

Lake diatom response to recent Arctic warming in Finnish Lapland

SANNA SORVARI*, ATTE KORHOLA* and ROY THOMPSON†

*Department of Ecology and Systematics, Division of Hydrobiology, PO Box 17 (Arkadiankatu 7), FIN-00014 University of Helsinki, Finland; †Department of Geology and Geophysics, The University of Edinburgh, Edinburgh EH9 3JW, Scotland

Abstract

High-resolution palaeolimnological data from a number of remote and nonpolluted lakes in Finnish Lapland reveal a distinct change in diatom assemblages. This parallels the post-19th century Arctic warming detected by examination of long-term instrumental series, historical records of ice cover and tree-ring measurements. The change was predominantly from benthos to plankton and affected the overall diatom species richness. A particularly strong relationship was found between spring temperatures and compositional structure of diatoms. The change is irrespective of the lake type and catchment characteristics, and is reflected by several other biological indicators, such as chrysophytes and zooplankton, suggesting that entire lake ecosystems have been affected. No corresponding change in the diatom-inferred lake-water pH was observed; hence, atmospheric fallout of acid substances cannot have been the driving force for the observed biological change. The mechanism behind the diatom response is unclear, but it may be related to decreased ice-cover duration, prolonged growing season and increased thermal stability. We postulate that 19th century Arctic warming, rather than acidic or other anthropogenic deposition, is responsible for the recent ecological changes in these high latitude lakes.

Keywords: Arctic warming, diatoms, ecosystem change, lakes, Lapland, long time-series

Received 28 April 2001; revised version received and accepted 6 August 2001

Introduction

Northern Hemisphere temperature fluctuations during the past few centuries are becoming increasingly well documented (Mann *et al.* 1998). For example, there is growing evidence from long instrumental records, glaciers, tree-rings and marine and lacustrine sediments to suggest that Arctic regions experienced a pronounced warming that started around 1840 and peaked in the mid-20th century, marking the termination of the Little Ice Age in the area (Overpeck *et al.* 1997). Where quantitative estimates are available, it appears that the 19th- and 20th-century warming was 1–3 °C locally (Overpeck *et al.* 1997 and references therein), with atmospheric greenhouse gas concentrations playing an increasingly dominant role in the post-1920 warming (Crowley 2000). However, the full geographical coverage and the environmental effects of this Arctic warming have yet to be established. Such

information is essential not only for understanding past environmental dynamics, but also for predicting the impacts of projected future climate warming on high-latitude ecosystems.

A characteristic feature of many parts of the Arctic is the numerous lakes and ponds maintained by moisture received from rain and snowmelt. In contrast to temperate lowland lakes – which are often productive, characterized by high summer temperatures, and have transient ice-cover, large species diversity and complex food web structures – arctic or subarctic lakes often have ecosystems with low species diversity, low productivity and simple food webs at low temperatures with short open water seasons (Welch 1991; Rautio *et al.* 2000; Sorvari *et al.* 2000). High-latitude waters also are usually small and clear, and their water column and biological life are in close connection with the atmosphere. These factors render arctic and subarctic waters and their biota highly vulnerable to changes in climate (Douglas *et al.* 1994; Rouse *et al.* 1997; Korhola *et al.* in press a).

Correspondence: Atte Korhola, fax + 358/ 9 191 28701, e-mail atte.korhola@helsinki.fi

Yearly records of ice cover duration on high-latitude lakes and rivers provide a direct measure of climatic effects on water bodies. Recent compilations of historical time series of ice cover point to later freezing and earlier ice break-up dates for lakes and rivers in the Northern Hemisphere over the past 150 years that translate to increasing air temperatures at a rate of about 1.2 °C per 100 years (Magnuson *et al.* 2000). Shifts in annual average air temperature of 1–2 °C can be expected to have profound influences not only on the chemical and physical limnology of high-latitude lakes but also on species compositions. Furthermore, the resulting increased activity of the aquatic organisms are likely to lead to marked ecological changes and a consequent modification of the entire ecosystem. However, the general lack of long-term biological monitoring of remote arctic and subarctic waters has strongly hampered such impact assessment. High-resolution analyses of recent lake sediments provide a means to extend monitoring records to cover the full temporal range of recent warming. Unfortunately, apart from a few isolated exceptions (e.g. Douglas *et al.* 1994; Gajewski *et al.* 1997; Sorvari & Korhola 1998), the tremendous resource of lake sediments has not been fully utilized in the Arctic context. Thus, little information exists about the consequences of recent Arctic warming on the biology and biodiversity of high-latitude lakes.

In this article, we apply palaeoecological techniques to assess the responses of aquatic ecosystems to recent climatic fluctuations in the Arctic. We focus on diatoms (Class Bacillariophyceae), because they are known to provide one of the most sensitive records of environmental change (Stoermer & Smol 1999). These microscopic, unicellular algae are particularly important components in northern aquatic ecosystems because they contribute markedly to the primary production and therefore have an important role in the food webs of these waters (Douglas & Smol 1995). Moreover, because of their siliceous composition, they are usually well preserved in sedimentary deposits. For these reasons, diatoms are frequently used as an important indicator group in biomonitoring of both present and past environmental changes (Stoermer & Smol 1999).

We first examine the local spatio-temporal variation in air-temperature series in order to find out how closely climate development in northern Fennoscandia has followed the circum-Arctic climatic change as described in Overpeck *et al.* (1997). To this end, we statistically combine time-series of various indicators of climate consisting of long-term instrumental records, dendroclimatic, and historical ice-cover data to reconstruct the high-latitude air-temperature series at the annual and seasonal levels. Secondly, we explore the relationships between climate variation and changes in lake biology.

Finally, we discuss the relevance of our findings to global change as manifested in the circum-polar region.

Data and methods

Long-term instrumental or historical climate records from high latitudes that can be used for validation of proxy climatic records are very scarce. Lapland (Fig. 1) is unusual as homogenized instrumental data (e.g. Vardo at 70°N and Karesuando at 68.3°N) stretch back for over a century, while a suite of very long instrumental series (e.g. Trodheim, Uppsala and Leningrad to the south) go back to the 1700s. Furthermore, historical records of ice-cover (e.g. River Tornionjoki since 1693) and tree-ring width and density series (at the Scandinavian timberline) provide further climatic information with an annual resolution.

