559 m a.s.l. (Fig. 6, site 2). The lake surroundings are covered by mountain birch (*Betula pubescens* var. *tortuosa*) but most of the catchment area is above the tree-line. Lake Tsahkaljavri has the largest catchment area (3396 ha) and lake surface area (113 ha) of the five study lakes. The presence of mountain birch affects the water chemistry of the lake, DOC concentrations and colour values being slightly higher than in the other study sites. Lake Tsahkaljavri is a dimictic lake, with a maximum depth of 18 m.

Lake Masehjavri is a relatively shallow (maximum depth = 11.0 m), isothermal (unstratified) lake situated above the tree-line at an altitude of 687 m a.s.l (Fig. 6, site 3). The smooth slopes of the catchment area are covered by shrub-type subalpine vegetation. Special characteristics of the catchment area

are the presence of a small subalpine peatland in the inlet and an esker formation on the NW shoreline. Masehjavri is a nutrient poor clear-water lake, with low conductivity. Due to shallowness and clear water primary production is dominated by the microbenthic algae (Lindqvist 2001).

Lake Toskaljärvi is 100 ha large, oval-shaped lake situated at 704 m a.s.l. (Fig. 6, site 4). Lake Toskaljärvi is a dimictic lake with a maximum water depth of 22 m. A special feature of the catchment area is an underwater inlet, which has been formed in calcium-rich dolomite bedrock. Lake-water has relatively high conductivity (mean 50.6 $\mu\text{S cm}^{-1}$), pH (7.2 unit) and calcium concentration (Ca 4.2 mg l^{-1}) compared to the other study sites as well as lakes in Finnish Lapland in general (Blom *et al.* 2000, Korhola *et al.*, submitted). The lake is an oligotrophic, clear-water lake with low primary production (Chlorophyll a < 1 mg l^{-1}).

Lake Stuoramohkki is situated at an altitude of 1024 m (Fig. 6, site 5) and has the most harsh climate conditions of the study sites. Although Lake Stuoramohkki is relatively deep (maximum 27 m) it is isothermal or only weakly stratified during the short open-water

season. The maximum measured surface temperature is 8.9°C in the end of July. Lake Stuoramohkki is dilute, highly transparent clear-water lake, where the photosynthetic layer for the primary production extends to the bottom of the lake. In the mid-summer, when the benthic production is at its highest, the highest oxygen values can be measured from the bottom water of the lake. More details about the physico-chemical characteristics of the study sites can be found in Table 1.

3. Methods

All the materials and methods where the author was responsible for collection, analysing and/or data processing excluding dating methods, are presented below. Detailed references for the methods, including those followed by other authors in papers I-V, are listed in Table 3. (end of this section).

3.1. *Physical, chemical and biological parameters*

The study lakes were monitored for their physical and chemical characteristic in 1996-2000. At the main study site, Lake Saanajärvi, more detailed monitoring was carried out in order to obtain better understanding of the basic functions and ecosystem dynamics of a subarctic lake. Water samples from Lake Toskaljärvi and Lake Stuoramohkki have been collected more randomly due to the remoteness of these sites from the nearest roads and settlements. The number of sampling visits and the number of specific water chemistry analyses are listed in Table 2. All the water profile samples have been taken with a Limnos-type water sampler (volume 2 l) from the deepest part of the lake basins.

Oxygen, pH, temperature and conductivity standardised to +25°C were measured in the field using the hand-operating equipment of HANNA Instruments. The Secchi disk transparency was determined by using the white disk of the Limnos water sampler. Water profile samples were taken for analyses of alkalinity, Ca, Na, Mg, K, SO₄, Cl, NH₄-N, NO₂+NO₃-N, TN, PO₄-P, TP, SiO₂ and TOC (or DOC). Alkalinity for Lake Saanajärvi was determined in the laboratory of the Kilpisjärvi biological station within 24 hours from the sampling by one point titration method (SFS 3005 1981). Alkalinity for the other study sites was analysed in the Lapland Regional Environment Centre at Rovaniemi. Major ions and nutrients were first analysed (1996-1998) in the Laboratory of Physical Geography, University of Helsinki using standard methods of the National Board of Waters in Finland as well as MOLAR water chemistry protocols. During 1998-2000 analyses were conducted in the Lapland Regional Environment Centre using standard procedures (Table 3). Total organic carbon (TOC) and dissolved organic carbon (DOC) were measured from the frozen samples at the Lammi Biological Station using the high temperature combustion method described in Salonen (1979).

From all the sampling sites where chlorophyll-a was determined, 2-3 l of water was filtered through the GF/C or GF/F Whatman filters in the field or in the laboratory during winter time. The filters were immediately frozen for further laboratory analysis. At the Lammi Biological Station, chlorophyll-a was extracted in 90% acetone overnight at room temperature in the dark. After the extraction, samples were filtered and measured with a spectrophotometer. The chlorophyll-a concentrations were calculated after Jefferey & Humphrey (1975).

Table 2. Number of measurements and analyses performed during the limnological monitoring of the study lakes in 1996-2000.

	Lake Saanajärvi	Lake Tsahkaljavri	Lake Masehjavri	Lake Toskaljärvi	Lake Stuoramohkki	Total
Number of sampling visits	46 (Jun 1996-Sep 2000)	5 (May 1998-Apr 1999)	19 (May 1998-Sep 2000)	3 (Jul 1998-Sep 2000)	4 (Jul 1998-Sep 2000)	77 (Jun 1996-Sep 2000)
Sampling depth (m)	0, 1, 2, 4, 6, 8, 10, 12, 16, 20, 22	0, 1, 2, 5, 10, 15	0, 1, 3, 6, 9	0, 1, 6, 12, 16, 18	0, 1, 3, 6, 9, 12, 15, 18, 21, 24, 26	39
Temperature	401	25	68	9	11	514
pH	398	23	68	7	9	505
Conductivity	393	25	68	7	11	504
Oxygen	297	5	12	7	11	332
Alkalinity	203	5	5	2	2	217
Ca, Na, Mg, K	275	20	54	2	10	361
SO ₄ -S	263	25	55	2	10	355
Cl	265	20	54	2	10	351
NH ₄ -N	367	24	68	4	10	473
NO ₂ +NO ₃	358	25	68	3	10	464
TN	367	25	68	4	11	475
TP	362	25	68	4	11	470
PO ₄ -P	110	25	68	3	10	216
SiO ₂	238	25	4	1	10	278
TOC or DOC	80	2	2	2	2	88
Colour	2	2	2	2	2	10
Chl-a	277	1	53	2	2	335
Total	4656	302	785	63	142	5948

For studies of the recent diatom communities (II), different habitats from Lake Saanajärvi were sampled in 1996-1997. Two parallel cylindrical sediment traps were placed in the deepest point of the lake in July 1996 at a depth of 23 m, i.e. one meter above the sediment surface. The traps were emptied monthly during the open-water season in 1996 and 1997, and after the autumn overturn traps were left exposed for the ice-cover period. Seven samples were investigated during the study period. In addition to diatoms, chrysophyte cysts were also determined from the trap material.

In addition to the sediment traps, 12 diatom samples were collected in 1997 from Lake Saanajärvi along the transect extending from the lake shore to the deepest point of the lake. The first 8 samples were removed from stones

by toothbrush and distilled water, and the rest of the samples (4) were taken from the sediment surface. Sampling was performed by diving and by using a 5 cm diameter Glew gravity corer (Glew 1991).

After collection, all the diatom samples were preserved with acid Lugol's Iodine. Transect samples were concentrated using centrifugation from 200 ml to approx. 10 ml and trap samples from 500-1000 ml to 10 ml in the laboratory. Lugol's Iodine was then removed from the samples by 5-step centrifugation dilution. After centrifugation, samples were heated at 90°C in a solution of H₂O₂, until all organic material was oxidised. A few drops of 37% HCl were added to remove the remaining H₂O₂ and carbonates. The resulting diatom suspension was washed by 5-step centrifugation procedure. Slides

were mounted on an objective glass using Naphrax as the mounting medium. The weakness of the performed procedure was that living diatom cells could not be distinguished in detail from the sedimented dead diatom cells from other habitats. Therefore only the most dominant diatom taxa in each habitat was discussed in more details.

Industrially produced microspheres (Battarbee 1982) were added into trap samples to estimate the total diatom and cyst concentrations. Diatom and chrysophyte cyst concentrations are expressed as number of sedimented valves $\text{day}^{-1} \text{ l}^{-2}$ in order to enable comparison. The diatom to chrysophyte cyst ratio (D:C) was calculated from formula $D:C = (\text{number of diatom frustules} / \text{number of chrysophyte cysts} + \text{number of diatom frustules}) \times 100$ (Smol 1985) in order to compare roughly the seasonal variability of these two algal groups. For more detailed description of methods see paper II.

3.2. Sediment studies

Numerous surface-sediment cores were retrieved from each lake in order to obtain a sufficient amount of sediment material for diatom and other palaeolimnological analyses. Firstly, from Lake Saanajärvi, a 30 cm long surface sediment core was collected with a Limnos type gravity corer in July 1995 (III). The core was immediately sectioned in the field into 1 cm sub-samples. Secondly, in May 1996, a 20 cm long surface sediment core was taken from Lake Saanajärvi with a 5 cm diameter Glew gravity corer (Glew 1991) for detailed diatom and chrysophyte cyst analyses. Sediment was extruded and sliced at 2 mm intervals in the field and stored in small plastic bags (II, IV, V). Several parallel cores were taken for supplementary sediment studies. Single sediment cores were taken from Lake Tshakaljavri was taken in May 1997, Lake Masehjavri in May 1998, and from the Lake Toskaljärvi in July 1998; in

each case the Glew miniature gravity corer was used. Cores from Lake Tshakaljavri, Lake Masehjavri and Lake Toskaljärvi were sub-sampled at 0.5 cm intervals. Sediment core from the Lake Stuoramohkki was taken in July 1999 and this was extruded and sliced into 2 mm sub-samples. The rationale for sampling the cores at different intervals was based on the rough a priori estimation of the sedimentation rates (catchment characteristics, altitude etc.). All the cores taken in May 1996-1998 were sampled from the deepest part of the lake basins from the ice, while the cores collected in July 1998-1999 were taken from an inflatable boat in calm weather conditions.

The sediment was divided into two fractions. Most of the wet sediment was placed in plastic tubes for diatom analysis and the rest of the sediment was placed in 1.5 ml Eppendorf tubes and dried immediately for dry weight (DW) and loss-on-ignition (LOI) determinations (III-V). Water content, DW and LOI were analysed according to the methods described by Dean (1974). Sediment was dried overnight at 105°C. Organic content of the sediment was defined from the ignition loss after heating the samples at 550°C for 2 hours (Heiri *et al.* 2001). Because of the small sample size, quartz crucibles were used instead of porcelain crucibles in order to improve accuracy (Olander *et al.* 1999, Heiri *et al.* 2001).

