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Comparing palaeolimnological and instrumental evidence of climate change for remote mountain lakes over the last 200 years

Richard W. Battarbee[1], John-Arvid Grytnes[2], Roy Thompson[3], Peter G. Appleby[4], Jordi Catalan[5], Atte Korhola[6], H.J.B. Birks[1,2] , Einar Heegaard[2] & Andrea Lami[7]
[1]*Environmental Change Research Centre, University College London, 26 Bedford Way, London WC1H 0AP, UK (E-mail: rbattarb@geography.ucl.ac.uk)*
[2]*Botanical Institute, University of Bergen, Allegaten 14, N-5007 Bergen, Norway*
[3]*Department of Geology and Geophysics, University of Edinburgh, West Mains Road Edinburgh, EH9 3JW, Scotland, UK*
[4]*Department of Applied Mathematics and Theoretical Physics, The University of Liverpool, P.O. Box 147, Liverpool, L69 3BX, UK*
[5]*Department d'Ecologia, Universitat de Barcelona, Diagonal 645, E- 08028 Barcelona, Spain*
[6]*Department of Ecology and Systematics, Division of Hydrobiology, P.O. Box 17 (Arkadiankatu 7), FIN-00014 University of Helsinki, Finland*
[7]*C.N.R. Istituto Italiano di Idrobiologia, Largo Tonolli 50, Verbania, I-28048 Pallanza, Italy*

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Abstract

This paper compares the palaeolimnological evidence for climate change over the last 200 years with instrumental climate data for the same period at seven European remote mountain lakes. The sites are Øvre Neådalsvatn (Norway), Saanajärvi (Finland), Gossenköllesee (Austria), Hagelseewli (Switzerland), Jezero v Ledvici (Slovenia), Estany Redó (Spain, Pyrenees), and Nižné Terianske Pleso (Slovakia). We used multiple regression analysis to transfer homogenised lowland air temperature records to each of the sites, and these reconstructions were validated using data from on-site automatic weather stations. These data showed that mean annual temperature has varied over the last 200 years at each site by between 1 and 2 °C, typical of the high frequency variability found throughout the Holocene, and appropriate, therefore, to test the sensitivity of the various proxy methods used. Sediment cores from each site were radiometrically dated using ^{210}Pb, ^{137}Cs and ^{241}Am and analysed for loss-on-ignition, C, N, S, pigments, diatoms, chrysophytes, Cladocera and chironomids. Comparisons between the proxy data and the instrumental data were based on linear regression analysis with the proxy data treated as response variables and the instrumental data (after smoothing using LOESS regressions) as predictor variables. The results showed few clear or consistent patterns with generally low or very low r^2 values. Highest values were found when the data were compared after smoothing using a broad span, indicating that some of the proxy data were capturing climate variability but only at a relatively coarse time resolution. Probable reasons for the weak performance of the methods used include inaccurate dating, especially for earlier time periods, the influence of confounding forcing factors at

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some sites e.g., air pollution, earthquakes, and the insensitivity of some methods to low amplitude climate forcing. Nevertheless, there were trends in some proxy records at a number of sites that had a relatively unambiguous correspondence with the instrumental climate records. These included organic matter and associated variables (C and N) and planktonic diatom assemblages at the majority of sites and chrysophytes and chironomids at a few sites. Overall for longer term studies of the Holocene, these results indicate the need to be cautious in the interpretation of proxy records, the importance of proxy method validation, the continuing need to use reinforcing multi-proxy approaches, and the need for careful site and method selection.

Introduction

Lake ecosystems of all types are likely to be sensitive to changes in climate. While the specific response of any lake will be individual we might expect that lakes of similar types (e.g., closed basin lakes, crater lakes, mountain lakes) will react to climate forcing in a broadly similar way. If we are to use lake sediments to reconstruct climate change we need to understand how the climate change signals in lake sediments are generated, and for any individual lake or type of lake we need to know which climate proxies perform best. This can be achieved by studying the contemporary relationship between climate variability and water column processes and by comparing the recent palaeolimnological record and the instrumental record for the time-span covered by the instrumental record. A key problem, however, is that human impact on most lake ecosystems, especially in Europe, potentially confounds the climate signal. In this study we have attempted to avoid this problem by focussing on remote mountain lakes.

The climatic impact on mountain lakes is mediated mainly through changes in temperature, precipitation and wind regimes that affect snow and ice cover, catchment hydrology, and water column stratification and mixing. These, in turn, control many chemical and biological processes such as primary production, nutrient cycling, hypolimnetic O_2 consumption, alkalinity generation and water column pH, and have a strong influence directly on habitat characteristics and distribution, and on biological life-cycles.

The extent to which any such change can be identified in the sediment record depends on (i) the suitability of study sites, especially their lack of disturbance from non-climatic influences; (ii) the quality of the sediment record and the rate of sediment accumulation; (iii) the availability and quality of the instrumental climate data that can be used at any particular site; (iv) the sensitivity of the various proxy methods to low amplitude variability; (v) the extent to which sites and species are forced across important physical, chemical or biological thresholds; and (vi) an understanding of the processes that link climate forcing and lake response, and that link lake response and the formation of the permanent sediment record.

In this paper we assess these issues with respect to the data from the Mountain Lake Research (MOLAR) sub-project on climate change described in the previous papers in this volume. Further details of the MOLAR project are presented by Battarbee et al. (in press).

Sites

In Europe it is difficult to find ‘pristine’ lakes that are ideal for a study of this kind. Most lowland lakes and many upland lakes are affected by land-use change and eutrophication and many upland and mountain lakes are also influenced by air pollution. However, whilst all sites in Europe are contaminated by fly ash, metals and trace organic compounds (e.g., Rose, 1995; Bindler et al., 2001; Grimalt et al., 2001) and receive acid deposition, it is possible to identify sites where these problems are minimised. In this study we have assumed that trace metals and trace organic contaminants, whilst demonstrably present at all sites, have had little impact on the overall structure of mountain lake ecosystems, and we have further assumed that problems of acid deposition can be avoided either by selecting sites in low deposition areas or sites that are well buffered against acidity.

Three of the sites selected in this study (Figure 1) were included in the AL:PE.2 study (Wathne et al., 1997), and belong to the group of sites identified in that project to be least influenced by acid deposition and other pollutants. Additional sites that provide the study with a wider geographical and chemical range are located in Finland, Austria, Switzerland and Slovenia.

The sites are: Øvre Neådalsvatn (Norway), Saanajärvi (Finland), Gossenköllesee (Austria), Hagelseewli (Switzerland), Jezero v Ledvici (Slovenia), Estany Redó (Spain, Pyrenees), and Nižné Terianske Pleso (Slovakia).