Multiple regression methods were used to estimate seasonal and annual air temperature anomalies (°C) for NW Finnish Lapland. Spring (MAM) and summer (JJA) temperatures (annually from 1693) were based on a least-squares regression of the Julian day of ice-break of River Tornionjoki (E. Kuusisto, pers. comm.), tree-ring width and maximum density, of tree stands at the Scandinavian timberline (data deposited by F.H. Schweingruber in the International Tree-Ring Data Bank, available from the World Data Centre (WDC) for Palaeoclimatology,

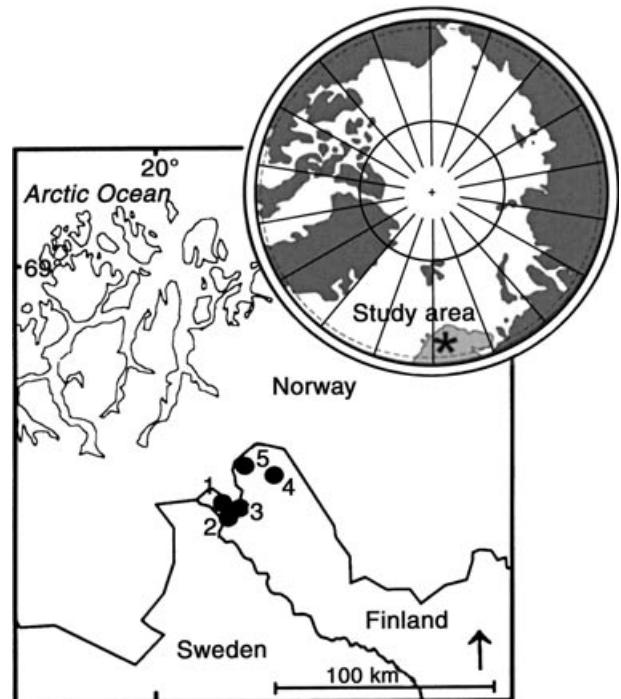


Fig. 1 Map of the NW Finnish Lapland. The study sites are indicated by solid dots (1, Saanajärvi; 2, Tsahkaljärvi; 3, Masehjärvi; 4, Toskaljärvi; and 5, Stuuramohkki).

Boulder), and central England air temperature (Manley 1974). For more recent times (1780–1999) our regressions are based on the monthly mean air temperatures of 20 homogenized air temperature series from lowland regions across Europe (data principally taken from the GHCN database at the WDC for Meteorology, Asheville). Air temperature for all four seasons were reconstructed (Fig. 2). All our regression analyses use Karesuando as the target series and have been extensively tested using cross-validation (Geisser 1975). In order to emphasize the long-term trends the seasonal and annual temperature series were smoothed using a low-pass filter. Bloomfield's (1976) least-squares approximation method was used to construct a filter with a pass frequency of 10 years. Finally, a loess smoother (Cleveland & Devlin 1988), adjusted to match the characteristics of the low-pass filter,

was used to extend the smoothing to cover the full temporal range of the data series.

We retrieved sediment cores from five subarctic lakes in NW Finnish Lapland, representing different lake types and environmental settings (Fig. 1). All five lakes are located above the present tree-line in small, rocky catchments at altitudes between 559 and 1024 m a.s.l. The lakes are clear, oligohumic, dilute, and ultra-oligotrophic, with a maximum depth between 11 and 27 m (Table 1). All the lakes studied were cold habitats; their ice season normally extends from October to June. Three of the lakes (Saanajärvi, Tsahkaljavri, Toskaljärvi) stratify thermally during summer and show a typical dimictic mixing pattern, while two of the lakes (Masehjavri, Stuuramohkki) are more or less isothermal throughout the year. In terms of atmospheric pollution, the study

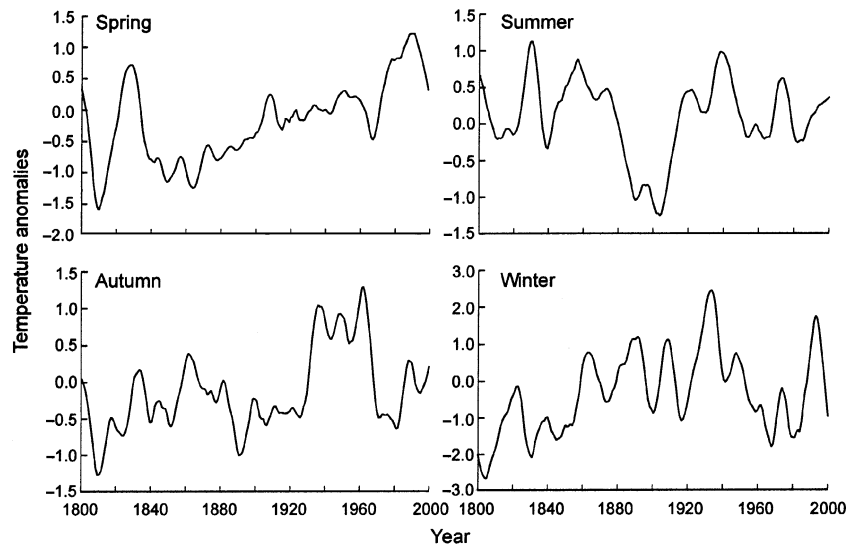


Fig. 2 Seasonal mean air-temperature anomalies ($^{\circ}\text{C}$) for NW Finnish Lapland based on the reference period 1890–1999. Each temperature series has been smoothed using a 10-y low-pass filter. Very different long-term trends are found for the individual seasons, but all seasons contribute towards the high temperatures of the 1930s and 1940s.

Table 1 Locations and environmental characteristics of the study lakes

Parameter	Saanajärvi	Tsahkaljavri	Masehjavri	Toskaljärvi	Stuuramohkki
Latitude ($^{\circ}\text{N}$)	69°05'	69°01'	69°05'	69°19'	69°14'
Longitude ($^{\circ}\text{E}$)	20°87'	20°55'	20°59'	21°27'	21°04'
Altitude (m a.s.l.)	679	559	687	704	1024
Area (ha)	70	113	17	100	18
Catchment area (ha)	461	3396	173	1433	98
Maximum depth (m)	24	18	11	22	27
Temperature ($^{\circ}\text{C}$)*	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	0.9
Color (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

*Measured in the end of July 1998

area represents one of the cleanest environments in Europe (Rühling 1992). There are little or no signs of direct human activity near any of the studied lakes; the closest settlements and roads are several kilometres away at lower elevations.

Parallel sediment cores were taken in the central part of the lakes from ice using the Glew gravity corer (Glew 1991). Samples from the master cores of each site were analysed for ^{210}Pb , ^{226}Ra , and ^{137}Cs by direct gamma assay in the Liverpool University Environmental Radiometric Research Centre, using Ortec GWL series well-type coaxial low background intrinsic germanium detectors and the technical procedures described in (Appleby *et al.* 1986). The separate cores were correlated with the master core by the variations in their dry weight and loss-on-ignition profiles. Relatively constant sedimentation was observed in all the study cores, the mean sedimentation rates varying between $0.017 \pm 0.02 \text{ cm y}^{-1}$ (Stuoramohkki) and $0.052 \pm 0.05 \text{ cm y}^{-1}$ (Masehjavri). In Tsahkaljavri, however, the very sharp decline in unsupported ^{210}Pb activity at 2.5 cm and the detection of what appear to be significant levels of unsupported ^{210}Pb between 5 and 5.5 cm suggest that this apparent equilibrium may in fact be a hiatus in the record, possibly the result of a sediment slump or an brief episode of rapid input from the catchment (Fig. 3).