The parallel core from each site was analysed for ^{210}Pb , ^{226}Ra , and ^{137}Cs by direct gamma assay in the Liverpool University Environmental Radiometric Research Centre (Table 3). The parallel cores were then correlated with the dated master core by the variations in their dry weight and loss-on-ignition profiles using the sequence slotting method (Thompson & Clark 1993). The preliminary diatom record from Lake Saanajärvi had no exact dating (paper III). Nevertheless, the studied core was correlated approximately to the dated diatom core taken from the lake in 1996, using LOI variation and specific marker horizons in the diatom

stratigraphy, particularly on the first appearances of *Cyclotella glomerata* and *C. comensis*.

Approximately 0.2 g of wet sediment was used for qualitative diatom and chrysophyte cyst analyses (III-V) and a known amount of wet sediment (*ca.* 0.1 g) was used for quantitative analyses (II). All the sediment samples for diatom and chrysophyte cyst analyses were treated with H₂O₂ for 2-4 hours on a hotplate and then a few drops of 37 % HCl were added to the samples. Residuals of the acids were washed away by repeated centrifugation. A known amount of microspheres was added to the quantitative samples. Cleaned diatoms, chrysophyte cysts and microspheres were mounted on microscope slides with Naphrax mounting medium. Diatoms were counted along randomly selected transects using Olympus BX40 microscope with x1000 final magnification, with phase contrast and immersion oil. A minimum of 500 diatom valves was counted per sample and the total number of chrysophyte cysts was enumerated simultaneously with diatom counts. Quantitative diatom concentrations were calculated from the formula: $c = (xav)/(bw)$, where c=concentration, x=counted diatoms, a=added amount of microspheres, v=1, b=counted microspheres and w = sample weight.

The main diatom flora used for diatom identification were Krammer & Lange-Bertalot (1986-1991), Mölder & Tynni (1967-1973), Tynni (1975-1980), Camburn & Kingston (1986), Håkansson (1990) together with special taxonomic papers such as the notes of the Arctic-Antarctic Diatom Workshop held in Quebec, Canada (Laing 1997) and MOLAR identification guide (1997). Much effort was put forward in order to obtain good taxonomic quality in the diatom studies. Taxonomic harmonisation was achieved through several workshops and with an international diatom quality control exercise held in 1996. In addition, photos of the most dominant diatom species in Lake

Saanajärvi have been published in paper III. Nomenclature mainly followed Hartley (1986). Results of the diatoms were processed and presented graphically using the computer program TILIA (Grimm 1990).

3.3. Data-analyses

Constrained cluster analysis (CONISS) was performed for the full percentage diatom data in paper III to facilitate the stratigraphical interpretation of TILIA diatom diagram. In addition, optimal partitioning with untransformed species percentage data was used in paper V to identify statistically the periods of the time with the most significant shifts in the diatom stratigraphical data of the study lakes. The computer program ZONE (Lotter & Juggins 1991) was used to perform the constrained cluster analysis and the optimal partitioning. The broken-stick model and the associated approach described by Bennett (1996) were used to identify the number of statistically significant partitions and hence the stratigraphical levels where the most distinct floristic changes occur in the diatom core data (V).

The diatom species data was square-root transformed for multivariate analyses in order to stabilise the variance and to optimise the signal-to-noise-ratio in the data set (Prentice 1980). Water chemistry parameters were tested for skewness and, when needed, transformed closest to the Gaussian distribution (I). Diatom data files (II-V) were transformed with the computer program TRAN (Lotter & Juggins 1991) from TILIA format to Condensed Cornell format, which was used in the ordination analysis in the CANOCO program (ter Braak 1988, 1990).

An indirect ordination technique of detrended correspondence analysis (DCA) (Hill & Gauch 1980) was used first to determine whether linear- or unimodal-based numerical techniques were more appropriate for the taxon data (ter Braak & Prentice 1988). If this analysis yielded a gradient length longer than 2.0 standard deviation (S.D.) units for the first

DCA axis, the species data was interpreted as behaving in unimodal manner in response to the underlying environmental gradient. If the gradient length is less than 2.0, the samples respond linearly along the major underlying gradient. Principal component analysis (PCA) was used for linear data to systematise and interpret the major patterns of variation in the chemical and physical (I), and biological data (IV, V). In paper II, diatom data produced a mathematical artefact, an 'arch effect' in the ordination diagram (Hill & Gauch 1980) when performing correspondence analysis (CA). DCA was used instead with detrending by segments, rescaling axis and downweighting the rare species. The results of PCA and DCA are expressed graphically in the form of ordination bi-plots using the first two ordination axes. The PCA, CA and DCA were performed using the FORTRAN program CANOCO, version 3.10 (ter Braak, 1988, 1990).

Diatom inferred lake-water pH was reconstructed in order to examine whether the lakes have been exposed to acidification in the last 200 years. Past pH was reconstructed using the unimodal-based techniques of weighted averaging (WA) and weighted averaging partial least squares regression (WA-PLS) (ter Braak and Juggins 1993). Three different training-sets of surface-sediment diatom assemblages with associated water chemistry data were available during the preparation of the manuscripts and were best suited to the available data (Weckström *et al.* 1997b, Cameron *et al.* 1999, Weckström & Korhola, unpublished data). In paper III the calibration data set comprises of 37 lakes from northern Finland (Weckström *et al.*, 1997b). The predictive ability of the WA transfer function was strong for pH after cross-validation by leave-one-out jackknifing ($r^2 = 0.91$, $r^2_{\text{jack}} = 0.72$, $\text{RMSE}_{\text{jack}} = 0.39$ pH units). The AL:PE training-set of 118 lakes from European mountain regions (Cameron *et al.* 1999) were used in paper IV to reconstruct lake-water pH for Lake Saanajärvi. The predictive power of the training set, as

assessed by statistical cross-validation, is 0.33 pH units for the 3-component WA-PLS model. The AL:PE data set has been screened to include only appropriate arctic and alpine lakes. For all study sites in paper V, an expanded Weckström *et al.* 1997b data-set consisting of 64 lakes was used (Weckström & Korhola 2001). The predictive power of the diatom – pH prediction model is, after cross-validation, 0.36 pH units ($r^2_{\text{jack}} = 0.69$) and the training set is most appropriate for the lakes studied here because it is a regional data set. In all the reconstructions, diatom taxonomy was harmonised with the training-set material. For more detailed descriptions of the data sets, see III-V. All the pH calibrations were performed by the computer program CALIBRATE (Juggins & ter Braak, unpublished program).

Although available, a direct diatom-temperature model by Weckström *et al.* (1997b) was not used in the present-day study, because this local diatom-temperature model was not considered appropriate for the present data. All the study sites are cold habitats and represent the uttermost coldest end of the temperature gradient in the modern calibration set data of Weckström *et al.* (1997). Moreover, the WA-PLS regression used to create the diatom-temperature model is based on inverse calibration, for which reason there is always a systematic discrepancy, or bias, in the model estimates – i.e. the model have a tendency to underestimate the values in the higher and overestimate the values in the lower end of the environmental gradient (the so-called "edge effect") (Birks 1998, Robertson *et al.* 1999). Therefore the model simply has a limited capacity to extrapolate over the extreme situations as would be the case when applying it to the data used in the study. In contrast, the available modern calibration data set by Weckström *et al.* (1997) suites well for pH reconstruction because study sites are not extreme in respect to pH but are lying in the middle of the pH range in the modern data set.

Table 3. Analysis and references of the methods used in papers I-V.

Parameter	Analytical method	References
Oxygen	<i>in situ</i> measurement	HANNA Instruments
pH	<i>in situ</i> measurement	HANNA Instruments
Conductivity	<i>in situ</i> measurement	HANNA Instruments
Alkalinity	Potentiometric titration	SFS 3005
NO ₂ +NO ₃ -N	Spectrophotometric determination	SFS 3030
NH ₄ -N	Spectrophotometric determination	SFS 3032
TN	Spectrophotometric determination	Valderrama (1981), Eaton (1995)
PO ₄ -P	Spectrophotometric determination	SFS 3025
TP	Spectrophotometric determination	Valderrama (1981), SFS 3025
Ca, Mg, Na, K	Flame atomic absorption spectrometric method	Eaton (1995)
SO ₄ -S	Turbidimetric method & spectrophotometric determination	SFS 5738
Cl	Colorimetric method & potentiometric titration	Grimshaw <i>et al.</i> (1989)
SiO ₂	Spectrophotometric determination	
TOC	High temperature combustion of carbon	Salonen (1979)
Colour		SFS-EN ISO 7887
Chl-a	Fluorometric method	
Phytoplankton	Chamber settlement method & inverted microscope identification, counting units: cells, colonies and trichomes with a length of 100 µm	Utermöhl (1958)
Zooplankton	Chamber settlement method & binocular and inverted microscope identification	Utermöhl (1958)
Transect diatoms	25 % hydrogen and 37% HCl treatment	Battarbee (1986)
Trap diatoms	25 % hydrogen and 37% HCl treatment	Battarbee (1986)
Sediment coring	Limnos sediment & Glew gravity corer	Glew 1991
Dry weight	Over night oven dry at 105°C	Dean (1974), Heiri <i>et al.</i> (2001)
Organic content	Loss-on-ignition at 550°C	Dean (1974), Heiri <i>et al.</i> (2001)
Core correlation	Sequence slotting method	Thompson & Clark (1993)
²¹⁰ Pb, ²²⁶ Ra & ¹³⁷ Cs	Direct gamma assay, Ortec GWL series well-type coaxial low background intrinsic germanium detectors	Appleby <i>et al.</i> (1986, 1992).
SCP	Nitric acid, HF and HCl treatment	Rose (1994)
Sediment C, N, S	NCS elemental analyser determination	
Mineral magnetics	Vibrating sample magnetometer, pulse magnetisers & spinner magnetometer methods	Thompson & Oldfield (1986), Dearing <i>et al.</i> (1998), Walden <i>et al.</i> (1999).
Fossil pigments	Spectrophotometric & HPLC chromatographic determination	Guilizzoni <i>et al.</i> (1983), Züllig (1982)
Fossil diatoms	25 % hydrogen and 37% HCl treatment	Battarbee (1986)
Cladocera remains	10 % Kaliumhydroxide treatment	Korhola & Rautio (in press)
Climate variables	Based on ice-break date & tree-ring proxies, local, regional and European-wide meteorological data, least-squares regression, cross-validation, low-pass filter & LOWESS smoothers	Thompson & Augusti-Panareda (in press), Grytnes & Birks (in press), Geisser (1975), Bloomfield (1976), Cleveland & Devlin (1988)
Correlations for PCAs and temperature	Pearson correlation coefficients	

In paper V, changes in diatom diversity were studied from the core data using the N^2 index from Hill's family of diversity indices (Hill 1973). The diatom species diversity was estimated from the constant sample counts; exactly 500 diatom valves were counted from selected transects across microscope slides.