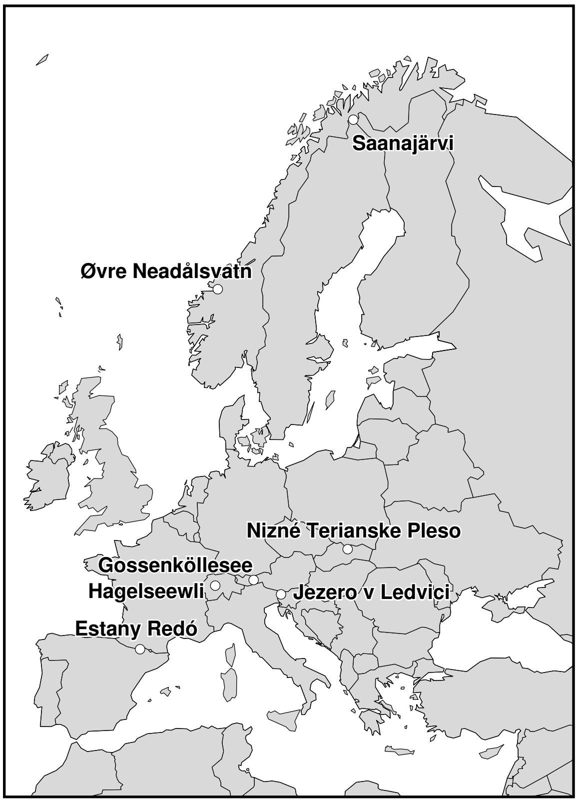

Figure 1. Location map of lake sites (from Battarbee et al. this issue).

Instrumental climate data

In the MOLAR study we have used multiple regression analysis to transfer homogenised lowland air temperature records to upland sites. Following lapse rate corrections for differences in altitude this has allowed us to reconstruct monthly mean temperature for each study lake for the period from 1781–1997. Details of the methods used are given in Agustí-Panareda et al. (2000), and Agustí-Panareda and Thompson (this issue).

The accuracy of the individual reconstructions was tested using data from the on-site automatic weather stations for 1996 and 1997, and these comparisons showed that typical reconstruction errors were about 1.3 °C for low-sun months and 0.98 °C for high-sun months.

The mean annual temperature reconstructed from the instrumental records for each study site is shown in Figure 2. The data show some nineteenth century cooling at the easternmost sites (Nižné Terianske Pleso, Jezero v Ledvici) but, despite considerable decadal variability, there is little overall trend at other sites during the nineteenth century. During the twentieth century all sites show a warming trend during the first few decades of the century, peaking in approximately 1950 at most sites but in the 1930's at the two Fennoscandian sites (Øvre Neådalsvatn, Saanajärvi). All sites show a relatively steep warming trend over the last 10–20 years of the century.

The data also show changes in other climate variables that may have ecological significance such as monthly or seasonal means and continentality (winter-summer). In addition the period of ice-cover can be calculated as the number of days with temperature below zero, or by subtracting the number of negative degree days from the number of positive degree days for each year (Agustí-Panareda et al., 2000). However, at Hagelseewli in Switzerland the relationship between air temperature and water temperature was poor due to the shading effect of a high cliff face on the south side of the lake.

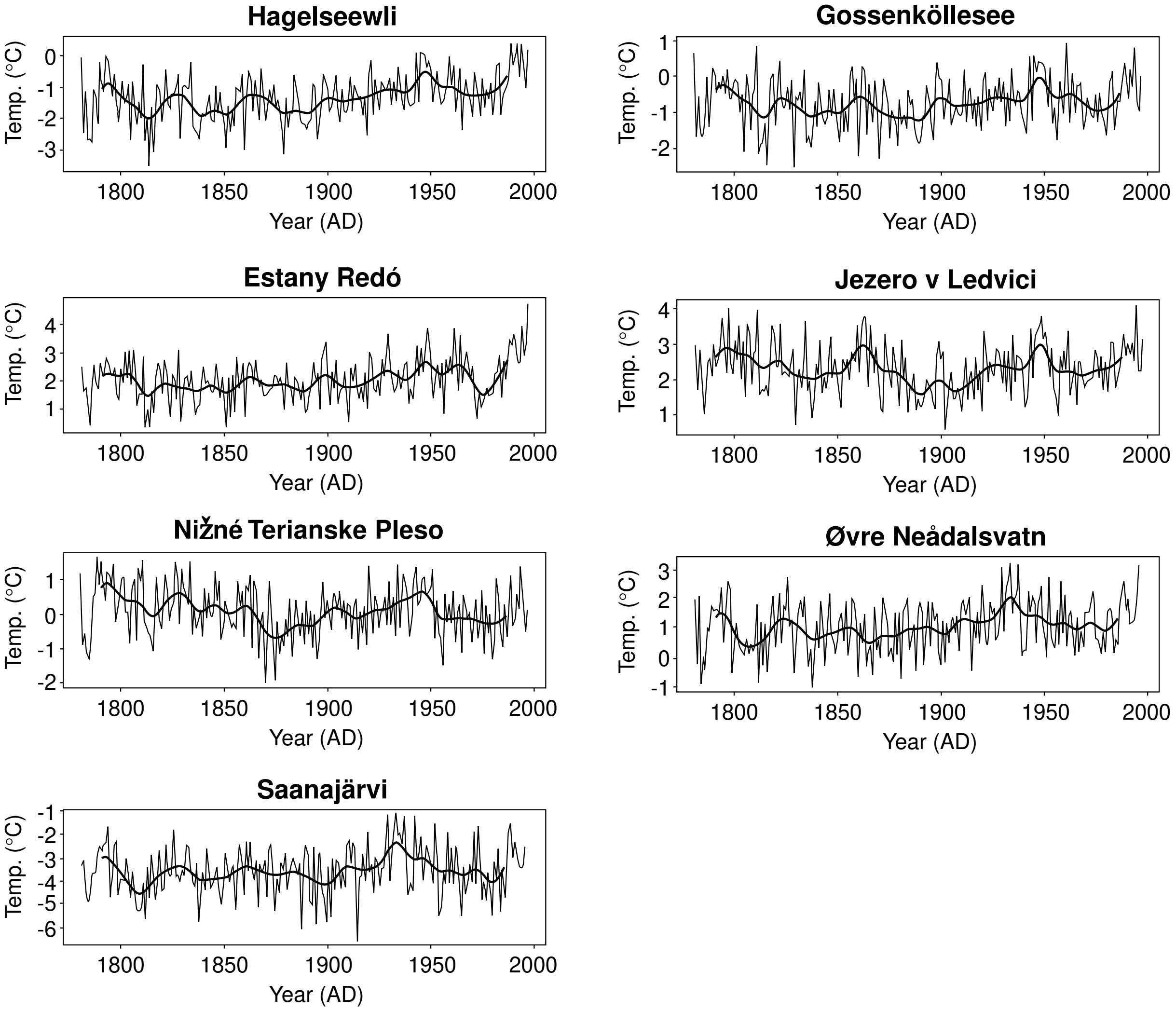

Figure 2. Time series of air-temperature reconstructions from 1791–1997 for the seven lakes shown in Figure 1. The annual means are represented by thin lines and the decadal variabilities are represented by the thick lines.