The cores were subsampled in fine intervals of 2 mm (Saanajärvi, Stuoramohkki) or 5 mm (Toskaljärvi, Masehjavri, Tsahkaljavri), equivalent to a temporal resolution of about 3–10 y. Diatom samples were treated with H_2O_2 and 37% HCl (Weckström *et al.* 1997) and residual acid was washed away by the centrifugation procedure. Cleaned diatoms were mounted with Naphrax® mounting medium and diatom slides were counted using Olympus BX40 with $\times 1000$ magnification, with phase contrast and immersion oil. A minimum of 500 diatom valves was counted per sample.

Diatom species diversity at constant sample counts was estimated using the index N_2 from Hill's family of diversity indices (Hill 1973). The 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). This relatively simple index is particularly well suited for stratigraphical species data and has been shown to meet basic mathematical and ecological assumptions (Hill 1973; Peet 1974).

In an attempt to identify the periods of time of the most significant shifts in the diatom assemblages, we used optimal partitioning with untransformed species percentage data for the diatom core data (Birks & Gordon 1985). The analysis was implemented using the programme ZONE (Lotter & Juggins 1991). The broken-stick model and the associated approach described in Bennett (1996) was used to identify the number of statistically significant

partitions and hence the levels where diatom floristic changes have been most distinct.

Principal component analysis (PCA) was used to summarize the major trends in the diatom assemblages. Although all the sediments were subsampled at regular depth increments, variations in accumulation rate naturally lead to unequal spacing through time. The radiometric dating of sediment allows us to assess the temporal coherence of the major principal components. We can express the mutual coherence of the PCAs in terms of a correlation coefficient by firstly interpolating the PCAs at equal (5-y) time intervals using a linear interpolation scheme. The 5-y time interval was selected to be roughly equivalent to the average length of time each sample took to form. Secondly, Pearson correlation coefficients were calculated between the regularized PCA time series.

The relationship, since 1800, between diatom assemblage and change in air temperature at the five lakes were studied quantitatively. The analysis was carried out for each of the four climatic seasons and for the complete year. For each sediment horizon, in each lake, the average air temperature during the period of its accumulation was calculated. Five climatic time-series (the four seasonal temperatures and the annual temperature) were thus generated for each of the five lakes (data not shown). An important statistical point is that care was taken to use a method which only involved integration of the air temperatures and which avoided smoothing. Over-smoothing is a major statistical concern as it inevitably generates autocorrelation in time-series, and consequently leads to spuriously high correlations (Ramsey & Schafer 1996).

Past pH was reconstructed from the relative abundance of fossil diatoms using the unimodal-based technique of weighted averaging partial least squares (WA-PLS) regression (ter Braak & Juggins 1993). The inference model is based on the modern calibration dataset of surface-sediment diatom assemblages and associated water chemistry data collected from 64 lakes in the study region, and therefore appropriate for the five study lakes (Weckström & Korhola, 2001). The calibration dataset is expanded from the one described in Weckström *et al.* (1997), so that 26 new sites—mainly from high-elevation sites—have been added into it. The pH range in this updated training dataset is 5.0–7.8, and the predictive power of the diatom–pH prediction model, as assessed by leave-one-out cross-validation (jack-knifing), is 0.36 pH units (r^2_{jack} between the observed and predicted pH = 0.69) (Weckström, unpubl.).

Results and discussion

Figures 2 and 4 present the temperature anomalies and trends since 1800, the period for which the diatom