Hill's N^2 index determines the effective occurrence of species in a sample and is therefore sensitive to the changes in abundance of common species (Hill 1979). Moreover, it is well suited for the stratigraphical species data (Hill 1973). Species diversity analyses were implemented using the computer program CALIBRATE (Juggins & ter Braak, unpublished program).

Additionally, the squared Chi-square distance method (Flower *et al.* 1997) was used to determine the degree of the similarity of diatom assemblages in different habitats in paper II. The method uses weighted diatom proportions to analyse the difference between the diatom samples (Overpeck *et al.* 1985). The calculated values of squared Chi-square distance vary from zero to two, with zero indicating an identical assemblage. The formula for the distance measure is:

$$D_{ij}^2 = \sum_{k=1}^m \left[\frac{(Y_{ik} - Y_{jk})^2}{(Y_{ik} + Y_{jk})} \right]$$

Where Y_{ik} is the proportion of diatom taxon k in samples I , D_{ij} is the Chi-squared distance between sample i and j . Deep-water sediment samples were removed from the analysis because they originate from the same accumulation zone as the sediment core samples.

4. Results and discussion

4.1. Limnological characteristics of subarctic lakes

The northern landscape is characterised by numerous water bodies, yet these ecosystems have been poorly studied around the circumpolar region. Typically, high latitude lakes are small, shallow, and highly exposed to the wind (Hobbie 1973, Duff *et al.* 1999). Furthermore, more northerly lakes above the tree-line have special physical, chemical and biological characteristics due to the extreme climate conditions and catchment characteristics (Kalff & Welch 1974, Pienitz *et al.* 1997, Blom *et al.* 2000, Korhola *et al.*, submitted). In this chapter some of these characteristics are discussed in more detail using the study lakes and monitoring data as examples.

The temperature and thermal structure of lakes depend on their location, altitude, landscape morphometry, mean lake-depth, and the lake surface volume ratio (Hutchinson 1957). Generally, three different thermal structures can be found in high latitude lakes: 1) dimictic lakes, with two mixing periods, 2) cold monomictic lakes with one mixing at temperature of 4°C in the open-water season (Wetzel 1983) and 3) isothermal lakes, with one mixing period or with brief, weak stratification during the open-water season (Fig. 8). In isothermal lakes the temperature may rise up to 10 – 15°C in the whole water column (Brodersen & Anderson 2000, Lindqvist 2001) creating unique thermal conditions for benthic flora and fauna.

Of the five lakes studied Lake Saanajärvi, Lake Tsahkaljavri and Lake Toskaljärvi are dimictic (V), and it seems that the inter-annual variability of their thermal structure is insignificant under present climate conditions. The monitoring data from Lake Saanajärvi show almost an identical pattern of the thermal structure in years 1996–1998 (I).

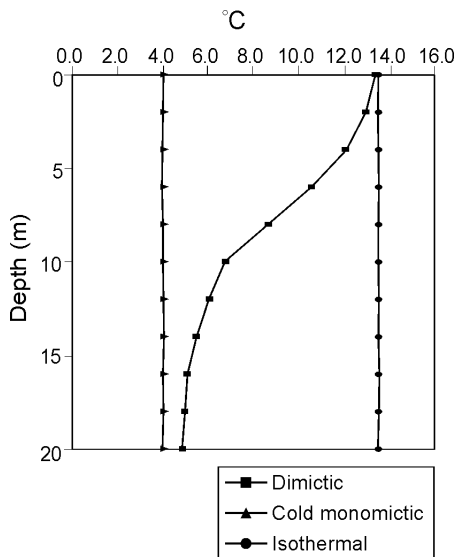


Figure 8. Schematic representation of different thermal structures found in high latitude lakes.

Lake Saanajärvi was ice-free for 126 days in 1996, and for 111 days in 1997. Summer stratification lasted 41 (1996) and 55 days (1997), while autumnal overturns were almost similar in length - 52 and 47 days, respectively (I). Spring overturn was 34 days in 1996 due to the early ice break-up but lasted only 9 days in 1997 when the ice break-up was later than normally observed. The difference in the length of the spring overturn was the only distinguishing factor in thermal pattern between the monitoring years. In all study lakes, maximum surface water temperatures were reached in the end of July or the beginning of August, maximum temperatures ranging from +8.9°C (Lake Stuoramohkki) to +15.4°C (Lake Saanajärvi and Lake Masehjavri). In general, surface water temperatures tended to react with a time lag of about 15 d to air temperature rise. A time lag between air and water temperatures were detected in the case of Lake Saanajärvi (Sorvari *et al.* in prep.). Because of this time lag, the epilimnion tends to be colder than the overlying air in June and July, but warmer than air in August and September. In the hypolimnion, temperature stayed below +5 - +7°C in the studied dimictic lakes, while the

hypolimnion temperature seemed to be positively related to the length of the spring overturn in Lake Saanajärvi (I). Lake Masehjavri and Lake Stuoramohkki are isothermal lakes, and in general, temperatures in the hypolimnion are clearly higher in these lakes. For example, in Lake Masehjavri, hypolimnion temperature varied from +8 to +13.5°C in July-August 1998 (Lindqvist 2001). The study lakes begin to freeze in mid-October and the ice thickness increases linearly towards the spring, reaching a maximum thickness of (1 m by May. The study lakes are ice-free for 3-4 months.

Subarctic lakes are dilute, clear water lakes with low within-lake productivity in part due to the poorly developed vegetation and soils in the catchment area (Pienitz *et al.* 1997, Weckström *et al.* 1997b, Rühland & Smol 1998, Korhola *et al.* 1999, Duff *et al.* 1999). In the study lakes, DOC concentration ranged from the detection limit of 0.5 mg l⁻¹ (Lake Stuoramohkki) to 3.4 mg l⁻¹ (Lake Tsahkaljärvi) (V). These lakes are among the most DOC-poor lakes in Finnish Lapland (Korhola *et al.* 1999, Rautio & Korhola, submitted). In Lake Saanajärvi, TOC values were steadily near or under the lower detection limit (1 mg l⁻¹) throughout the monitoring period. They also indicate minor variation in TOC concentrations during the open-water season (I). Water colour of the lake varied from 2.5 PT mg l⁻¹ (Lake Toskaljärvi, Lake Stuoramohkki) to 10 PT mg l⁻¹ in Lake Tsahkaljärvi (V). Generally, in lakes in Finnish Lapland the colour values range from 2.5 PT mg l⁻¹ to 80 PT mg l⁻¹, while in Finnish boreal lakes colour values are much higher (median 120 PT mg l⁻¹) (Kortelainen 1999). In dilute, clear water lakes, the photosynthetic layer can be defined as 2-3 times greater than the Secchi depth due to the low dissolved material and pelagic production (Tilzer & Schwarz 1976). This means that the photosynthetic layer extends to the bottom of the study lakes even in their deepest parts of the basins. In Lake Saanajärvi, the highest Secchi values were observed in spring during mixing period,

while the lowest values were during the autumnal production maximum indicating that the lake transparency is determined largely by biological production (I).

All the study lakes have circumneutral waters, their mid-summer pH being 6.6 – 7.2. The mean pH was 7.1 in Lake Saanajärvi in 1996–1998. The two years monitoring on Lake Saanajärvi and less intensive monitoring at the other study lakes revealed that the ion concentrations of the lakes are relatively stable throughout the year. The only exception is in springtime when acid but nutrient-containing melt water drain into the lakes (Lindqvist 2001, Catalan *et al.* in press, I, II). At that time, pH values drop suddenly below 6.0. A sulphate maximum occurred during the snow melt period (I). Fortunately, the lakes are situated in an alkaline bedrock area, and they therefore have a good buffering capacity against acid melt waters. Moreover, the acid melt-water pulse is extremely short in duration (less than 2 weeks). The mean alkalinity in Lake Saanajärvi was 161.4 μeq^{-1} during the monitoring period. Palaeolimnological studies from eastern Lapland show that the acid spring pulse has had no detectable effects on lake biology although the melt waters in the area are even more acid because of the vicinity of the smelter industry in the Kola Peninsula, Russia (Korhola *et al.* 1999).

All the study lakes are oxygen saturated during the open-water season but during the long winter, oxygen depletion gradually occurs in the bottom of the lakes due to respiration and loss of oxygen to the sediments. During times of the oxygen depletion, ions are released from the sediment surface, which can be seen by twofold or greater increases in the hypolimnetic conductivity and the concentrations of base cations (I, Sorvari *et al.*, in prep.). Generally, conductivity and base cation concentration are extremely low in subarctic lakes (Blom *et al.* 2000, Korhola *et al.*, submitted). For example, conductivity values ranged from 7.1 (Lake Stuoramohkki) to 39.0 $\mu\text{S cm}^{-1}$ (Lake

Toskaljärvi) in the study lakes, while values in Lake Saanajärvi varied from spring surface-water minimum of 8.5 $\mu\text{S cm}^{-1}$ to a spring deep-water maximum of 45.1 $\mu\text{S cm}^{-1}$ (mean 27.6 $\mu\text{S cm}^{-1}$) (I).

In a treeless area, the nutrient status of the lakes is usually poor and most of the lakes are oligotrophic (TP < 10 $\mu\text{g l}^{-1}$) or even ultra-oligotrophic (TP < 5 $\mu\text{g l}^{-1}$) (Rautio *et al.*, unpublished data). This is also the case in these study lakes. The lowest nutrient values were observed in Lake Stuoramohkki and the highest values in Lake Masehjavri. Total phosphorus values varied in the studied lakes from the lower detection limit (2 $\mu\text{g l}^{-1}$) to 13 $\mu\text{g l}^{-1}$, and PO₄-P was under its detection limit of 2 $\mu\text{g l}^{-1}$ in all study sites during the whole monitoring period. Nitrate (NO₃-N) concentration had a median of 22 (g l⁻¹ and ammonium (NH₄-N) a median of 6.5 (g l⁻¹. The main sources of inorganic nutrients into the lakes are from the melting snow that has accumulated nutrients during the long winter and surface runoff from the catchment area. Lake Saanajärvi featured a clear seasonal variability in NO₃-N with values from mid-summer 0 to the spring maximum of 383.5 $\mu\text{g l}^{-1}$. Ammonium (NH₄-N) displayed a range from 0 to 68.9 $\mu\text{g l}^{-1}$. It has been demonstrated that lakes with low nitrate values reveal a higher variability in nutrient concentrations than lakes with higher nitrate concentrations, suggesting that in low-nitrate-lakes nitrogen and phosphorus may alternate as the limiting nutrient in the course of the year (Catalan *et al.*, in press). In the case of Lake Saanajärvi, it seems that phosphorus is the limiting nutrient for primary production, with only a short exchange from phosphorus limitation to nitrogen limitation during the spring (I). Because of the nutrient poor nature, the study lakes have extremely low productivity (Chl-a 0.5 – 2.0 $\mu\text{g l}^{-1}$). During the period of most intensive plankton production in autumn the water column may lack NH₄-N and NO₂+NO₃ together with PO₄-P completely (I, II). In Lake Saanajärvi, the production maximum occurred during autumn at mixing. This is reverse of what is observed

in most temperate lakes where the production maximum occurs during the spring overturn (Wetzel 1983). However, in shallow isothermal Lake Masehjavri, the production maximum occurred after the ice break-up in 6 m water depth in 1998 (Lindqvist 2001).