Lake characteristics

The lakes in this study are all situated above or beyond the regional tree-line, and they have sparsely vegetated catchments with thin soils. Although different in depth and climate setting they share some physical characteristics. They have a winter ice-cover (typically from 5–9 months) and a weak summer thermocline. Summer water temperature rarely exceeds 15 °C.

The lakes are well-oxygenated in summer but all, especially the small, shallow lakes, Gossenköllesee and Hagelseewli, show significant oxygen depletion in winter during the ice-cover period. Total phosphorus values are extremely low with mean values between 0.1 and 1 μmol l^{-1} and phosphorus is generally the limiting nutrient in all the lakes and at most time periods (Catalan et al., this issue (a)). Chl*a* values (not shown) range from from less than 1 μg l^{-1} to about 4 μg l^{-1}. Lakes with a short ice-free period showed a single chlorophyll maximum between August and October during the period of summer stratification, whereas Redo, with a longer ice-free period showed two peaks, one at the beginning of the ice-free period in July/August and the second towards the end in October/November (Catalan et al., this issue (a)). In all cases, as is typical for mountain lakes, the chl*a* maximum is found in sub-surface zones, close to the bottom in shallow lakes, such as Gossenköllesee and Hagelseewli, and in the lower part of the metalimnion in the deeper lakes Saanajärvi, Nižné Terianske Pleso and Redó.

The pH of the lakes reflects their catchment bedrock. Hagelseewli in the Swiss Alps and Jezero v Ledvici in the Slovenian Triglav have pH values varying between 7.8 and 8.0, whilst most other sites situated on crystalline bedrock have acidic mean pH values between 6 and 7. Shorter periods of lower values occur at some sites associated with the spring ice-melting. The mean alkalinity data between lakes follow the pH pattern, and the seasonal data indicate that the increase in alkalinity generated within the lake during the winter ice-cover period is offset by the increase of acidity during the spring-melt.

Sediment chronology

The extent to which the sediment record can be compared with the instrumental climate record depends not only on the sensitivity of the various proxy methods but also on sedimentological factors such as the degree of mixing (by physical, biological or chemical processes), the rate of sediment accumulation and the precision and accuracy of the chronology.

Whilst none of the sites has laminated sediments the sharpness of the stratigraphical changes suggests that physical and biological mixing at all the study sites is relatively low. This may in part reflect their low productivity and in part indicate, despite their altitude and exposure, that they are sufficiently deep in relation to their surface area for sediment resuspension to be unimportant.

At all sites more than one core was needed to provide an adequate quantity of sediment to carry out analyses. In all cases a master core was designated and this core was the one used for radiometric dating by ^{210}Pb, ^{137}Cs and ^{241}Am. The methodology and results are given in detail in Appleby (2000). Dates from the master cores were transferred to the other cores using depth correlations using a sequence-slotting algorithm based on loss-on-ignition and other sediment data (Thompson & Clark, 1989).

The ^{210}Pb dating horizon was at most sites around 1830–1850, and dates for the earlier part of the period of climate reconstruction were obtained by extrapolating the ^{210}Pb chronology back to 1781. Figure 4 shows age-depth plots for all sites back to 1800. Plots of sediment accumulation rates vs. time are given in Appleby (2000). At four of the sites, Øvre Neådalsvatn, Saan-

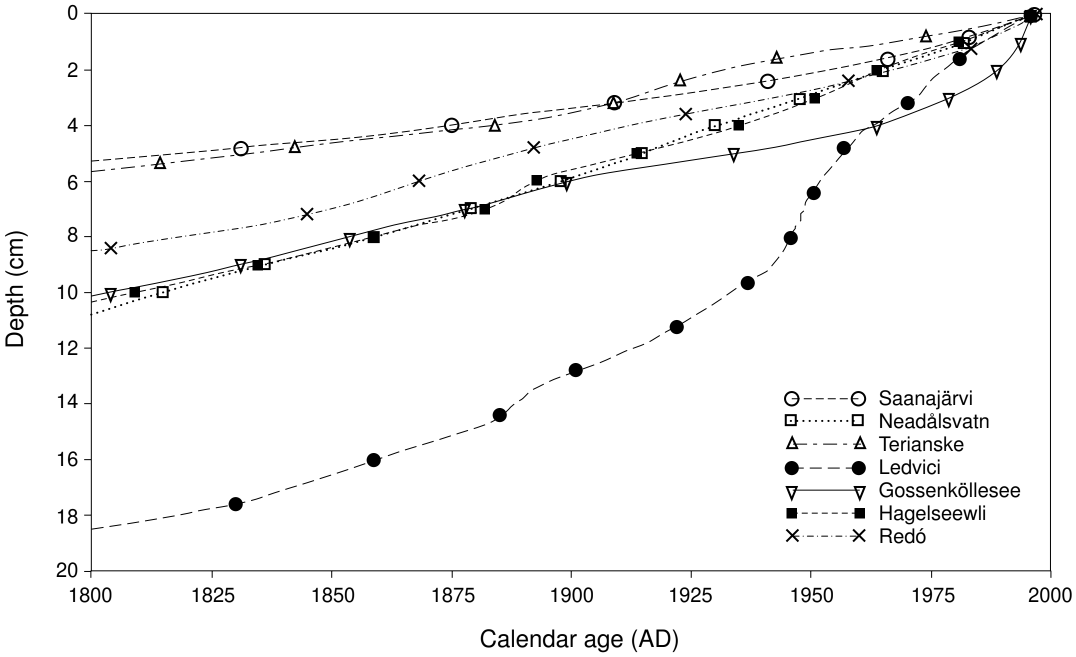

Figure 3. Plots of sediment depths vs. calendar age for all sites. Dates below the ^{210}Pb dating horizon (c. 1830–1850) have been obtained by extrapolation of the ^{210}Pb chronology.