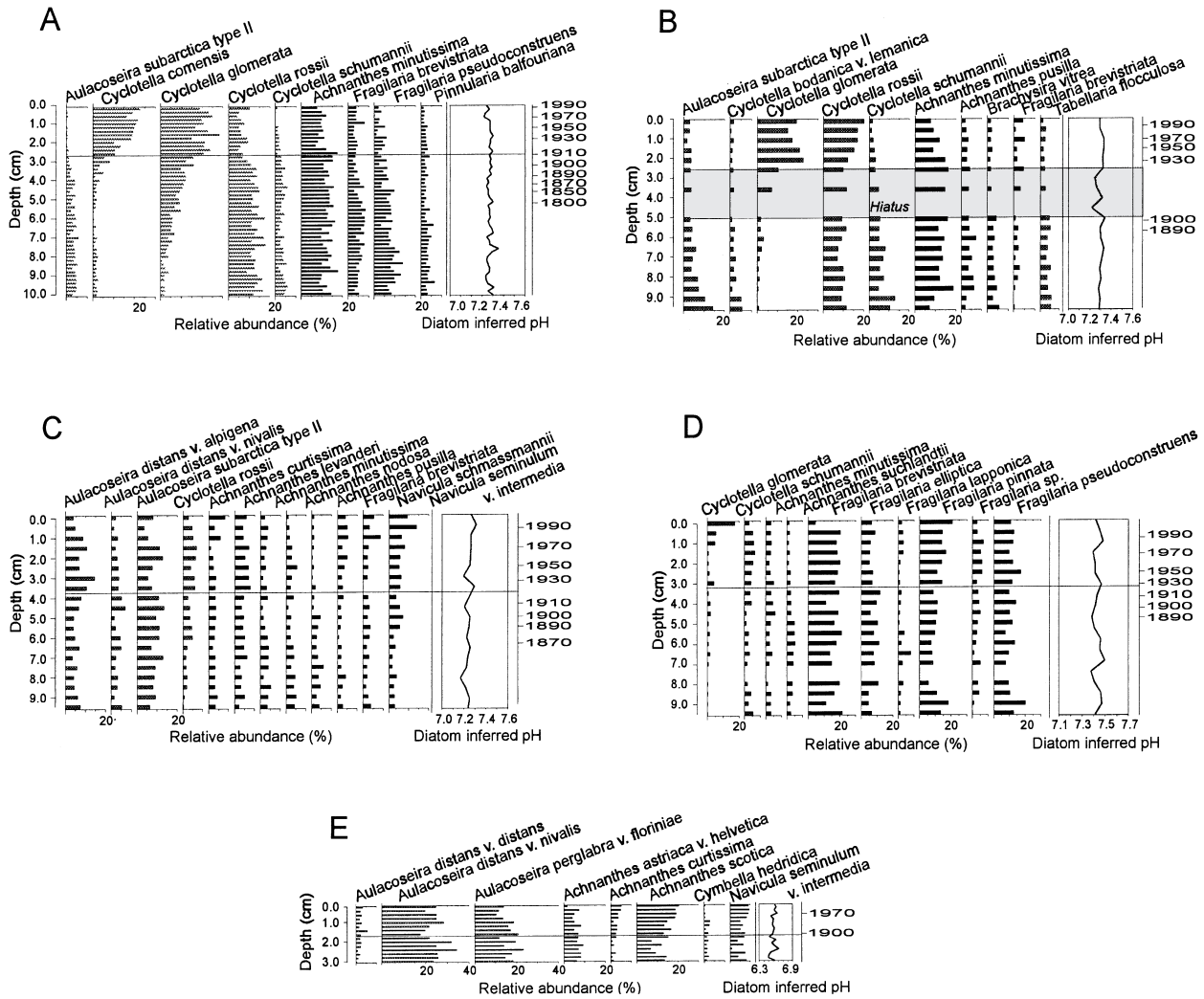


Fig. 3 Relative frequency diagrams of the most dominant (>5%) diatom taxa recorded in the sediments of the five study lakes, and diatom based pH reconstructions. A total of 356 diatom taxa were identified. The planktonic and tychoplanktonic taxa are shown in grey and the benthic taxa in black bars. Horizontal lines (in the case of Tsahkaljärvi the shaded area) indicate the locations of the statistically significant shifts in diatom assemblages as defined by optimal partitioning (Birks & Gordon 1985) and comparison with the broken-stick model (Bennet 1996). Saanjärvi (a), Tsahkaljärvi (b), Masehjärvi (c), Toskaljärvi (d) and Stuuramohkki (e).

assemblages are known. Seasonal trends in NW Finnish Lapland are plotted in Fig. 2, while annual trends for NW Finnish Lapland are displayed in Fig. 4(c) and the Arctic pattern in Fig. 4(d). The local post-18th century warming trend for NW Finnish Lapland (Fig. 4c) is found to have been rather similar to the northern hemispheric average. Both reveal an underlying general warming trend with periods of more rapidly rising temperatures through the 1920s and 1930s and from the mid-1970s onwards. A particularly pronounced increase in mean annual temperature, of about 1.5 °C, occurred in Lapland between the late 1880s and the mid-1930s (Fig. 4c). At the seasonal level, pronounced temperature fluctuations are again

found for Lapland. Each season follows its own pattern. Spring temperatures during the last 200 years (Fig. 2 and Fig. 4b) have shown the most rapid increases, rising fairly steadily since 1800 at an average rate of 0.005 °C y⁻¹. This increase is especially important as it forms part of an even longer warming trend in spring temperatures, since at least 1690, as revealed by the dates of ice break-up on river Tornionjoki. Although summer temperatures rose rapidly in the early 1900s, gradually falling summer temperatures at other times have resulted in there being a slight decline in summer temperatures over the last 200 years (Fig. 2). Although the 1940s saw a sharp rise in autumn temperatures, a subsequent steep fall in the 1970s

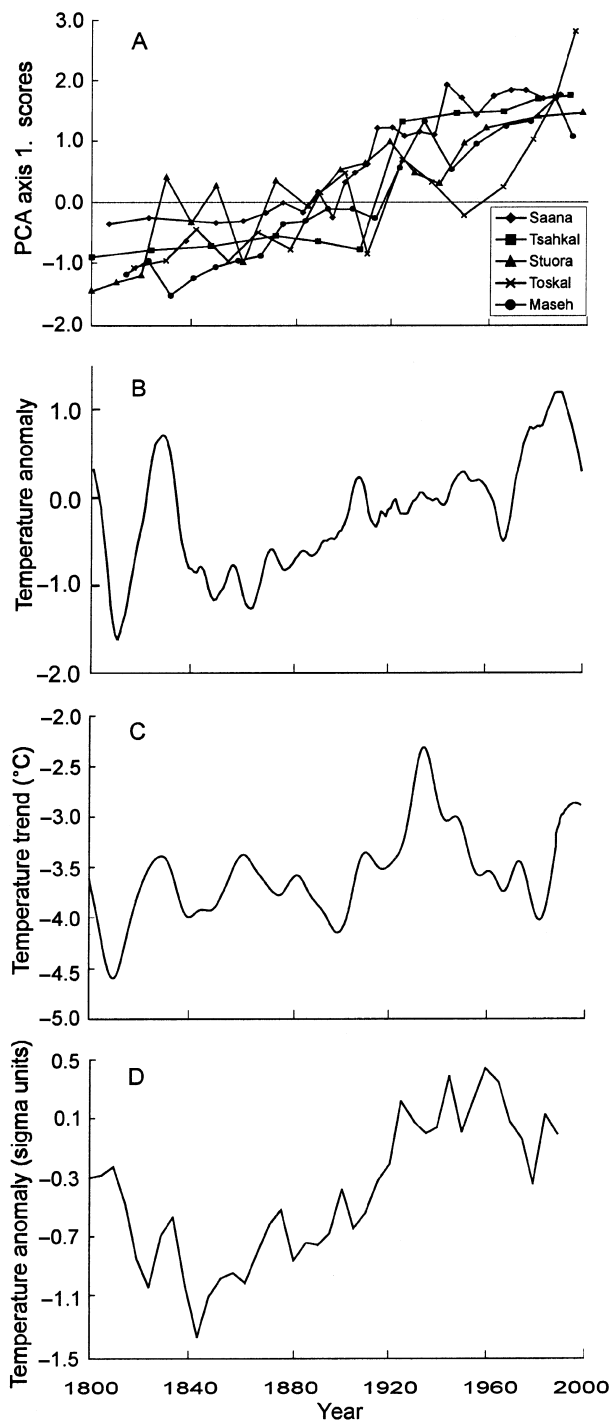


Fig. 4 Comparison of the diatom assemblage changes with the regional and Arctic-wide temperature anomalies. Principal components analysis (PCA) primary axis scores derived from the correlation matrices of the diatom percentage counts of the five study sites (a). Spring (MAM) temperature anomalies ($^{\circ}\text{C}$) for NW Finnish Lapland, smoothed using a 10-y low-pass filter (b). Annual air-temperature trend ($^{\circ}\text{C}$) for NW Finnish Lapland, smoothed using a 10-year low-pass filter (c). Standardized proxy Arctic-wide summer-weighted annual temperature, plotted as sigma units (d) (from Overpeck *et al.* 1997).

has left only an overall $0.003\text{ }^{\circ}\text{C y}^{-1}$ rise in autumn temperatures since 1800 (Fig. 2). Winter temperatures in Lapland are well known to show marked fluctuations from one year to another. These short-term fluctuations lead to the oscillatory nature of the smoothed winter temperature series of Fig. 2 which is superimposed on an overall winter warming trend of $0.008\text{ }^{\circ}\text{C y}^{-1}$.