The growing season is short due to the long polar night and harsh climate. The food web structure in subarctic lakes is simple, especially considering the relatively low productivity per unit area of subarctic lakes (Welch 1991). High latitude lakes have normally four well-defined trophic levels. Phytoplankton and benthic algae are the most important groups responsible for primary production (Welch 1991). The shallowness and clarity of the lake water allow microbenthic flora to constitute for most of the primary production which can be up to 80% of production in shallow lakes and ponds (Niemi 1996). Macrophytes are generally absent from the littoral area. Zooplankton (mainly copepod and cladoceran zooplankton), benthic larvae (e.g. chironomid larvae) and benthic crustaceans are the most abundant grazers (Welch 1991, II). Arctic char (*Salvelinus alpinus*) and lake trout (*Salmo trutta m. lacustris*) are the most common fish in subarctic lakes (I, II). Due to the low productivity a few arctic char or lake trout may become cannibals, and thus creating the fourth trophic level. Nutrients seem to have a relatively strong controlling effect for primary production in high latitude lakes (Jeppesen *et al.* 2000) and for this reason changes in fish populations do not necessarily have a straightforward cascading effect for primary production (Kling *et al.* 1992, Jeppesen *et al.* 2000) as is usually the case in oligotrophic lakes (Brönmark & Hansson 1998). However, the structure and the function of the food webs have to be studied more carefully in the study lakes in the future in order to better understand the effects of the changing fish populations on the overall ecosystems. The simple food web structure and the fact that the most of the species live at the edge of their distributional ranges, render subarctic lake ecosystems particularly vulnerable to

environmental changes (Pienitz *et al.* 1997, Rouse *et al.* 1997, Blom *et al.* 2000, Weckström & Korhola 2001, Korhola *et al.*, submitted).

4.2. Seasonal variability of planktonic diatoms

Planktonic diatoms, like all phytoplankton, exhibit clear seasonal variability, which is affected by several physical, chemical and biological factors (Reynolds 1984, Sommer 1986). In temperate lakes, diatoms generally have a maximum in spring when nutrient-rich and turbulent water masses favour plankton growth (Reynolds 1984). Seasonal variability of phytoplankton, particular focus on diatoms and total chrysophyte cyst concentrations, were studied in Lake Saanajärvi during the open-water seasons 1996 and 1997 (II). Phytoplankton biomass and densities were found to be low in Lake Saanajärvi, varying from 5700 to 220 000 counting units 100 ml^{-1} (Forsström 2000, II). In contrast to temperate lakes, the maximum biomass in both monitoring years occurred during the autumn overturn with chrysophytes as the most abundant group (Forsström 2000, II). Diatoms were the second most abundant algal group, constituting up to 62 % of the total phytoplankton density (Forsström 2000, II). In general, diatoms are, compared to other algae groups, cold water tolerant and therefore they are successful in early spring, even under ice, if sufficient amount of light penetrates through the ice-cover (Reynolds 1984, DeNicola 1996). However, late summer or autumnal phytoplankton maxima are relatively common in high altitude and high latitude lakes (e.g. Pechlaner 1971, Kerekes 1973, Hinder *et al.* 1999, Medina-Sánchez *et al.* 1999, Lotter & Bigler 2000, Catalan *et al.* in press, II). It is unclear why phytoplankton, and especially diatoms, do not have a vernal maximum in these lakes, when environmental conditions should be ideal for blooming (e.g. maximum nutrient concentrations, turbulent water, low grazing pressure). It simply seems

that the lakes with longer ice-free periods tend to develop two production maxima and lakes with a short ice free period exhibit only a single production peak from late August to October (Catalan *et al.* in press).

In temperate lakes, *Asterionella* species are normally the first to peak in spring, followed by *Cyclotella*, *Fragilaria* and *Tabellaria* spp. in the spring maximum (Wetzel 1983). In addition, *Aulacoseira* species are common in the water column in early spring due to their low light and high water turbulence requirements (Reynolds 1984, Kilman *et al.* 1996). Turbulent conditions are important in particular for *Aulacoseira* because of its rapid sinking rate resulting from the high silica content (Round *et al.* 1990). In Lake Saanajärvi, small *Cyclotella* species, such as *C. comensis* Grunow in Van Heurck, *C. rossii* Håkansson, *C. glomerata* Bachmann, along with *Thalassiosira pseudonana* (Hustedt) Hasle & Heimdal and *Aulacoseira subarctica* (O. Müller) Haworth were the most dominant diatoms found in the water column (II). *Cyclotella* spp. and *Thalassiosira pseudonana* had their maximum bloom during the autumn overturn when the thermal stratification broke down and available nutrients were released from the hypolimnion into the water column (cf. Elo *et al.* 1998, I, II). At the same time also the grazing pressure of *Daphnia longispina* decreased (II). *Aulacoseira subarctica* was the most abundant planktonic diatom in the water column in the early summer 1997.

Although diatom taxa were present in high numbers in the water column of Lake Saanajärvi in 1996, they were almost absent during the open-water period in the following year. In 1997, chrysophyte species dominated the water column, composing over 90 % of the total phytoplankton density (Forsström 2000, II). Total chrysophyte cyst concentrations were also highest in July 1997 in the trap material, supporting the observations from the water column studies. Such inter-annual variability among the different planktonic components is a common

feature in arctic lakes. Similar shifts from chrysophytes to diatoms and *vice versa* has been noted in the monitoring records of Arctic Char Lake and in Meretta Lake (Canada) in 1969-1971 (Kalff *et al.* 1975). The inter-annual variability is most probably due to competition from limited nutrients between the various algal groups. Natural phosphorus concentrations in the high latitude lakes are low and phosphorus is commonly the limiting factor for algal growth (Catalan *et al.* in press). Most of the bio-available phosphorus ($\text{PO}_4\text{-P}$) is continuously taken up by the organisms and is therefore difficult even to measure. In contrast to phosphorus, nitrogen concentrations are relatively high in high latitude lakes (Catalan *et al.* in press). From the sources of nitrogen, diatoms utilise the ammonium ($\text{NH}_4\text{-N}$) first and then nitrate ($\text{NO}_3\text{-N}$) compounds (Wetzel 1983). Generally, diatoms are good competitors for phosphorus, but are strongly dependent on silica (Reynolds 1984, Sommer 1991). In northern waters, concentrations of silica are relatively stable over time. Only heavy diatom blooms can periodically reduce the silica concentrations and affect the production of diatoms (Schelske 1999). The critical limit of silica for diatom growth is not straightforward to define (Reynolds 1984), but 0.5 mg l^{-1} of SiO_2 has been considered to form a threshold value below which the growth is limited (Sas 1989). In Lake Saanajärvi, phosphorus and nitrogen concentrations were relatively similar during both monitoring years. However, mean silica concentrations were slightly lower during the autumn overturn in 1997 than in 1996 (0.47 mg l^{-1} and 0.59 mg l^{-1} , respectively). Thus, lower silica concentration resulted from the shorter spring overturn might have at least partly caused the shift in phytoplankton compositions from diatoms to almost sole dominance of chrysophytes in 1997.

An interesting feature of the sediment trap data was the very low accumulation rate of *Cyclotella glomerata* in Lake Saanajärvi throughout the study period (II). However, evidence from the sediment studies (II-V)

show that *C. glomerata* is one of the most abundant diatom taxa in this lake (21.3% abundance in uppermost sediment sample) or at least it has been abundant until the recent times. The low accumulation rate in the trap is probably a result of resuspension of diatoms from blooms earlier in the year, and therefore *C. glomerata* did not necessarily inhabit the water column during the study period. Unfortunately, little is known about the ecology of *C. glomerata*. Reynolds (1998) classifies *C. glomerata* as a taxon typical of ultra-oligotrophic, clear-water lakes. Kalff *et al.* (1974) found *C. glomerata* to dominate plankton in Meretta Lake in arctic Canada during the period of declining light in October, which may indicate that the species blooms late in autumn overturn or under the ice. However, many problems are also associated with the ecology and taxonomic identification of the small *Cyclotella* taxa (Haworth & Hurley 1984, Krammer & Lange-Bertalot 1991a), for which reason comparisons between the few ecological descriptions are somewhat questionable. A particularly good example of these difficulties is *C. comensis*-complex that has several morphotypes and different autecological requirements (Wunsam *et al.* 1995, Hausmann & Lotter 2000).

4.3. Benthic diatoms and habitat factors

Most of the studies concerning unicellular algae are focused on phytoplankton (Lowe 1996) whereas little is known about the ecology of benthic microalgae. These, however, can be the main contributors to the primary production in subarctic lakes (Niemi 1996). The most abundant benthic algae are blue-green algae (*Cyanophyta*), green algae (*Chlorophyta*) and diatoms (Stevenson 1996). Transect samples from Lake Saanajärvi were analysed in order to obtain more information of specific habitats of benthic diatoms in 1997 (II). Epilithon samples were analysed from the littoral, from water depths 0.5 to 6.0 m. *Achnanthes minutissima* Kützing, *Brachysira vitrea* (Grunow) R. Ross in Hartley and *Denticula tenuis* Kützing were the most common taxa in the epilithon communities along with *Achnanthes*, *Cymbella* and *Gomphonema* spp. It seems that diatoms capable of attaching tightly to the substrate were most common in the upper littoral zone where high-energy wave disturbance is constant. *Achnanthes nodosa* Cleve-Euler, *A. kriergerii* Krasske, *A. pusilla* Grunow in Cleve & Grunow, *Denticula tenuis*, *Brachysira vitrea* were most abundant in water depths 0.5 to 3.0 m. *Cocconeis placentula* Ehrenberg had