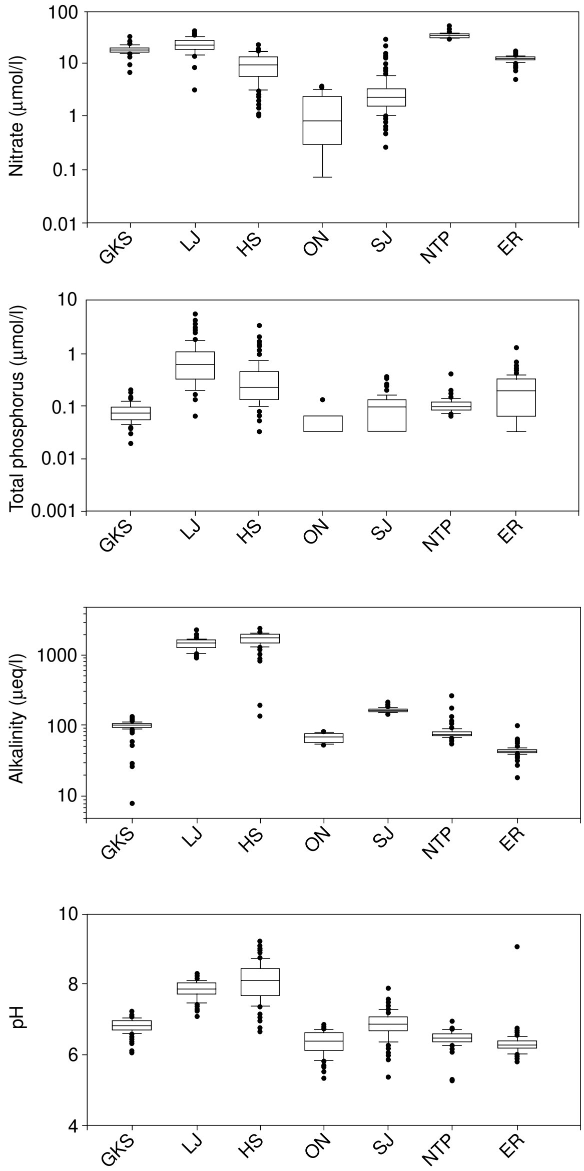

Figure 4. Box plots of nitrate, total phosphorus, alkalinity and pH for the seven lakes shown in Figure 1. 10, 25, 50, 75 and 90% percentiles are indicated.

ajärvi, Gossenköllesee and Redo, accumulation rates (and ^{210}Pb supply rates) appear to have been relatively stable throughout most of the ^{210}Pb period. Variations in accumulation rates have mostly taken place during the past few decades and they have been validated by stratigraphic dates based on the ^{137}Cs and/or ^{241}Am records. At these sites the extrapolations could be made with a high degree of confidence. Results for Terianske, Ledvici and Hagelseewli were more problematic. At each of these sites there was evidence of one or more brief episodes of rapid accumulation superimposed on longer periods of slow stable accumulation. Associated (but disproportionate) variations in ^{210}Pb supply rates during these episodes meant that dates had to be calculated using a composite piecewise CRS model (Appleby, 1998). Although the recent parts of the chronologies were relatively secure due to good ^{137}Cs/^{241}Am stratigraphic dates, variable accumulation rates in the earlier parts of the record make the older dates less certain. In spite of these difficulties, good agreement between the tabulated 1848 dates and the 99% equilibrium depths (Appleby, 2000) suggests that gross errors at any of these sites are unlikely.

Sediment accumulation rates are relatively low and typical of what would be expected for unproductive lakes with no or only small inflow streams, though there are significant differences between the sites. Contemporary values of the dry mass sediment accumulation rates vary by a full order of magnitude, from 0.0038 g cm^{-2} yr^{-1} at Nižné Terianske to 0.039 g cm^{-2} yr^{-1} at Saanajärvi. Corresponding volumetric accumulation rates vary from 0.044 cm yr^{-1} (Nižné Terianske) to 0.45 cm yr^{-1} (Gosssenköllesee). Table 1 gives values of both measures of the accumulation rate for each site, for the present day, 1900 and 1850. This table also gives a measure of the temporal resolution of the sediment records, expressed as the number of years encompassed by a 2.5 mm slice. For contemporary records it ranges from less than 1 year at Gosssenköllesee to about 6 years at Nižné Terianske. For records from 1850, at 5 of the 7 sites it is in the range 4–6 years, though at Saanajärvi and Nižné Terianske the resolution is in excess of 12 years due to the very low volumetric accumulation rates at these two sites.

Establishing chronologies and assessing their uncertainty is crucial in studies where palaeolimnolgical data are being compared with calendar-based historical data. For the MOLAR sites in this project a range of errors and uncertainties were considered. Standard errors in the ^{210}Pb dates were calculated from the 1-σ standard errors in the radiometric measurements, using the calculus of propagation of errors. Post-1963 errors due to deviations in the ^{210}Pb supply rate from the CRS model assumption of a constant flux were corrected using ^{137}Cs and ^{241}Am stratigraphic markers. Pre-1963 variations cannot be corrected for this uncertainty, and for this reason greatest confidence must be placed in results from those sites where the pre-1963 unsupported ^{210}Pb activity varies more or less exponentially with depth. At these sites it is reasonable to suppose that

Table 1. For each site: Accumulation rates at the present day, 1900 and 1850 in terms of both dry matter (g cm^{-2} yr^{-1}) and volume (cm yr^{-1}), and numbers of years spanned by a 2.5 mm slice at each of these times

	Sediment accumulation rates						Years per 2.5 mm slice		
	1996		1900		1850		1996	1900	1850
	g cm^{-2} yr^{-1}	cm yr^{-1}	g cm^{-2} yr^{-1}	cm yr^{-1}	g cm^{-2} yr^{-1}	cm yr^{-1}	yr	yr	yr
Saanajärvi	0.039	0.086	0.011	0.022	0.0086	0.016	2.9	11.4	15.6
Øvre Neådalsvatn	0.010	0.079	0.010	0.057	0.010	0.045	3.2	4.4	5.6
Nizné Terianske	0.0038	0.044	0.0083	0.032	0.0034	0.020	5.7	7.8	12.5
Gossenköllesee	0.013	0.45	0.0027	0.040	0.0022	0.045	0.6	6.3	5.6
Hagelsee	0.0043	0.064	0.014	0.047	0.011	0.042	3.9	5.3	6.0
Ledvicah	0.0058	0.096	0.0051	0.066	0.0050	0.057	2.6	3.8	4.4
Redó	0.010	0.096	0.0059	0.041	0.0076	0.054	2.6	6.1	4.6

accumulation rates and ^{210}Pb supply rates have both remained relatively uniform throughout the pre-1963 period. Standard errors in dates for these sites (Øvre Neådalsvatn, Saanajärvi, Gossenköllesee, Redo) are typically ±2 yr for 1960 and ±8 yr at 1850 (Appleby, 2000), though at Saanajärvi the 1850 uncertainty is much higher (±19 yr). Although the remaining sites (Hagelseewli, Nižné Terianske, Ledvici) have comparable standard errors, these do not take account of the possible impact of variations in the ^{210}Pb supply rate. However, since the (model independent) 99% equilibrium depths do not differ from the calculated 1848 depths by more than 11% (16 years), and the mean deviation for all sites is just 5% (7 years), these two figures can be regarded as providing a credible estimate of the mean and maximum uncertainties in the mid 19th century dates.