Many of the broad features of the annual and seasonal fluctuations in Lapland temperatures described here have also been noted in the Helsinki (1829 onwards) record (Heino 1978). Their wide spatial coherence and regional importance is further confirmed in the long Uppsala and Stockholm data-series (Moberg & Bergstrom 1997). The early 20th century summer and winter seasonal warming which resulted in high temperatures in the 1930s and 1940s (Figs 2b and 2d), are particularly widespread (e.g. Jones & Briffa 1992). In Arctic time-series, in addition to Lapland, these climatic features are found as far afield as western Siberia (Salehard) and western Greenland (Godthaab), while southwards the same warming pattern is observed in Europe (e.g. Uppsala, Vienna and Budapest). Indeed summers in the 1930s were warmer than average over all northern continents, especially central North America (the dustbowl years), Greenland, NE Europe and parts of Siberia (Jones & Briffa 1992). Geographically coherent zones of regional climate change are not uncommon. They often form highly organized wave-like or alternating patterns. The Southern (Walker & Bliss 1932), North Atlantic (van Loon & Rogers 1978) and Arctic (Thompson & Wallace 1998) oscillations, with scale lengths of many thousands of kilometres, are well known examples. These large-scale pressure and temperature anomalies display positive correlations over distances of 2000-km or more (e.g. Hansen & Lebedeff 1987). Precipitation rates, instead, depend on vertical motions, moisture availability and vorticity in addition to advection of air masses, and consequently rainfall anomalies tend to occur over much shorter horizontal scales than those of pressure or temperature. Thus, aquatic ecosystem responses to climate change, especially those responses linked to temperature, can be expected to show consistency over wide geographical regions as opposed to being restricted to individual lakes or ponds.

Diatom assemblages showed clear changes in all study profiles (Fig. 3). The most conspicuous features were the increasing values of small planktonic *Cyclotella* and the reciprocal decrease in several benthic forms in the upper strata of the study cores of the thermally stratified lakes, whereas in isothermal lakes the species shifts occurred among the tychoplanktonic and benthic algae. Only one major, statistically significant zone boundary was discovered in each study profile by optimal partitioning and comparison with the broken stick model (see methods). This zone boundary, which indicates the

Table 2 Principal components analysis (PCA) of diatom data of each study site. Eigenvalues of the first four PCA axes

Lake	PCA axes			
	1	2	3	4
Saanajärvi	0.76	0.08	0.04	0.03
Tsahkaljavri	0.65	0.14	0.06	0.04
Toskaljärvi	0.61	0.20	0.07	0.04
Stuoramohkki	0.45	0.16	0.13	0.05
Masehjavri	0.29	0.17	0.14	0.08

Table 3 Correlation coefficients between the first PCA axis scores of the five study sites. All correlations are statistically highly significant at $P < 0.0001$

	Saanajärvi	Tsahkaljavri	Stuoramohkki	Toskaljärvi	Masehjavri
Saanajärvi	1.00	0.95	0.84	0.74	0.94
Tsahkaljavri	0.95	1.00	0.77	0.75	0.93
Stuoramohkki	0.84	0.77	1.00	0.75	0.82
Toskaljärvi	0.74	0.75	0.75	1.00	0.86
Masehjavri	0.94	0.93	0.82	0.86	1.00

main period of change in the diatom compositions, occurred more or less synchronously between the study sites dating between *c.* 1900 (Stuoramohkki) and 1920 (Masehjavri) (Fig. 3).

The first PCA axis captured between 29% (Masehjavri) and 76% (Saanajärvi) of the total variance in the species data (Table 2). Table 3 shows the PCA axis scores to be highly mutually correlated (average correlation coefficient +0.84); all 10 coefficients are statistically significant at $P = 0.001$. This mutual coherence, along with the fact that the first principal components capture in most cases (with exception to Masehjavri) more than three times the total floristic variance of the second PCA axis (Table 2), suggests consistent changes in diatom assemblages between the five lakes.

The sample scores on the primary PCA axis are plotted stratigraphically in Fig. 4(a). Gradually increasing PCA axis 1 scores from the mid-19th century indicate changes in species compositions, with the most pronounced floristic shift occurring around the turn of the 20th century. The overall patterns in the curves follow closely the reconstructed climate history in this region (Fig. 4b,c) as well as the reconstructed Arctic summer temperature anomalies (Fig. 4d). The correlation coefficients of the five climate series (four climatic seasons and the complete year) with the first principal component for each lake are tabulated in Table 4. Only the coefficients that are significant at $P < 0.05$ are shown. All five lakes are found

to have significant correlations between spring (March to May) mean air temperature and PCA axis 1 sample scores. Three of the lakes also reveal significant correlations with the mean annual temperatures. However, the diatom response was evidently not fully linear to climate forcing, but the lake systems seemed to contain internal thresholds which, once crossed, have led to positive feedback and consequent rapid stepwise shift to a new equilibrium state.

A noticeable difference between the temporal validation approach to elucidating the climatic control on diatom communities, as employed here, and the more usual spatial calibration methodology (e.g. Pienitz *et al.* 1995; Lotter *et al.* 1997; Weckström *et al.* 1997) is that herein spring, rather than summer, temperatures show a significant relationship with compositional structure. One explanation for this difference could be that the training sets of the local elevation gradients commonly used in the spatial studies, have insufficient information content to differentiate satisfactorily between the climatic seasons (i.e. their seasonal climatic 'lapse-rates' vary colinearly). By contrast, over decadal and centennial time periods, seasonal temperatures reveal quite different trends and, hence, provide a potentially richer approach to climate calibration. Thus, through the temporal study of five lakes we have been able to identify a springtime climate signal.

The overall diatom diversity (N_2 index) in our five study sites was found to be negatively correlated with

Table 4 The statistically significant ($P < 0.05$) correlation coefficients between the first PCA axis and mean air temperature

	Saanajärvi	Tsahkaljavri	Stuoramohkki	Toskaljärvi	Masehjavri
Year	0.39	0.62	–	–	0.55
MAM	0.52	0.68	0.53	0.70	0.56
JJA	–	–	–	–	–
SON	0.39	–	–	–	–
DJF	–	–	–	–	0.45

Year, Mean annual temperature; MAM, March, April, May; JJA, June, July, August; SON, September, October, November; DJF, December, January, February

altitude/temperature with the highest species diversity in the warmest and lowest-lying lake (Masehjavri) and the lowest diversity in the coldest and highest site (Stuoramohkki). In their survey on modern diatom distributions in northern Fennoscandia, Weckström & Korhola (2001) similarly found highest diatom diversity in lakes of the mountain birch woodland zone from where the diversity declined progressively towards the cold, arctic lakes in the tundra.