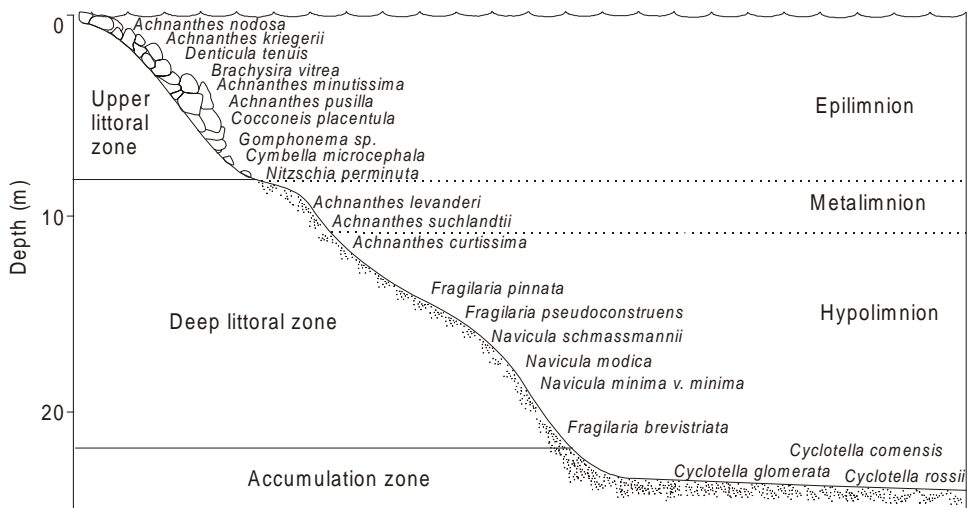


Figure 9. Most abundant diatom species found in different benthic habitats in Lake Saanajärvi.

its highest proportions in the water depth of 3.0–6.0 m with *Cymbella microcephala* Grunow in Van Heurck, *Gomphonema* sp. and *Nitzschia perminuta* (Grunow in Van Heurck) Peragallo, favouring more stable environmental conditions with low-energy wave action (Fig. 9). Stockner and Armstrong (1971) found the upper littoral area of large oligotrophic soft-water lakes to be dominated by stalked diatoms (*Gomphonema*, *Cymbella*), whereas in smaller lakes adnate forms, such as *Achnanthes* and *Brachysira* dominated the communities. These findings support the results from a medium size (70 ha) Lake Saanajärvi as observed here.

The deep littoral habitat was represented by transect samples taken from 7–16 m water depth (II). The deep littoral zone is characterised by low light, minor wave action and thermal stability because most of the zone is situated at or below the thermocline. Typical benthic diatom species, such as *Fragilaria brevistriata* Grunow in Van Heurck, *F. pseudoconstruens* Marcinjak, *Navicula minima v. minima* Grunow in Van Heurck, *N. modica* Hustedt and *N. schassmannii* Hustedt, were found in high numbers in this zone.

Planktonic species such as *Cyclotella comensis*, *C. glomerata*, *C. rossii* and *Thalassiosira pseudonana* increased markedly in proportions when moving from rock surfaces to the accumulation zone of the lake basin (samples from 21 m and 24 m water depth). *Fragilaria pinnata* Ehrenberg was most common benthic diatom in these deep-water sediments. Detrended correspondence analysis (DCA) classified transect samples into three clear habitat groups, where the two DCA first axes captured 40.8% of the total variance in the species data (II). The first group was characterised by littoral epilithic samples, and the second group comprised soft-bottom, deep littoral habitats. The third group was characterised by planktonic taxa in the accumulation zone.

4.4. Diatom representation in the sediment archives

Sediment distribution in a lake is a function of many external factors, such as hydrological flow, topography, shelter and climate, which influence physical limnological processes (e.g. thermocline depth, time of turnover, wave action). On the basis of the operation of these processes a lake basin can be divided into three different zones: an erosion zone, a transportation zone and an accumulation zone (Håkanson & Jansson 1983). The accumulation zone is least affected by wind-driven turbulence, allowing accumulation of even fine-grained sediments and resuspended material. Paleolimnological studies are generally based on the assumption that a single, centrally located core is representative of all the biological material derived from different microhabitats in the lake. Many studies seem to confirm this basic assumption (Frey 1988, and references therein). On the other hand, some studies clearly indicate that accumulation of biological remains and the representation of different communities of organisms may not be uniform (e.g. Meriläinen 1971, Battarbee 1978, Anderson 1989, 1990, 1994).

The representation of diatoms in sediment core material was estimated by studying different recent diatom community components and comparing the species proportions to the topmost 1 cm of the central sediment core of Lake Saanajärvi (II). Trap samples were thought to be a surrogate for plankton habitat, whereas, according to DCA, transect samples formed three different groups, epilithic upper littoral assemblages (0–6 m), deep littoral assemblages (7–16 m) and accumulated sediment assemblages (21–24 m). With analog matching there was a very good congruence between planktonic assemblages found in the trap material and the plankton in the sediment core material, whereas the similarity of non-planktonic assemblages to the sediment core assemblages was only moderately good (II). In addition,

several tests in Lake Saanajärvi have shown that diatom and cladoceran changes observed from the sediment sequence can be repeated from other sediment cores taken in the deepest point of the lake. Based on these studies, it was evident that the sediment core taken from the deepest point of the Lake Saanajärvi was representative for the entire diatom community in the lake and proof of this representativeness forms a good basis for further sediment studies.

4.5. Sedimentation rates in subarctic lakes

The origin of lake sediments are commonly from atmosphere, catchment, groundwater and lake itself (Charles *et al.* 1994). Atmospheric input to the lake include volcanic ash, some of which can also be utilised in sediment dating and in studying sediment accumulation rates. Catchment input material such as radioactive nuclides, carbonaceous particles, pollen grains and lake input consists mainly of inorganic and organic materials which may accumulate. In the study lakes, the sediment is composed of a relatively minerogenic gyttja (IV, V), with loss-on-ignition values varying from 16.9% (Lake Stuoramohkki) to 24.8% (Lake Masehjavri) in surface sediments. Such low LOI values are typical of high latitude sites with low primary production and low input of allochthonous organic matter from their poorly vegetated catchment area (Douglas *et al.* 1994, Korhola *et al.* 1999, IV). The typical colour of the upper sediment layers in the cores was light grey with several reddish-yellowish bands. The layers with reddish-yellow colour result most probably from the oxidation by the oxygen-saturated bottom waters (Prof. Rick Battarbee, Environmental Change Research Centre, University College London, personal communication).

The choice of the dating method depends on the time span of interest and the temporal resolution required by the study. For high-resolution studies considering the recently

accumulated sediments (last ~150 years), ^{210}Pb dating is the most widely applied dating tool (Oldfield & Appleby 1984) if annually laminated sediments are not available, which is unfortunately the case for northern Fennoscandian lakes. Lead-210 dating is based on the naturally occurring radioisotope in the ^{238}U -decay series following the decay of atmospheric ^{222}Rn . More details about ^{210}Pb dating are given in Appleby & Oldfield (1983) and Oldfield & Appleby (1984). Lead-210 dating can be verified by analysing Cesium-137 activity from the sediment sequence. Normally, two clear peaks of ^{137}Ce activity are presumed to be found; the more recent peak records the fallout from the Chernobyl reactor accident in 1986, and that the earlier peak records the 1963 fallout maximum from the atmospheric testing of nuclear weapons (Appleby *et al.* 1991).

^{210}Pb activity was measured from the study lakes (II, IV, V) and relatively constant sedimentation rates were observed in all the study sites (Fig. 10). The only exception was the increased sedimentation rates in Lake Toskaljärvi at the turn of the 20th century. The slowest sedimentation rates (the slowest ever measured in the Environmental Radioactivity Laboratory in University of Liverpool, Peter Appleby, personal communication) were observed from Lake Stuoramohkki, where $^{210}\text{Pb}/^{222}\text{Ra}$ equilibrium (~150 yrs) occurs at the depth of 3 cm, the mean sedimentation rates varying between $0.017 \pm 0.02 \text{ cm yr}^{-1}$ (Fig. 10). In harsh climate conditions at the altitude of Lake Stuoramohkki (1024 m a.s.l.), allochthonous material from the rocky catchment and autochthonous inputs from lake production are minimal, resulting in an extremely slow sedimentation rate. The highest sedimentation rate was measured in Lake Masehjavri, where the uppermost *ca.* 7 cm represents the last 130 years, indicating greater catchment inputs and perhaps also more productive conditions within the lake. The sedimentation rate at Lake Masehjavri was approximately $0.052 \pm 0.05 \text{ cm yr}^{-1}$. Due to the slow sedimentation rates, sediment cores were sub-sampled at

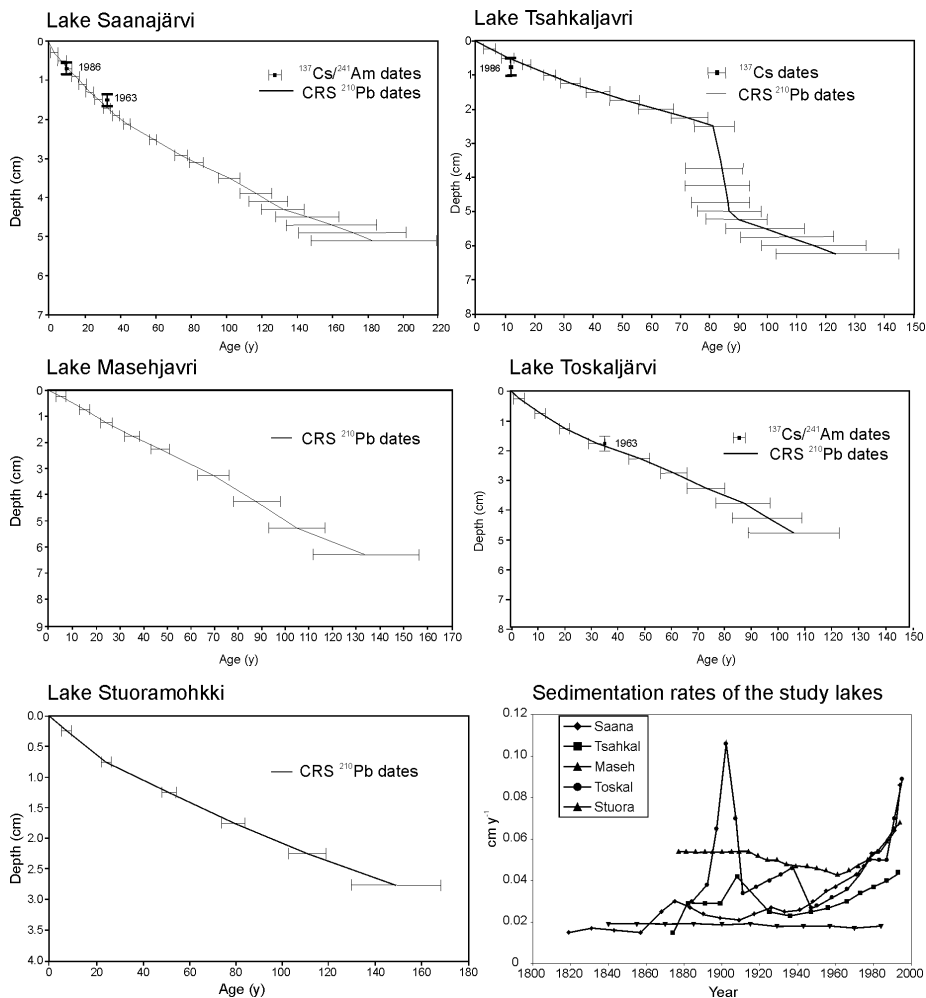


Figure 10. Results of ^{210}Pb datings and sedimentation rates of the study lakes.

high-resolution. 2 mm was used in Lake Saanajärvi and in Lake Stuuramohkki, while 5 mm resolution was applied to Lake Toskäljärvi, Lake Masehjavri and Lake Tsahkaljavri with slightly higher sedimentation rates. The sampling resolution is equivalent to *ca.* 3 to 10 years. In Tsahkaljärvi, however, there has been change in the flux of ^{210}Pb to the lake around 1900 which may be result of a sediment slump or a brief episode of inwash from the catchment. This hiatus has been taken into account when interpreting the diatom results.