A further source of uncertainty is the potential error in core correlation. Although most analyses were carried out on the dated master cores, cores used for chironomid and other additional analyses were correlated with the master core using loss-on-ignition values and a slot-sequencing routine (Thompson & Clark, 1989). However, because the loss-on-ignition record at all sites showed clear patterns that are easily correlated between cores, this process is not considered to be a major source of uncertainty in the final age models adopted at each site (Appleby, 2000).

Comparisons between proxy data and instrumental climate records

Comparisons between the sediment record and the instrumental climate record are complicated by the differing nature of the two records. The climate record is reconstructed from average monthly air temperature data (Agustí-Panareda & Thompson, this issue) to provide mean values for a range of climate variables for each year since 1781 whilst the sediment record provides values for samples that are 2.5 mm thick, whose age span varies between sites and over time at a site. To harmonise the two records, the climatic predictor variables were smoothed along time with a LOESS regression (Cleveland et al., 1993), and an estimate of the climate variable was interpolated for the dated midpoint of each sediment sample.

At each site linear regression analysis was then used to find any potential relationships between the proxy climate response variables and the instrumentally reconstructed climatic predictor variables. The species composition data for diatoms, chironomids, chrysophytes, cladocerans and pigments were summarised as principal components prior to being used as response variables. In this discussion we consider these regressions proxy by proxy to identify the strongest relationships. Because the results may be sensitive to the degree of smoothing applied to the climatic variables, three different spans were applied to the six climatic predictors, namely 0.5, 0.1, 0.05. The span decides the amount of smoothing in the LOESS by setting the fraction of data to be used in estimating the fit at each point of the predictor. A narrow span gives smoothed curves that follow the original data closely, and a broader span gives much smoother curves. This means that the narrow span captures the fine-scale variability of climate whereas the broadest span captures the broad-scale trends in climate. This provides the opportunity to study relationships at different temporal scales, and to investigate whether the different biological groups in this study respond to climatic changes at different temporal scales. We predict the regression results (Tables 2–11) for the various response variables in relation to the six predictor variables when smoothed with three different spans, although little discussion is made of the results with the smallest span because the regression models usually had the lowest r^2 values. Results for all spans are presented to provide an overview of response relationships at varying temporal scales and lags.

Loss-on-ignition

Loss-on-ignition (LOI) is a routine but quite powerful measurement carried out in most palaeolimnological studies and is mainly used as a measure of sediment organic matter content. However, its interpretation can be quite complex as the values are influenced by varying inputs of inorganic matter (e.g., silts, carbonates, diatoms) as well as by changing inputs and changing preservation of organic matter. In addition, both inorganic matter and organic matter can be derived from a variety of different sources, both from within the lake and from the catchment. For remote mountain lakes that have sparsely vegetated catchments, with thin and poorly developed soils, few significant inflow streams and very restricted aquatic macrophyte populations, the situation is somewhat simplified. Our main hypothesis at the sites on crystalline bedrock is that the organic matter inputs to the sediment are driven mainly by the primary productivity of the water column (cf. Willemse & Törnquist, 1999; Battarbee et al., 2001; Nesje & Dahl, 2001), and that the LOI record is enhanced by a positive feedback mechanism associated with improved organic matter preservation during periods of reduced hypolimnetic oxygen concentration. The hypothesis of an in-lake source of organic matter is supported by the low C:N ratio which is generally below 10. In the absence of nutrient enrichment from human activity, variations in primary production might then be related to climate either through increased external loading from the catchment or atmosphere or through re-cycling processes in the water column (Catalan et al., this issue (a)). For the base-rich site Jezero v Ledvici, LOI may also be controlled by primary production, but in a more complex way associated with the production and preservation of authigenic calcite in the lake as well as the organic matter production.

Table 2 shows the relationship between LOI and the various predictor climate variables for the seven study sites. The correlations differ strongly between sites and between seasons, and the highest correlations are found using the 0.5 span. This latter observation suggests that either the lake response, or more likely the representation of the lake response in the sediment record is a relatively coarse one, limited perhaps by the slow rate of sediment accumulation, bioturbation and inaccuracies in matching the sediment dates to calendar dates. It is also possible that lake responses to climate forcing are lagged, although for the proxies used here it is unlikely that the lags are significant and could be expected to be less than the resolution of the sediment record itself.

The strongest relationships shown by the data are for Hagelseewli and Terianske Pleso followed by Øvre Neådalsvatn and Redo, with the lowest values for Jezero v Ledvici. At almost all sites the highest values are for winter temperature and for annual mean temperature, indicating perhaps the importance of reduced winter ice cover in generating increased primary production in the water column. The lack of response at Jezero v Ledvici where the relative amounts of organic matter in the sediment are probably controlled by the carbonate content is not surprising, and the data overall indicate that LOI may be a good indicator of varying mean annual temperature in lakes especially in soft water systems where the sources of organic matter are mainly autochthonous. The only major caveat to this interpretation arises if the observed correlation is dependent on very recent increases in organic content close to the core surface caused by a delay in the mineralisation of organic matter and not on a recent increase in temperature.

Table 2. LOI vs. climate

	Summer1 temperature			Summer2 temperature			Autumn temperature			Winter temperature			Continentality index			Annual temperature		
Span	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05
Gks	0.12	0.05	0.07	0.14	0.04	0.08	0.32	0.11	0.06	0.28	0.24	0.17	0.26	0.15	0.10	0.27	0.14	0.12
Hage	0.41	0.11	0.11	0.29	0.10	0.07	0.64	0.37	0.26	0.72	0.58	0.44	0.66	0.41	0.29	0.69	0.49	0.36
Ledv	0.06	0.06	0.05	0.06	0.08	0.07	0.07	0.10	0.10	0.04	0.01	0.01	0.01	0.01	0.00	0.10	0.12	0.12
Ovne	0.12	0.06	0.05	0.08	0.03	0.03	0.29	0.20	0.17	0.44	0.28	0.19	0.38	0.31	0.22	0.61	0.31	0.22
Redo	0.11	0.17	0.12	0.11	0.18	0.08	0.18	0.17	0.06	0.34	0.14	0.06	0.09	0.00	0.00	0.25	0.22	0.16
Saan	0.09	0.06	0.08	0.19	0.10	0.13	0.18	0.08	0.05	0.14	0.02	0.02	0.16	0.04	0.05	0.31	0.07	0.06
Teri	0.35	0.06	0.03	0.37	0.04	0.02	0.18	0.04	0.06	0.52	0.15	0.11	0.60	0.15	0.06	0.15	0.02	0.01

Carbon, nitrogen and sulphur

Carbon, nitrogen and sulphur measurements in softwater lake sediments are related strongly to the amount and composition of the organic matter in the sediment. Total carbon values are closely correlated with LOI values, whereas N and S values are likely to vary independently according to the source of organic matter and its degree of preservation. A relationship with primary production may be expected for all three elements and the C:N ratio is often used as an indicator of organic matter sources. The C:N ratios for the sites here indicate that the sedimentary organic matter is predominantly autochthonous (mean of ca. 10). The only exception is Øvre Neådalsvatn (C:N = 18).