In the case of the three stratified lakes, the temporal change in diatom composition was also reflected by diatom species richness. Diatom diversity exhibited an inverse relationship with the PCA sample scores; since 1800 there was a gradual decrease in species richness followed by a sharper fall around 1900 (Fig. 5). Diversity in the two unstratified lakes showed either no response (Stuoramohkki) or revealed only a slightly decreasing trend (Masehjavri) during the studied time interval.

Because of the major importance of diatoms to the food webs and general functioning of the northern freshwaters, one might expect that the impacts of the diatom change would reflect on other ecosystem levels as well. Our detailed work on one of the sampled lakes (Saana-järvi) has corroborated this expectation; the change in diatom assemblages was accompanied by simultaneous shifts in other biological indicators, such as zooplankton and chrysophytes, and was further reflected by increased rates of organic matter accumulation and higher pigment concentrations (Korhola *et al.* in press b). These synchronous stratigraphic changes of many proxy indicators point to a major ecosystem change in the region beginning in the late 19th century.

The mechanisms underlying the proposed relationship between diatom species shifts and temperature are not immediately obvious. Diatoms might reflect climate variability in several different ways: direct temperature effects (Raven & Geider 1988), stratification and mixing (Bradbury 1988; Gaedke *et al.* 1998), through water quality change (Psenner & Schmidt 1992; Anderson *et al.* 1996), and through habitat change (Smol 1988; Lotter & Bigler 2000; Rautio *et al.* 2000).

Climatic warming is expected to affect directly the productivity, life history and reproduction of diatoms through the increased average and maximum water temperatures, extended growing season and increased light penetration during shorter periods of surface freezing. The duration of the ice-free period in these high-latitude waters is determined largely by spring (March to May) temperatures (Bilello 1964). Also the length of the snow cover season in northern Finland is determined predominantly by the spring temperature (Tuomenvirta & Heino 1996). Magnuson *et al.* (2000) reported significant trends toward reduced ice-cover during the last 150 years in their recent broadscale survey of northern hemispheric lakes and rivers. In line with their observations, we postulate that the post-Little Ice Age warming, in particular in spring temperatures (Fig. 2), may have lengthened the duration of the ice-free period – and hence growing season – and resulted in the development of the present steep summer stratification in three of the study lakes

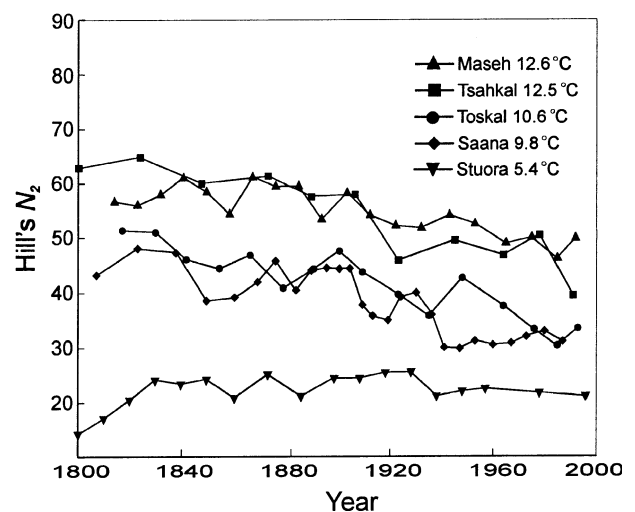


Fig. 5 Temporal variations in diatom diversity (Hill's N_2 diversity measured from Hill's (1973) family of diversity indices) in each study site. The present-day epilimnetic temperature of the lake is also indicated.

(see Hondzo & Stefan 1993; De Stasio *et al.* 1996). The water column stability is known to strongly affect the light, nutrient, oxygen and pH regime that planktonic organisms experience (Tilzer & Schwarz 1976; Gaedke *et al.* 1998). The increased thermal stability along with shorter ice-cover may thus have created more favourable conditions for the growth of plankton and may have changed the overall primary production from benthos to plankton (Lotter & Bigler 2000; Smol & Cumming 2000). This typological change resulted in the decreased species diversity. Higher temperature and increased resources have favoured the small planktonic species with rapid growth rates and these have become dominant enough to reduce the diversity.

In the two unstratified lakes, the species changes are somewhat weaker, as suggested by lower percentages explained by the PCA. In isothermal lakes primary production is shown to be controlled predominantly by internal factors in contrast to dimictic lakes, where the primary production seems to be more sensitive to external forcing, such as climate change (Agbeti *et al.* 1997). However, changes in ice-cover may also trigger alterations in species compositions within the periphytic diatoms (Smol 1988).

An alternative explanation for the present findings can be sought in acid deposition. At lower latitudes, the biota of lakes, especially those downwind of the major industrial regions of North America and Europe, have been modified strongly by the effects of acid rain (Battarbee *et al.* 1990). We therefore reconstructed the pH for each lake using a transfer function based on the local diatom-pH training dataset. However, only minor trends in the diatom-inferred pH values were noted in each site with all pH variation lying within the standard error of the model estimate (Fig. 3). The marked stability in the reconstructed pH values, and the fact that all diatom taxa that increase in the post-1900 sediments are indicative of nonacidic, neutral waters (Pienitz *et al.* 1996; Sorvari & Korhola 1998), lead us to conclude that the lakes studied herein have remained clean and that atmospheric fallout of acid substances thus cannot have been the driving force for the observed biological changes. Similarly, no evidence of acidification in northeastern Lapland lakes have been noted despite much higher local acid deposition from the smelter industry in Russia (Korhola *et al.* 1999).

Direct catchment impact by humans can almost certainly also be ruled out as a potential explanatory factor because the study area is remote, rocky, sparsely vegetated and hence unsuitable for any land use. There is also little evidence of atmospheric nutrient deposition either in the sedimentary deposits (in the form, e.g. eutrophication) or in the present limnology of the lakes. Finnish Lapland, nevertheless, receives some nutrient deposition from southern Scandinavia and Europe. The

values are, however, low: NO_3 $0.07 \text{ gN m}^{-2} \text{ y}^{-1}$, NH_4 $0.025 \text{ gN m}^{-2} \text{ y}^{-1}$ compared to values in southern Finland of $0.15 \text{ gN m}^{-2} \text{ y}^{-1}$ and $0.25 \text{ gN m}^{-2} \text{ y}^{-1}$, respectively (Järvinen & Vänni 1990). Catalan *et al.* (in press) compared nitrogen values in alpine and arctic lakes in Europe, and they found lowest nitrogen values in waters of northern Fennoscandia and Spain.