Although the lakes had a relatively good chronological control, some errors and inaccuracy are always present in the dating. Moreover, although modern statistical techniques were used to correlate the dated master cores to the parallel sediment cores, caution must be exercised when cross-correlating ages between cores. Therefore, statements of exact years have been avoided in the interpretation. Also yearly accumulation (influx) of diatoms was not calculated and only percentage diatom data were used to study the environmental history of the lakes.

4.6. Recent environmental history as interpreted from the sediment records

Douglas *et al.* (1994) documented massive diatom species shifts from *Fragilaria* spp. to other benthic taxa over the past 150 years in the Canadian High-Arctic. The study was one of the first to report recent environmental change in remote “pristine” high latitude aquatic ecosystems. Douglas *et al.* (1994) pointed out that the causes of the dramatic diatom assemblage change were uncertain, although all the proxy evidence favoured climate warming as the major explanatory factor for the changes. Stimulated by the study of Douglas *et al.* (1994) in paper III, we studied the recent environmental history of an undisturbed subarctic lake, Lake Saanajärvi. This study was the first to document recent diatom compositional changes from benthos (*Achnanthes* and *Fragilaria* spp.) to plankton (*Cyclotella* species) in the Eurasian Arctic. Because of the importance of diatoms in the food webs and general functioning of the northern freshwaters, it was considered that some changes might also occur among other organism groups and other ecosystem levels as well. Hence, a detailed multi-proxy study was carried out on Lake Saanajärvi (IV). The study clearly revealed that the change in diatom assemblages was accompanied by simultaneous shifts in other biological indicators, such as zooplankton, chrysophyte cysts, and pigment concentrations (IV). These synchronous stratigraphic changes in many proxy indicators point to a major ecosystem change in the region at the turn of the 20th century.

On the basis of the detailed sediment study of Lake Saanajärvi, it could be argued that the biological changes might be related to in-lake processes or to the ontogeny of this particular lake. Therefore, diatoms were studied also from four other lakes (Lake Tsahkaljavri, Lake Masehjavri, Lake Toskaljärvi and Lake Stuoramohkki) representing different environmental settings (V). Diatom community structure showed clear changes in

all study profiles and the changes were observed as concurrent in time, starting in the beginning of the 20th century (V). In the dimictic lakes (Lake Saanajärvi, Lake Tsahkaljavri, and Lake Toskaljärvi), the proportions of the tychoplanktonic *Aulacoseira* species and several benthic *Achnanthes* and *Fragilaria* species declined, while small planktonic *Cyclotella* species increased towards the core surfaces (III-V). In isothermal lakes (Lake Masehjavri and Lake Stuoramohkki) the diatom species shifts occurred among the tychoplanktonic and benthic forms (*Aulacoseira* and *Achnanthes* species) and the response was weaker than in dimictic lakes. Nevertheless, all the studied lakes showed synchronous floristic change, which can be clearly manifested by multivariate analysis of the diatom data (III-V).

Catchment disturbances, atmospheric deposition and climate change were put forward as the most plausible causes for the recent biological change in the study lakes. In the papers III-V, hypotheses have been discussed and evaluated in detail. The major points are summarised here:

Direct human impact as a causative mechanism for the observed changes can be ruled out since the study area is remote, rocky, sparsely vegetated and hence unsuitable for any land-use. However, the number of *reindeer* has significantly increased in the area in the last few decades (III). This may have been responsible for some the observed change. Nevertheless, preliminary limnological monitoring data (Lindqvist 2001) from Lake Masehjavri does not show any substantial increase in lake-water nutrients, although large numbers of reindeer have gathered in the catchment area for a few weeks each July for last *ca.* 30 years. In addition, the topmost surface sediments of Lake Masehjavri do not show any clear diatom species composition change at that particular time interval when the reindeer have been abundant (V). Moreover, the recent increase in the reindeer numbers

can not explain the diatom assemblage changes which occurred over 100 year ago.

Finnish Lapland receives some *atmospheric acid and nutrient deposition* from southern Scandinavia and Europe (Lien *et al.* 1993), although it is one of the cleanest areas in Europe (Rühling 1992). The study lakes have been subjected to atmospheric pollution since the late 19th century as shown by the SCP and mineral magnetic data from Lake Saanajärvi (IV). The SCP and mineral magnetic profiles of Lake Saanajärvi reveals typical features shown by SCP and mineral magnetic profiles throughout Europe. However, the pollution levels at Saanajärvi are extremely low in comparison with areas which show clear indications of pollution such as lake acidification. In addition, it is known from the limnological monitoring data that the study lakes receive acid melt waters from the catchment areas during spring time (Lindqvist 2001, I, Sorvari *et al.*, in prep.), which lower the pH values drastically for a few weeks. To examine the possible *effects of acid deposition*, inferred pH was calculated for all the study lakes using different diatom calibration data sets (III-V). The pH reconstructions revealed no or only minor trends in the pH values, whilst the variation lies well within the standard errors of the model estimates. The stability of the reconstructed pH values, and the fact that all diatom taxa showed increases toward the sediment surface are characteristic of non-acidic, neutral waters (Pienitz *et al.* 1996, Weckström *et al.* 1997b, II, III) indicating that the lakes are not impacted by acid fallout. This is most probably because of the episode of acid melt water is brief and occurs when primary production in the lakes is minor. Thus, there are no diatom blooms at that time to track and store this information to the sediment. All this leads to the conclusion that atmospheric fallout of acid substances can not have been the driving force for the observed biological change.

In addition to acid rain, another possible explanation for the recent diatom

compositional change is *increasing atmospheric nutrient pollution*. Unfortunately, no long-term monitoring data on atmospheric nutrient levels exist for the study region. Several possible explanatory factors such as prehistoric alkalisation (Renberg *et al.* 1993), macronutrients by pollen (Lee *et al.* 1996, Doskey & Ugoagwu 1989), and increased nitrogen deposition values (Järvinen & Vänni 1990, Catalan *et al.*, in press) have been discussed in the papers III-V. However, there is no evidence of increased nitrogen accumulation loadings in the sediments (measured TN concentrations are stable throughout the study period) of Lake Saanajärvi (IV). The limnological monitoring of the study sites reveals that the only period of major external nutrient inwash occurs during spring when nutrient compounds are transported into the lakes with melt waters. During the remainder of the open water period, nutrient levels are very low and constant, indicating little inflow from the catchment area. The remaining question is why no biological response is observed because of the increase in nutrients during spring. One possibility is that the nutrients from the melt water outflows from the lake during the heaviest snowmelt and runoff. Other studies in the Arctic (Welch 1991) show that dilute and cold melt waters float just below the melting ice sheet and above the more saline (heavier – higher conductivity) stable water column in spring. Therefore, dilute, cold surface water may leave the lake via outflow during maximum runoff takes place and the lake only experiences vertical mixing after ice-out. In Lake Saanajärvi, the most intensive inflows of melt waters from the catchment area occurred when the lake still had an ice cover. In addition, the water chemistry data clearly show that the surface water under the ice-cover is more dilute than the water underneath (I). As stated before, lakes are limited by phosphorus. Because direct fertilising by humans can be ruled out and phosphorus is unlikely to be transported via atmosphere to remote regions, atmospheric nutrient deposition is not a plausible explanation for the ecosystem

change. The third remaining hypothesis, climate change, is discussed in more detail in the next section.

4.7. Post-Little Ice Age climate warming

Several studies from high latitude regions (Moberg & Alexandersson 1997, Jones *et al.* 1998) suggest pronounced warming starting from the mid-19th century and peaking in the 1930's. Overpeck *et al.* (1997) found a similar transition across the Arctic from anomalously cold climate conditions of the 19th century to peak warm conditions of the 20th century. It appears that the 19th- to 20th-century warming was 1°C to 3°C locally and averaged about 1.5°C across the Arctic (Overpeck *et al.* 1997). Monthly air temperature reconstructions based on regional long-term meteorological data and available proxy data show roughly a similar trend in Finnish Lapland as for the whole Arctic region (IV, V). It seems that a substantial increase of 1-2°C in mean annual temperature (Alexandersson & Eriksson 1989) occurred in Finnish Lapland between the late 1880s and the mid-1930s. It was followed by slight cooling trend since the 1950s (V). From the mid-1970s onwards, temperatures have increased again (Tuomenvirta & Heino 1996, V). Monthly air temperature reconstruction allowed examination of the record at the seasonal level, and indicates pronounced temperature fluctuations with each season having its own pattern. Spring temperatures during the last 200 years have shown the most rapid increases. This increase is especially important because of its effect on the length of the ice cover duration and on precipitation. Summer temperatures rose rapidly in the early-1900s but have gradually declined since then. Autumn temperatures have been relatively stable in the 19th century, showing an increasing trend from the 1940s to 1960s. Winter temperatures were found to be similar to the mean annual temperatures.

The correlation between the four seasons as well as the complete year and the diatom assemblage change as expressed by PCA axis 1 sample scores were examined in paper V. All the five lakes were found to have significant correlations between diatom changes and spring (March to May) air temperatures over the last 200 years. Three of the lakes (Lake Saanajärvi, Lake Tsahkaljavri and Lake Masehjavri) also showed a significant relationship to the mean annual temperature (V). However, the lakes seemed to respond individually to climate forcing although the floristic shifts in all study sites were relatively synchronous. Physical and chemical differences between the lakes, the wide geographic coverage and concurrence of the change, as well as the nature of the change from benthos to plankton (mostly *Achnanthes* spp. to *Cyclotella* spp.) all indicate a regional, rather than local response. The rapid reorganisation of diatom assemblages and the increase of the plankton component in most of the lakes suggest that the post-LIA warming in the polar region some 100 years ago may have forced the ecosystems to shift from one equilibrium level to another after crossing a critical threshold (see Fig. 2d). The general cooling trend from the 1950's to 1970's cannot be observed in the diatom assemblages; either the cooling has not been sufficiently pronounced to affect diatom compositions or the temporal resolution of the study is too crude to note such short-term changes.