The correlations between climatic variables and N (Table 3) follow the pattern for LOI, with high values for Hagelseewli, Terianske and Øvre Neådalsvatn, and the lowest for Ledvici. Interestingly the highest correlation is for N and ”continentality” at Terianske, but it is unclear how this might be explained.

The S data (Table 4) are less clear with only Terianske showing any high correlation values, again with ‘continentality’. Although this site is not acidified because of its relatively high neutralising capacity it is in a zone of high S deposition in the Tatra Mountains and it is possible that this is a spurious relationship related to pollution rather than climate change or organic matter preservation.

Pigments

Pigment analyses of organic matter in lake sediments are used to identify the composition and source of primary producers in the lake and its catchment. Some compounds are specific to individual taxa and can be used as biomarkers, whereas aggregate measurements, e.g., total chlorophyll derivatives, total carotenoids, reflect overall primary production. In addition principal components analysis of the pigment assemblage can be used to reflect changes in the overall composition of the contributing algal, bacterial and higher plant groups. Pigment preservation is generally good throughout the cores from all the lakes (Lami et al., 2000). Nevertheless, it is possible that the sediment signal is biased by losses due to mineralisation, the rate of which varies amongst compounds. The interpretation of the data in terms of primary production, species change and climate change can be thereby somewhat compromised by this process, especially in the cases of lakes Nižné Terianske and Redo. The oscillations in pigment concentration, especially CD, TC, β-carotene, diadinoxanthin,

Table 3. N vs. climate

	Summer1 temperature			Summer2 temperature			Autumn temperature			Winter temperature			Continentality index			Annual temperature		
Span	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05
Gks	0.02	0.05	0.05	0.00	0.08	0.08	0.16	0.08	0.01	0.29	0.36	0.18	0.29	0.20	0.08	0.10	0.21	0.12
Hage	0.48	0.09	0.10	0.31	0.05	0.06	0.64	0.31	0.28	0.71	0.52	0.37	0.64	0.32	0.19	0.69	0.39	0.32
Ledv	0.01	0.00	0.00	0.02	0.02	0.01	0.04	0.04	0.06	0.09	0.00	0.00	0.01	0.00	0.00	0.05	0.02	0.03
Ovne	0.10	0.04	0.00	0.09	0.09	0.01	0.41	0.09	0.10	0.27	0.05	0.06	0.24	0.08	0.06	0.45	0.07	0.09
Redo	0.20	0.05	0.02	0.33	0.16	0.12	0.24	0.21	0.21	0.08	0.04	0.05	0.32	0.13	0.11	0.17	0.10	0.08
Saan	0.10	0.04	0.08	0.26	0.17	0.25	0.15	0.08	0.03	0.18	0.06	0.04	0.21	0.10	0.10	0.35	0.11	0.06
Teri	0.61	0.21	0.06	0.47	0.14	0.06	0.02	0.00	0.00	0.27	0.01	0.01	0.74	0.16	0.05	0.25	0.12	0.04

Table 4. S vs. climate

	Summer1 temperature			Summer2 temperature			Autumn temperature			Winter temperature			Continentality index			Annual temperature		
Span	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05
Hage	0.14	0.05	0.03	0.10	0.03	0.05	0.40	0.11	0.15	0.22	0.14	0.09	0.20	0.27	0.21	0.28	0.03	0.03
Ledv	0.15	0.10	0.06	0.17	0.06	0.04	0.06	0.00	0.00	0.00	0.02	0.03	0.31	0.09	0.09	0.05	0.01	0.00
Ovne	0.03	0.01	0.02	0.00	0.01	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00
Redo	0.19	0.02	0.01	0.24	0.08	0.06	0.33	0.20	0.19	0.23	0.05	0.01	0.01	0.00	0.00	0.33	0.06	0.04
Saan	0.05	0.01	0.01	0.11	0.13	0.13	0.23	0.14	0.03	0.12	0.06	0.05	0.13	0.08	0.07	0.21	0.11	0.05
Teri	0.46	0.15	0.04	0.39	0.10	0.03	0.03	0.00	0.00	0.35	0.03	0.04	0.69	0.17	0.07	0.18	0.06	0.01

and echinenone, at Redo are interesting in this respect. This lake has the highest concentration of sedimentary fossil pigments (Lami et al., 2000). As its morphometry is very different from other sites with a maximum depth of 70 m, and it has a deep and stable thermal stratification, sedimentation processes and pigment preservation conditions are probably different from the other study lakes.

β-carotene, the recommended indicator carotenoids of algal biomass (Leavitt, 1993) is much more abundant in pre-1800 periods than at present in Redo and Gossenköllesee. Hagelseewli and Nižné Terianske also have a high peak of this carotenoid in deeper sediments (Lami et al., 2000). Abundance of β-carotene and its keto-derivatives (e.g., echinenone) in high altitude lakes might be related to prolonged nutrient (e.g., N) deficiency (Lami et al., 1991).

To explore the quantitative relationship with climate we have taken the three summary variables, total carotenoids, total chlorophyll derivatives and PCA axis 1 (for all pigments) at each site for comparison with the 5 climate variables. Tables 5–7 show the results.