The planktonic diatoms (i.e. the small *Cyclotella* taxa) that play the most important role in the species compositional changes in the studied lakes all bloom during the autumnal overturn (Rautio *et al.* 2000) when alpine and arctic lakes with short ice-free period typically have their maximum algal productivity (Catalan *et al.* in press). However, the only period of major external nutrient influence occurs in the studied lakes during spring when nutrient compounds that are stored during long winter into the snow pack, are transported into the lakes with melt waters. During the rest of the open-water period, nutrient levels are constantly very low. In the five lakes studied herein, $\text{PO}_4\text{-P}$ was constantly under the detection limit, total phosphorus (TP) ranged between 3 and $6 \mu\text{g L}^{-1}$, $\text{NO}_3\text{-N}$ had a median of $22 \mu\text{g L}^{-1}$, and $\text{NH}_4\text{-N}$ had a median of $6.5 \mu\text{g L}^{-1}$. Although the sites may receive some extra nitrogen loading through atmospheric deposition, phosphorus is nevertheless the limiting nutrient for the primary production in these lakes as is the case for most of the Arctic waters (Schindler *et al.* 1974; McCoy 1983).

Although this study is the first to document concurrent changes in recent aquatic communities in the Euro-Asian Arctic, the present results are consistent with records of massive diatom species shifts over the past 150 years in the Canadian Arctic (Douglas *et al.* 1994; Gajewski *et al.* 1997; Rühland & Smol, pers. comm.). The physical and chemical differences between the lakes, the wide geographical coverage and concomitance of the changes, as well as the nature and magnitude of the changes (in many cases from benthos to plankton), all indicate a regional rather than a local cause. The rapid replacement of species populations in many lakes suggests that the warming in the Arctic some 150–100 years ago may have caused a critical threshold of ice cover and growing season duration on the lakes to be exceeded thereby altering the species compositions. If the rate of warming accelerates in the future, as has been consistently predicted by several generations of atmospheric general circulation models (e.g. Mitchell & Schlesinger 1989), we should expect biological and ecological changes in arctic and subarctic lakes to continue.

Acknowledgements

We thank J Weckström for help in pH reconstruction, M Rautio for fruitful discussions and help in the fieldwork, and JP Smol, V Jones and an anonymous journal referee for their constructive

comments on the original manuscript. We also thank the staff of the Kilpisjärvi Biological Station and The Finnish Forest Research Institute, Kilpisjärvi Branch, for their hospitality and for logistic help. The work was supported by the Academy of Finland (grant 101 7383), by the European Community, Environment and Climate Programme (MOLAR Project; Contract No. ENV4 CT95 0007) and by the NERC (grant GR9/04195).

References

- Agbeti MD, Kingston JC, Smol JP, Watters C (1997) Comparison of phytoplankton succession in two lakes of different mixing regimes. *Archiv für Hydrobiologie*, **140**, 37–69.
- Anderson NJ, Odgaard B, Segerström U, Renberg I (1996) Climate–lake interactions recorded in varved sediments from a Swedish boreal forest lake. *Global Change Biology*, **2**, 399–405.
- Appleby PG, Nolan PJ, Gifford DW *et al.* (1986) ^{210}Pb dating by low background gamma counting. *Hydrobiologia*, **141**, 21–27.
- Battarbee RW, Mason J, Renberg I, Talling J (1990). *Palaeolimnology and Lake Acidification* The Royal Society, London.
- Bennett KG (1996) Determination of the number of zones in a biostratigraphical sequence. *New Phytologist*, **132**, 155–170.
- Bilello MA (1964) Method for predicting river and lake ice formation. *Journal of Applied Meteorology*, **3**, 38–44.
- Birks HJB, Gordon AD (1985) *Numerical Methods in Quaternary Pollen Analysis*. Academic Press, London.
- Bloomfield P (1976) *Fourier Analysis of Time Series. An Introduction*. Wiley, New York.
- ter Braak CJF, Juggins S (1993) Weighted averaging partial least squares regression (WA-PLS). An improved method for reconstructing environmental variables from species assemblages. *Hydrobiologia*, **269/270**, 485–502.
- Bradbury J (1988) A. climatic-limnological model of diatom succession for paleolimnological interpretation of varved sediments at Elk Lake. *Journal of Paleolimnology*, **1**, 115–131.
- Catalan J, Ventura M, Brancelj A *et al.* (in press) Seasonal variability in remote mountain lakes: implications for climatic signals in their sediment record. *Journal of Paleolimnology*, in press.
- Cleveland WS, Devlin SJ (1988) Locally-weighted regression: an approach to regression analysis by local fitting. *Journal of the American Statistical Association*, **83**, 596–610.
- Crowley TJ (2000) Causes of climate change over the past 1000 years. *Science*, **289**, 270–277.
- De Stasio BT, Hill DK, Kleinmans JM, Nibbelink NP, Magnuson JJ (1996) Potential effects of global change on small north-temperate lakes: Physics, fish, and plankton. *Limnology and Oceanography*, **41**, 1136–1149.
- Douglas MSV, Smol JP (1995) Periphytic diatom assemblages from high Arctic ponds. *Journal of Phycology*, **31**, 60–69.
- Douglas MSV, Smol JP, Blake W Jr (1994) Marked post-18th century environmental change in high-arctic ecosystems. *Science*, **266**, 416–419.
- Gaedke U, Ollinger D, Kirner P, Bäuerle E (1998) The influence of weather conditions on the lake seasonal plankton development in a large and deep lake (L. Constance). III. The impact of water column stability on spring algal development. In: *Management of Lakes and Reservoirs During Global Climate Change* (eds George D *et al.*), pp. 71–84. Kluwer, Dordrecht.
- Gajewski K, Hamilton PB, McNeely R (1997) A. high resolution proxy-climate record from an arctic lake with annually-laminated sediments on Devon Island, Nunavut, Canada. *Journal of Paleolimnology*, **17**, 215–225.
- Geisser S (1975) The predictive sample reuse method with applications. *Journal of the American Statistical Association*, **70**, 320–328.
- Glew JR (1991) Miniature gravity corer for recovering short sediment cores. *Journal of Paleolimnology*, **5**, 285–287.
- Hansen J, Lebedeff S (1987) Global trends of measured surface air temperature. *Journal of Geophysical Research*, **92**, 13, 345–13, 372.
- Heino R (1978) Climatic change in Finland during the last hundred years. *Fennia*, **150**, 3–13.
- Hill MO (1973) Diversity and evenness. a unifying notation and its consequences. *Ecology*, **54**, 427–432.
- Hill MO (1979) *DECORANA. A FORTRAN program for detrended correspondence analysis and reciprocal averaging*. Section of Ecology and Systematics, Cornell University, Ithaca, NY.
- Hondzo M, Stefan HG (1993) Regional water temperature characteristics of lake subjected to climate change. *Climatic Change*, **24**, 187–211.
- Jones PD, Briffa KR (1992) Global surface air temperature variations during the twentieth century. *The Holocene*, **2**, 165–179.
- Järvinen O, Vänni T (1990) Bulk deposition chemistry in Finland. In: *Acidification in Finland* (eds Kauppi P, Anttila P, Kentlamies K), Springer, Berlin.
- Korhola A, Weckström J, Nyman M (1999) Predicting the long-term acidification trends in small subarctic lakes using diatoms. *Journal of Applied Ecology*, **36**, 1021–1034.
- Korhola A, Weckström J, Blom T (in press) Relationships between lake and land-cover features along latitudinal vegetation ecotones in arctic Fennoscandia. *Archiv für Hydrobiologie*, in press a.
- Korhola A, Sorvari S, Rautio M *et al.* (in press) A multi-proxy analysis of climate impacts on recent development of subarctic Lake Saanajärvi in Finnish Lapland. *Journal of Paleolimnology*, in press b.
- Lotter AF, Juggins S (1991) PLOPROF, TRAN and ZONE. Programs for plotting, editing and zoning of pollen and diatom data. INQUA Commission for the study of the Holocene; Working Group on Data Handling Methods, Newsletter 6. www.kv.geo.uu.se/inqua/nlindex.htm
- Lotter AF, Birks HJB, Hofmann W, Marchetto A (1997). Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. I. Climate. *Journal of Paleolimnology*, **18**, 395–420.
- Lotter AF, Bigler C (2000) Do diatoms in the Swiss Alps reflect the length of ice-cover? *Aquatic Science*, **62**, 125–141.
- Magnuson JJ, Robertson DM, Benson BJ *et al.* (2000) Historical trends in lake and river ice cover in the Northern Hemisphere. *Science*, **289**, 1743–1746.
- Manley G (1974) Central England temperature: monthly means 1659–1973. *Quarterly Journal of the Royal Meteorological Society of*, **100**, 389–405.
- Mann ME, Bradley RS, Hughes MK (1998) Global-scale temperature patterns and climate forcing over the past six centuries. *Nature*, **392**, 779–787.