4.8. Diatom response to climate forcing

The causes of the observed relationship between climate change and diatom species shifts are not obvious. The effects of climatic warming is mediated to the lake ecosystem in multiple ways, such as an ambient rise in lake temperature, changes in solar radiation and windiness, and decreased or increased rainfall, either directly to the lake or via runoff from the catchment area. Moreover, the factors controlling seasonal variability and

distribution of diatoms are numerous and the most important factors are often highly correlated. In this section some possible mechanisms between temperature and diatoms are discussed.

Most aquatic organisms are poikilothermic so that their internal temperature varies with environmental temperature. Therefore, temperature of their environment is an important factor in their life. Traditionally, diatoms have been classified into taxa with broad tolerance to temperature (*eurythermic* taxa) and those with narrow tolerance to temperature (*stenothermic* taxa) (Hustedt 1956, Patrick 1971). There seems to be a consensus that temperature has physiological importance for the diatom species (Hartig & Wallen 1986, Raven & Geider 1988, Michel *et al.* 1989), but it is yet unknown whether temperature affects directly diatoms at the community level (DeNicola 1996, Anderson 2000). At a physiological level, temperature mainly causes metabolic changes, i.e. changes in energy consumption, respiration and carbon fixing (Reynolds 1984). At a community level temperature effects can be direct or indirect. Direct effects may include changes in growth rates, reproduction and life cycles (Reynolds 1984). Indirect temperature effects are often related to changes in abiotic environment, such as changes in stratification and mixing periods (Bradbury 1988, Tilzer *et al.* 1991, Gaedke *et al.* 1998), changes in water quality (Psenner & Schmidt 1992, Anderson *et al.* 1996, Fritz *et al.* 1991), and changes in habitat (Smol 1988, Schmidt *et al.* 1990, Weckström *et al.* 1997a, Lotter & Bigler 2000).

It is widely known that a slight variation in climate can have dramatic effects on the diatom assemblages in environmentally sensitive high latitude and high altitude lakes (Smol *et al.* 1991, 1995, Douglas *et al.* 1994, Moser 1996, Rouse *et al.* 1997, Lotter & Bigler 2000). In extreme climate conditions in arctic and alpine lakes, diatom habitat, and therefore, some diatom taxa can be limited by ice-cover (Smol 1983, 1988). In cold, moist

climate conditions, floating ice and snow can remain in the central part of the lake for the whole summer leaving only a narrow moat on a lake shore, restricting the pelagic diatom communities and favouring littoral communities (especially *Achnanthes* spp. and *Fragilaria* spp.). In warmer summers, the ice-cover can disappear allowing plankton communities to develop and to dominate the diatom production. Such habitat changes are recorded in the fossil assemblages. Lotter & Bigler (2000), for example, demonstrated with sediment trap and sediment core studies a shift from benthic *Fragilaria* spp. to planktonic *Cyclotella* spp. due to the reduced ice-cover after the cold period of LIA in an high altitude lake Hagelseewli in the Swiss Alps. In NW Finnish Lapland, such severe climate conditions do not occur at present; all the lakes in the Kilpisjärvi region are ice-free for a few months during summer and most probably have been such during the last 200 years.

The formation of a thermocline, length of thermal stratification, and intensity of water column mixing are factors closely related to climatic variables, such as temperature, precipitation and storminess (Hondzo & Stefan 1993, Livingstone & Lotter 1998). These factors are important to diatom growth (Reynolds 1980, 1984, Kilman *et al.* 1996). Water-column mixing is one of the dominant controlling factors on algal communities and the seasonal variability of phytoplankton (Reynolds 1984). The timing of ice break-up and duration of overturns control light climate and the transport of the nutrients from hypolimnion to epilimnion (Kilman *et al.* 1996). Under such circumstances, the water column is commonly dominated by diatoms, that typically favour high nutrient conditions, low light and low temperature (Kilman *et al.* 1996). Generally, large, heavily silicified species, such as *Aulacoseira* spp. favour the changed conditions during spring overturn (Lund 1966, Round *et al.* 1990). When the water temperature increases, the viscosity and the density of the water changes and thus climate warming can strengthen or even

generate thermal stratification and therefore alter the diatom community composition (IV). Water column stability is known to strongly affect the light, nutrient, oxygen and pH conditions experienced by planktonic organisms (Rodhe 1955, Tilzer & Schwarz 1976, Gaedke *et al.* 1998). The importance of the stratification for diatoms can be indirectly via the duration of mixing periods, including in-lake nutrient cycling from the hypolimnion when ice cover or the thermal stratification breaks apart. For example, Bradbury (1988) showed at Elk Lake, Minnesota, US, that nutrient availability was linked to the timing of spring ice break-up and subsequent stratification. Late break-up led to early stratification and resulted in a diatom population with a characteristically high silica to phosphorus ratio. In contrast, the early spring break-up of ice cover resulted in a long period of mixing leading to a diatom community typical of high phosphorus loading. Agbeti *et al.* (1997) compared two lakes with different mixing regime (isothermal versus dimictic) and they clearly showed that in the isothermal lake, *Aulacoseira* species were abundant, whereas the small lightly-silicified diatoms were dominant in a dimictic lake.

In the lakes of Finnish Lapland, the situation seems to be similar: *Aulacoseira* spp. were most dominant in isothermal lakes, while small unicellular *Cyclotella* species predominated the thermally stratified lakes. The decrease of *Aulacoseira* species, benthic *Achnanthes* and *Fragilaria* taxa, and increase of *Cyclotella* species in the studied dimictic lakes led us to hypothesise that the post-LIA warming between 1880-1930s and especially the enhanced warming in springtime, may have lengthened the open-water season and therefore, may have created or prolonged the summer stratification in dimictic lakes. This in turn may have favoured the growth of small *Cyclotella* species. This assumption is supported by the fact that the duration of the open-water season in high latitude lakes is largely determined by spring (March to May) temperatures (Bilello 1964). According to our

regional air temperature reconstructions (IV, V), spring temperatures in particular have increased significantly between 1880 and the 1930's. Also the world's longest ice break-up record from the River Torniojoki (*ca.* 450 km south from the study area) reveals the same long-term trend toward earlier break-up dates between 1620 and 1995. Using data from the River Torniojoki, Magnuson *et al.* (2000) calculated break-up dates occurring 3.7 days earlier in 1850 than in 1701 and 6.6 days earlier break-ups in 1995 than in 1846. According to Magnuson *et al.* (2000), the change in ice cover period corresponds to increase in air temperatures of 1.2°C per 100 years.

Shifts in annual average air temperature of the magnitude of 1 to 2°C can be expected to have profound influences not only on species composition and overall production in high latitude lakes but also on species diversity. In shallow arctic ponds Douglas & Smol (1999) observed that in warmer summers, and hence during longer growing season, algal communities had higher overall productivity and they were more complex and diverse than in colder summers. More diverse diatom assemblages in warmer summers included moss epiphytes, and tube and stalked diatoms, as opposed to simply adnate diatom communities in cooler summers. In the study lakes, the species diversity seems to follow temperature. In the warmest lake (Lake Masehjavri) the species diversity and the overall algal productivity (measured as Chl-a) was highest, while in the coldest lake (Lake Stuoramohkki) diatom diversity and algal productivity was lowest (V). Weckström & Korhola (2001) recorded highest diatom diversity in lakes of the mountain birch woodland zone and a northward decline in diversity towards the cold, arctic lakes in the tundra. However, the temporal changes in diatom diversity exhibited an inverse relationship with an increasing temperature. Species diversity decreased toward the present-day warmer climate. We assume that higher temperature and associated increase in nutrient have favoured small planktonic

species with rapid growth rates and these have become dominant enough to reduce the overall diversity.

On examination all the alternatives and hypothesis (catchment disturbances, atmospheric deposition and climate change) discussed above, it seems that the most plausible explanation for the diatom assemblage change observed in lakes of Finnish Lapland is *climate warming*. The diatom response to the post-LIA climate warming is most probably a response to the increased thermal stability and shorter ice-cover duration in studied lakes. These changes in environmental conditions may thus have created more favourable conditions for the small *Cyclotella* species, such as *C. comensis* and *C. glomerata* to grow. The diatom response was weaker in the isothermal lakes (Lake Masehjavri and Lake Stuuramohkki). Agbeti *et al.* (1997) found similar differences in their unstratified and stratified lakes. They concluded that in isothermal lakes primary production was primarily controlled by a combination of internally-driven (autogenic) factors, while in thermally stratified lakes primary production was more sensitive to external forcing, such as climate change. Moreover, ecological effects of temperature at diatom community level can differ substantially between phytoplankton and periphyton (DeNicola 1996). These differences result primary from the manner in which temperature interacts with other environmental factors in the two habitats. The more variable physicochemical environment of the benthos relative to the plankton usually results in more complex spatiotemporal patterns in species distribution (DeNicola 1996).

5. Summary of the papers I-V

Paper I describes the general limnological features of the main study site, subarctic Lake Saanajärvi. Paper I was the first monitoring study of a subarctic lake in Finnish Lapland and it presents two years (1996-1998) seasonal and inter-annual variability of physical and chemical parameters. The aims of the study were to understand the ecosystem dynamics of a subarctic lake in order to interpret more carefully the recent environmental history of such lakes. Lake Saanajärvi is a relatively deep (24 m), dimictic, dilute (conductivity 27.6 $\mu\text{S cm}^{-1}$), circumneutral (pH 7.1) clear water lake (water colour 5.0 PT mg l^{-1}) with low productivity ($\text{Chl-a} < 2 \mu\text{g l}^{-1}$). The ion concentrations of the lakes were relatively stable throughout the year with only exceptions found in springtime, when at first, oxygen depletion caused ion concentrations to increase several fold in bottom waters, and afterwards, when acid but nutrient-containing melt water from the catchment area drained into the lake.

Paper II is a hydrobiological study of two years variability in planktonic diatoms and crustacean zooplankton in the Lake Saanajärvi. In addition, diatom and zooplankton species compositions were studied in different habitats. Species occurrence in different habitats was then compared to the results of quantitative diatom and cladocera sediment core studies, with an aim to examine representation of prevailing communities in a sediment core taken from the central part of the lake. One phytoplankton production maximum was observed during the open-water season. Planktonic *Cyclotella* and *Thalassiosira* species had their maximum bloom during the autumn overturn when the thermal stratification broke down and available nutrients were released from the hypolimnion to the whole water column. Inter-annual variability within the dominant algal groups was common. Typical habitat preferences were found among benthic communities;

Achnanthes, *Brachysira* and *Denticula* spp. were common in the upper littoral zone while *Fragilaria* and *Navicula* spp. were predominant in the deeper littoral zone. A single sediment core taken from the deepest area of a lake represents the overall diatom community of Lake Saanajärvi well.