The pigment PCA1 data generally show lower correlation coefficient values than LOI and N. The highest values are for Gossenköllesee winter temperatures and continentality, followed by Hagelseewli and Saan-

Table 5. Pigments PCA first axis vs. climate

	Summer1 temperature			Summer2 temperature			Autumn temperature			Winter temperature			Continentality index			Annual temperature		
Span	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05
Gks	0.06	0.12	0.15	0.09	0.01	0.03	0.40	0.09	0.06	0.58	0.37	0.25	0.55	0.16	0.07	0.38	0.27	0.24
Hage	0.29	0.02	0.03	0.11	0.02	0.01	0.38	0.23	0.15	0.39	0.30	0.20	0.34	0.24	0.13	0.36	0.16	0.11
Ledv	0.00	0.08	0.07	0.01	0.09	0.07	0.00	0.03	0.01	0.12	0.05	0.04	0.14	0.15	0.12	0.01	0.01	0.00
Ovne	0.07	0.03	0.01	0.13	0.16	0.06	0.29	0.05	0.04	0.13	0.00	0.00	0.13	0.00	0.00	0.26	0.00	0.01
Redo	0.03	0.00	0.02	0.05	0.00	0.00	0.03	0.02	0.01	0.02	0.01	0.01	0.07	0.00	0.00	0.01	0.00	0.00
Saan	0.10	0.05	0.04	0.28	0.19	0.19	0.10	0.12	0.06	0.31	0.06	0.02	0.32	0.12	0.05	0.37	0.10	0.05
Teri	0.79	0.45	0.19	0.72	0.37	0.20	0.00	0.00	0.00	0.15	0.00	0.01	0.75	0.27	0.15	0.31	0.23	0.06

Table 6. Total chl*a* derivatives vs. climate

	Summer1 temperature			Summer2 temperature			Autumn temperature			Winter temperature			Continentality index			Annual temperature		
Span	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05
Gks	0.04	0.11	0.15	0.04	0.01	0.02	0.21	0.04	0.03	0.38	0.23	0.10	0.36	0.08	0.01	0.20	0.18	0.14
Hage	0.28	0.01	0.01	0.14	0.02	0.00	0.42	0.23	0.20	0.44	0.27	0.18	0.40	0.23	0.16	0.40	0.14	0.10
Ledv	0.05	0.11	0.08	0.07	0.10	0.06	0.03	0.02	0.01	0.06	0.05	0.05	0.24	0.16	0.14	0.01	0.01	0.01
Ovne	0.14	0.07	0.02	0.19	0.19	0.05	0.32	0.05	0.04	0.21	0.00	0.00	0.21	0.01	0.01	0.32	0.00	0.01
Redo	0.25	0.02	0.03	0.28	0.08	0.06	0.32	0.17	0.11	0.05	0.01	0.00	0.03	0.01	0.03	0.32	0.07	0.05
Saan	0.05	0.02	0.04	0.21	0.14	0.18	0.29	0.16	0.09	0.25	0.05	0.03	0.23	0.08	0.05	0.49	0.14	0.06
Teri	0.72	0.34	0.14	0.69	0.30	0.19	0.02	0.02	0.01	0.27	0.04	0.05	0.83	0.32	0.17	0.28	0.16	0.04

Table 7. Total carotenoids vs. climate

	Summer1 temperature			Summer2 temperature			Autumn temperature			Winter temperature			Continentality index			Annual temperature		
Span	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05
Gks	0.03	0.09	0.10	0.05	0.00	0.00	0.011	0.02	0.02	0.22	0.09	0.04	0.21	0.02	0.00	0.11	0.08	0.06
Hage	0.28	0.02	0.01	0.15	0.03	0.01	0.37	0.25	0.20	0.42	0.25	0.18	0.38	0.20	0.14	0.38	0.14	0.10
Ledv	0.06	0.13	0.09	0.08	0.13	0.08	0.02	0.03	0.02	0.03	0.05	0.04	0.23	0.17	0.13	0.01	0.02	0.01
Ovne	0.00	0.01	0.00	0.02	0.07	0.02	0.05	0.00	0.00	0.00	0.09	0.03	0.00	0.05	0.02	0.04	0.04	0.01
Redo	0.43	0.06	0.07	0.47	0.18	0.14	0.49	0.28	0.18	0.08	0.01	0.00	0.06	0.03	0.06	0.050	0.13	0.10
Saan	0.04	0.02	0.05	0.17	0.12	0.17	0.18	0.13	0.07	0.21	0.05	0.02	0.19	0.08	0.05	0.45	0.15	0.07
Teri	0.59	0.24	0.07	0.63	0.21	0.11	0.04	0.03	0.03	0.35	0.07	0.10	0.80	0.29	0.15	0.24	0.10	0.02

ajärvi. There are also high values for Redo on PCA axis, not shown here. At Terianske especially high values are observed for the relationship between pigment PCA axis1 and summer temperature and continentality.

The chlorophyll *a* (chl*a*) data show the same pattern as for PCA axis 1 scores, and, with the exception of Jezero v Ledvici, generally show higher values for the relationship with winter and mean annual temperatures suggesting either increased primary production in warmer years or better preservation of chl*a*. The former may be more likely as preservation is not necessarily enhanced by increased winter temperatures and reduced ice cover. The opposite, however, may be the case for Terianske where high correlation coefficient values for both chl*a* (Table 6) and carotenoid concentrations (Table 7) are linked to summer temperatures and continentality. Either the steep increase in pigment concentration towards the surface of the core (Sporka et al., this issue) is the result of delayed mineralisation in a deep, strongly stratified lake or the result of a real increase in primary production associated with summer temperature increases, possibly coupled with an improvement in preservation conditions related to a decrease in hypolimnetic oxygen concentrations in summer.

Redo also shows this pattern with a relatively high correlation between summer temperature and both chl*a* and carotenoid concentrations. As Redo is also a deep lake with strong summer stratification, this observation reinforces the view that summer temperature and summer oxygen concentration are important for pigment preservation. What is unclear is whether this is a transient phenomenon or a longer term trend in increasing primary production, potentially linked to climate change.

Diatoms

Diatoms might reflect climate variability in several different ways, including direct temperature effects via stimulation of photosynthesis and growth (Hartig & Wallen, 1986; Raven & Geider, 1988; Michel et al., 1989), through 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; Weckström & Korhola, 2001). Climatic warming may also affect directly the productivity, life history and reproduction of diatoms through the increased average and maximum water temperatures and growing season, and increased light penetration during shorter periods of surface freezing. Recently, several studies have shown that diatom compositional changes in lakes situated in extreme environments (e.g., high altitude and high-latitude ecosystems) may be directly related to climatic patterns (Pienitz et al., 1995; Lotter et al., 1997; Weckström et al., 1997a,b). Transfer functions have been created for temperature using modern calibration reference data sets of limnological and surface-sediment diatom data, and the first applications of such transfer functions demonstrate that diatoms may yield reliable quantitative information of Holocene climatic fluctuations (Korhola et al., 2000).

In this study we focussed on changes in species composition expressed here as PCA axis 1 scores (Table 8). Details of individual diatom changes for each site are included in the respective papers in this volume.