- McCoy GA (1983) Nutrient limitation in two arctic lakes. *Alaska Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 1195–1202.
- Moberg A, Bergstrom H (1997) Homogenization of Swedish temperature data. Part III: The long temperature records from Uppsala and Stockholm. *International Journal of Climatology*, **17**, 667–699.
- Overpeck J, Hughen D, Hardy R *et al.* (1997) Arctic environmental change of the last four centuries. *Science*, **278**, 1251–1256.
- Peet RK (1974) The measurement of species diversity. *Annual Review of Ecology and Systematics*, **5**, 285–307.
- Pienitz R, Smol JP, Birks HJB (1995) Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories, Canada. *Journal of Paleolimnology*, **13**, 21–49.
- Pienitz R, Douglas MSV, Smol JP, Huttunen P, Meriläinen J (1996) Siliceous algal and protozoan distributions along a latitudinal transect in Fennoscandia. *Ecography*, **18**, 429–439.
- Psenner R, Schmidt R (1992) Climate-driven pH control of remote alpine lakes and effects of acid deposition. *Nature*, **356**, 781–783.
- Ramsey FL, Schafer DW (1996) *The Statistical Sleuth: a Course in Methods of Data Analysis*. Duxbury Press, Belmont, California.
- Rautio M, Sorvari S, Korhola A (2000) Diatom and crustacean zooplankton communities, their seasonal variability, and representation in the sediment of subarctic Lake Saanajärvi. *Journal of Limnology*, **59**, 81–96.
- Raven J, Geider R (1988) Temperature and algal growth. *New Phytologist*, **110**, 441–461.
- Rouse WR, Douglas MSV, Hecky RE *et al.* (1997) Effects of climate change on the freshwaters of arctic and subarctic North America. In: *Freshwater Ecosystems and Climate Change in North America* (ed. Cushing C), pp. 55–84. John Wiley & Sons, Chichester.
- Rühling Å (1992) *Atmospheric heavy metal deposition in northern Europe 1990*. Nordic Council of Ministers, Copenhagen
- Schlesinger M, Mitchell J (1987) Climate model calculations of the equilibrium climate response to increased carbon dioxide. *Review of Geophysics*, **25**, 760–798.
- Schindler DW, Welch HE, Kalff J *et al.* (1974) Physical and chemical limnology of Char Lake, Cornwallis Island (75° N Lat.). *Journal of Fisheries Research Board of Canada*, **31**, 585–607.
- Smol JP (1988) Paleoclimate proxy data from freshwater arctic diatoms. *Verhandlungen der Internationalen Vereinigung für Limnologie*, **23**, 837–844.
- Smol JP, Cumming BF (2000) Tracking long-term changes in climate using algal indicators in lake sediments. *Journal of Phycology*, **36**, 986–1011.
- Sorvari S, Korhola A (1998) Recent diatom assemblage changes in subarctic Lake Saanajärvi, NW Finnish Lapland, and their palaeoenvironmental implications. *Journal of Paleolimnology*, **20**, 205–215.
- Sorvari S, Rautio M, Korhola A (2000) Seasonal dynamics of subarctic Lake Saanajärvi in Finnish Lapland. *Verhandlungen der Internationalen Vereinigung für Limnologie*, **27**, 507–512.
- Stoermer EF, Smol JP (eds) (1999) *The Diatoms. Applications for the Environmental and Earth Sciences* Cambridge University Press, Cambridge.
- Thompson DWT, Wallace JM (1998) The Arctic Oscillation signature in the wintertime geopotential height and temperature fields. *Geophysical Research Letters*, **25**, 1297–1300.
- Tilzer M, Schwarz K (1976) Seasonal and vertical patterns of phytoplankton light adaptation in a high-mountain lake. *Archiv für Hydrobiologie*, **77**, 488–504.
- Tuomenvirta H, Heino R (1996) Climatic changes in Finland – recent findings. *Geophysica*, **32**, 61–75.
- van Loon H, Rogers JC (1978) The seesaw in winter temperatures between Greenland and Northern Europe. Part I: General description. *Monthly Weather Review*, **106**, 296–310.
- Walker GT, Bliss EW (1932) World Weather V. *Memoirs of the Royal Meteorological Society*, **4**, 53–84.
- Weckström J, Korhola A (2001) Patterns in the distribution, composition and diversity of diatom assemblages in relation to climatic factors in Arctic Lapland. *Journal of Biogeography*, **28**, 31–45.
- Weckström J, Korhola A, Blom T (1997) The relationship between diatoms and water temperature in 30 subarctic Fennoscandian lakes. *Arctic and Alpine Research*, **29**, 75–92.
- Welch H (1991) Comparison between lakes and seas during the arctic winter. *Arctic and Alpine Research*, **23**, 11–23.