Paper III was the first diatom surface sediment core study carried out in the NW Finnish Lapland. The aim of the study was to achieve information about the environmental history of a subarctic lake for the last 200 years. A distinct diatom assemblage change from benthos to plankton was detected from the sediment sequence. Three hypotheses were put forth to explain the recent environmental change, namely atmospheric pollution, catchment disturbances, and climate change. These hypotheses were discussed and evaluated in the paper. The data seemed to support climate change as the predominant causative force.

Paper IV is a high-resolution multi-proxy study carried out in Lake Saanajärvi to examine more closely the three hypotheses established in paper III. The aims of the study were to explore several biological indicators simultaneously and their responses to environmental change. The multi-proxy evidence shows synchronous change in diatom, cladocera, chrysophyte cyst assemblages, and in fossil pigments. Post-Little Ice Age climate warming seemed to explain most of the changes in biota. In the paper, several possible underlying mechanisms for the change were discussed.

Paper V is a detailed diatom study on five lakes in NW Finnish Lapland. The aim was to expand the study from Lake Saanajärvi to additional lakes in the area and to assess the relationship between recent climate warming and diatom community changes. Independent monthly air temperature reconstructions were made for the study region that enabled the

direct comparison of the diatom assemblage changes as expressed by the PCA axis 1 sample scores to the air temperature reconstructions. A statistically highly significant correlation was found between air temperature data and diatom changes, with spring temperatures explaining most of the variation in the diatom species data. Temperature effects and mechanisms behind the changes in the diatom species composition were discussed.

6. Conclusions

The purpose of this thesis was to understand the basic limnology and ecosystem dynamics of poorly studied subarctic lakes and to study recent environmental history of these remote and environmentally sensitive lakes (the last 200 years) in NW-Finnish Lapland. The present study shows that the subarctic lakes in the Kilpisjärvi region are dilute, circumneutral, clear water lakes with low productivity (I, II, V). Two different thermal structures were recognised: dimictic lakes (Lake Saanajärvi, Lake Tshakaljavi, Lake Toskaljärvi) with brief spring overturn, a few weeks of stratification and relatively long autumn overturn, and isothermal lakes (Lake Masehjavri, Lake Stuuramohkki), which were unstratified during the entire open-water season (V). Subarctic lakes were ultra-oligotrophic and their primary production was phosphorous-limited (I, II, V). In dimictic lakes, only one phytoplankton production maximum was observed during the autumn overturn (I, II). The shallowness and clarity of the lake water resulted in microbenthic flora to be an important component of the primary production (II). The comparison of habitat samples and sediment trap communities to surface sediment core data demonstrated that a sediment core representing a deep basin constitutes a “surrogate” of all the habitats of the lake (II).

Extremely slow sedimentation rates were typical for the study lakes due to low primary

production and low input of material from their poorly vegetated catchment areas (IV, V). Diatom studies from the sediment cores demonstrated a floristic change from benthos (*Achnanthes* and *Fragilaria* species) to plankton (small *Cyclotella* species) in dimictic lakes (III, IV, V). In isothermal lakes the diatom species shifts occurred within the tychoplanktonic and benthic forms (*Aulacoseira* and *Achnanthes* spp.) (V). Statistical analyses revealed that the diatom assemblage change was concurrent within the study lakes dating to the turn of the 20th century (IV, V). Multi-proxy analyses from Lake Saanajärvi demonstrated that the change in diatom assemblages was accompanied by simultaneous shifts in cladoceran species composition, concentrations of chrysophyte cyst assemblages and fossil pigments, indicating an overall ecosystem change (IV). Monthly air temperature reconstruction based on the regional long-term meteorological and available proxy data shows a 1-2°C increase in mean air temperatures from 1880-1930 in the Kilpisjärvi region (V). At the seasonal level, spring temperatures showed the most rapid increase during the last 200 years (V). A significant relationship was found between the reconstructed air temperatures and the diatom species shift in each lake (V). The most significant correlation was found between the spring (March to May) mean air-temperature and the diatom assemblages (V). Despite the high correlations, lakes seemed to respond individually to the climate forcing, with isothermal lakes showing a somewhat weaker response (V). The most powerful explanatory factor for the diatom assemblage change was climate warming. Alternative hypotheses, such as atmospheric pollution and catchment disturbances were critically assessed (III, IV, V).

The exact causative mechanism(s) between climate warming and the diatom species shifts are discussed but remain somewhat open. The nature and timing of the diatom floristic shifts and highly significant correlations between climate parameters and diatom assemblages suggest that the post-Little Ice Age climate

warming (especially the increase in spring temperatures) may have lengthened the overall open-water season. The changes in the duration of the ice cover and changes in the mixing periods and summer stratification may have favoured the growth of small *Cyclotella* species. The weaker response of diatoms to climate forcing in isothermal lakes was probably associated with the fact that the benthic dominated primary production in isothermal lakes is predominately controlled by internally-driven factors whilst climate change has more of an effect on the productivity of dimictic lakes (Agbeti *et al.* 1997).

Despite the similar and concurrent observations from other circumpolar sites (Douglas *et al.* 1994, Gajewski *et al.* 1997; Rühland & Smol, personal communication), multi-proxy evidence from Lake Saanajärvi (IV) and the significant correlation between independent air temperature reconstructions and floristic change (IV, V), there is still lot to be done in order to understand more comprehensively the causative mechanisms between diatom response and climate warming. Further long-term proxy-data on other climate parameters (e.g. precipitation and windiness) are needed to achieve a more holistic picture of the past climate conditions and associated ecosystem response. Also palaeolimnological studies of earlier climatic events such as early Holocene warm period and subsequent Neoglacial cooling of the study site should broaden our understanding of the diatom response to the climate forcing. In addition, more monitoring data and possible laboratory experiments are needed to relate diatom response to climate forcing. This includes additional studies in dynamics of the thermal structure, diatom autecology and lake trophic interactions. Several studies are already in progress and we may expect to receive more information to test these assumptions in the near future.

Acknowledgements

It all started in my first study years when I participated several lectures given by dos. Atte Korhola. I was astonished by his enthusiasm towards both palaeolimnology and science in general. His inspiration and motivation in science, and ability to truly enjoy life was something special and it radiated hundreds of meters from him. So in the end, it was not too difficult to knock on his door to ask if there was any possibility to do a MSc. thesis in palaeolimnology and if he would like to supervise the study. That's when my interesting and enjoyable journey into the world of palaeolimnology started, a journey that has now culminated in a Ph.D. thesis. I owe my greatest and warmest thanks to my SUPER-supervisor Atte Korhola, who is simply the best supervisor in the world. He has always encouraged me during hard times, and in good times he has been the most entertaining company to work with. My closest colleague, a twin sister, Milla Rautio deserves the biggest thanks for standing my company during numerous field- and meeting trips. We have shared thousands of experiences, varying from dangerous snowstorms in the Halti area to extravagant shopping in Europe's biggest cities. These years have made us a seamless team without any conflicts! Milla, I have always enjoyed working with you and I highly appreciate our team. I hope we have many years of working together ahead of us. I have also been privileged to work in the funniest and most relaxed research group, the Environmental Change Research Unit (ECRU). I thank the whole ECRU group (Marjut Nyman, Jan Weckström, Kaarina Weckström, Laura Karjalainen, Raino-Lars Albert, Paavo Junttila, Tuomas Perkkiö) for good times at work; you have made the present study much easier to do. Special thanks belong to Jan Weckström, who has always unselfishly helped me with computers and with complicated software. I am grateful to the people at Department of Ecology and Systematics, especially in the Division of

Hydrobiology for welcoming our group so warmly a few years ago. I also acknowledge the Laboratory of Physical Geography for the facilities during the years 1997-1999, with special thanks to Juhani Virkanen and Marketta Eerola for helping with water chemistry analyses.

I have worked in several big EU projects and Atte made sure that I attended many meetings around the world. During these years, I have made many good friends in the mountain lake and palaeo research communities. I thank you all for stimulating discussions and great bar sessions. I would like to express my gratitude to my Swiss colleagues, André Lotter, Oliver Heiri, Sonja Hausmann and Karin Koinig, who took very good care of me during my visit to Bern for 3 months. I am grateful to my external reviewers Dr. Vivian Jones and Dr. Johanna Ikävalko, and my professor Markku Viitasalo for critical and constructive comments on the manuscript, and to Phillippa Noon for kindly improving my inadequate English.

Because most of the work has been done in Kilpisjärvi and I am indebted to numerous people in Lapland. I acknowledge the Lapland Regional Environment Centre for help with water chemistry analyses and the staff of the Kilpisjärvi Biological Station for providing comfortable accommodation and the opportunity to use the Rantasauna every now and then. I would also like to thank the "Rantasauna gang" and house keepers of the station for good discussions and enjoyable company after hard days in the field. I would like to thank Seppo Lahti for being the godfather and for helping us in critical situations. Without the help of Kuisma Ranta and Viktor Mannela from the Finnish Forest Research Institute, Kilpisjärvi Branch this work would not have been finished. Without the logistic help and field experience of these tough Laplanders most of the samples would still lie in remote subarctic lakes. In addition to the help in the field, I have learned so much about life from Kuisma and Viktor. I will never forget you and the time we spent

together in the field. I am indebted to several people who have helped me in field and I am certain that this list is incomplete, my apologies. I would not have managed without your help: Petri Shemeikka, Phillipa Noon, Maria Laamanen, Oula Kalttopää, Antti Kalttopää, Sinikka Tikkinen, Laura Försström, Lasse Lindqvist, Mari Hakojärvi, Ullariikka Erola, Paavo Junttila, and Tuomas Perkkiö. Special thanks go to the helicopter pilots Ari Tiittanen and Sampo Laitila for smooth flights during these years.

I want to thank all of my friends for understanding my long absence during field seasons and for standing my endless, boring monologues about my work. I am very proud to have you all around me. My family has always supported me and I am certain that you have sometimes had more faith in this project than I have. I am very grateful to my family that they have always provided me a necessary contrast to research, by organising all kinds of refreshing activities in their garden or in our summer cottage. Last but not least, I want to express my super-thanks, hugs and kisses to my sweetheart and best friend Tero Huttunen, who has put up with me coming home very late from work just mumbling something illogical about diatoms and subarctic lakes. You have taken good care of me mentally and physically during these hectic months. Without you, Tero, I would not be here writing my acknowledgements of my doctoral thesis. Thank you for being the sun of my life!

Financial support from the following sources is gratefully acknowledged: Academy of Finland (grant 101 7383) and the European Community, Environment and Climate Programme (MOLAR Project ENV4 CT95 0007 and EMERGE project EVK1-CT-1999-00032).

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