Except for three sites the data show little or no relationship between diatom species compositional change (PCA axis 1) and temperature. The exceptions, Redo, Saanajärvi and Terianske, however, show quite strong correlations. For Redo the correlation is with summer and autumn temperature and annual temperature, for Saanajärvi it is with annual temperature and for Terianske it is for summer temperature and continentality. In the case of both Redo and Saanajärvi the correlation is based on the shifts in the composition of the planktonic diatoms with *Cyclotella pseudostelligera* and *Fragilaria nanana* expanding during the last few dec-

Table 8. Diatom PCA axis 1 vs. climate

	Summer1 temperature			Summer2 temperature			Autumn temperature			Winter temperature			Continentality index			Annual temperature		
Span	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05
Gks	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.02	0.00	0.00	0.02	0.00	0.00	0.01	0.00	0.00
Hage	0.00	0.03	0.02	0.09	0.06	0.10	0.00	0.06	0.03	0.01	0.03	0.03	0.01	0.01	0.01	0.02	0.10	0.07
Ledv	0.05	0.03	0.01	0.08	0.03	0.01	0.36	0.08	0.10	0.00	0.06	0.04	0.05	0.01	0.02	0.23	0.15	0.12
Ovne	0.08	0.07	0.01	0.10	0.13	0.05	0.08	0.10	0.07	0.01	0.01	0.03	0.02	0.04	0.04	0.05	0.04	0.01
Redo	0.75	0.32	0.26	0.81	0.55	0.37	0.87	0.68	0.40	0.35	0.09	0.04	0.01	0.06	0.3	0.88	0.41	0.32
Saan	0.00	0.00	0.00	0.04	0.03	0.01	0.39	0.19	0.08	0.32	0.03	0.04	0.22	0.03	0.04	0.63	0.17	0.14
Teri	0.70	0.16	0.01	0.55	0.08	0.00	0.02	0.00	0.01	0.33	0.08	0.03	0.61	0.27	0.05	0.19	0.06	0.04

ades in Redo (Catalan et al., this issue (b)) and *Cyclotella glomerata* and *C. comensis* increasing in Saanajärvi over a similar time-scale (Sovari & Korhola, 1998; Korhola et al., this issue). In Saanajärvi the change can be explained as a result of an increase in the population size of planktonic diatoms in autumn stimulated by greater nutrient availability during autumn overturn and extended warmth before the onset of winter ice-cover. In Redó *Fragilaria* appears in September and *Cyclotella* in October, when the lake is still stratified. These taxa consequently appear to be stimulated by the warmer condition during the later part of the stratification period. For Teriankse the interpretation is less clear. The diatom compositional change is associated not with the development of planktonic taxa but with changes in benthic taxa since the 1930's. pH reconstruction (Sporka et al., this issue) shows that a slight acidification may have occurred over this time period despite the relatively high alkalinity of the water column. However, this is unsurprising as the lake is situated in one of Europe's regions of highest acid deposition and the SCP data (Sporka et al., this issue) also show a steep increase in the concentration of particles coincident with the diatom change. On the other hand, an additional and independent impact of increased summer warming cannot be ruled out.

Planktonic diatom populations also seem to respond positively to temperature increase at Gossenköllesee and Hagelseewli, although these relationships are not apparent from the PCA axis 1 data (Table 8). For Gossenköllesee there is a significant relationship between diatom plankton percentages and the 15 year smoothed mean annual temperature for the alpine regions (Koinig et al., this issue), although it is also possible that diatom changes at this site may reflect changing nutrient conditions linked to past changes in the intensity of grazing in the catchment (Kamenik et al., 2000). For Hagelseewli benthic *Fragilara* taxa alternate in dominance with planktonic *Cyclotella* taxa, suggesting that climate variability at this extremely cold site has an impact on the diatom assemblage through ice-cover and habitat availability. *Cyclotella* dominance is characteristic of warmer conditions when open water occurs in summer and *Fragilaria* dominance is associated with colder conditions when only marginal benthic habitats are available for diatom growth (cf. Smol, 1988; Lotter et al., this issue). This habitat response is not reflected in the statistical analysis shown in Table 8.

The diatoms at Øvre Neådalsvatn show no response to climate. The lack of plankton at this more acidic site precludes the kind of evidence indicated by Redo and Saanajärvi but a response related to pH (cf . Psenner & Schmidt, 1992) might have been expected. However, there is little evidence of any compositional change in the diatom assemblage and the data indicate that the diatom assemblage is insensitive to the degree of climate change that has occurred over recent decades at this site. Jezero v Ledvici is a complete outlier. The data show little correlation between changes in diatom composition and air temperature (Table 8). Although diatom changes occur at this site in the twentieth century the reasons for the change are unclear as sediment accumulation rates and lake conditions may have been influenced by earthquake activity and enrichment from air pollution (Brancelj et al., this issue) as well as climate change.

Chrysophytes

Chrysophytes are a diverse group of primarily freshwater algae with over one thousand known species. They are an important component of phytoplankton assemblages of temperate and cold oligotrophic lakes (Sandgren et al., 1995). They produce resting siliceous cysts, and there is a robust correlation between the number of live cells and the number of cysts produced (Sandgren, 1988). Because of the importance of cysts in palaeoecological studies, floras specifically for cysts have been developed (Duff et al., 1995; Pla, 2001), and their distributions have been linked to environmental factors. Some recently developed transfer functions have shown a good relationship between chrysophyte cysts assemblages and mean annual air temperature (e.g., Pla & Catalan, personal communication).

In the MOLAR sites relatively strong relationships between cyst assemblage changes and temperature (Table 9) are seen for Redó and Saanajärvi, following the pattern observed in the diatom data. As chrysophytes are almost exclusively planktonic the similar response of planktonic diatoms and chrysophytes at these two sites indicates, not unexpectedly, that phytoplankton composition is especially influenced by climate change. This influence, however, is not necessarily a direct result of temperature variability, but related more indirectly to temperature and wind-induced changes in stratification, overturn, nutrient availability and ice cover.

Cladocera

Cladocera are a major component of the micro-crustacean fauna in freshwater lakes and ponds. They play a

Table 9. Chrysophyte PCA axis 1 scores vs. climate

	Summer1 temperature			Summer2 temperature			Autumn temperature			Winter temperature			Continentality index			Annual temperature		
Span	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05
Gks	0.01	0.07	0.05	0.05	0.02	0.01	0.28	0.04	0.08	0.11	0.12	0.12	0.09	0.20	0.17	0.17	0.01	0.03
Hage	0.45	0.13	0.15	0.44	0.13	0.19	0.14	0.04	0.10	0.21	0.20	0.20	0.13	0.09	0.07	0.25	0.16	0.24
Ledv	0.04	0.00	0.00	0.07	0.00	0.01	0.32	0.05	0.08	0.00	0.00	0.00	0.03	0.00	0.00	0.31	0.05	0.03
Ovne	0.16	0.01	0.00	0.19	0.08	0.04	0.27	0.11	0.08	0.28	0.06	0.03	0.27	0.06	0.03	0.37	0.08	0.04
Redo	0.42	0.10	0.05	0.44	0.21	0.14	0.45	0.26	0.20	0.08	0.05	0.05	0.06	0.01	0.00	0.46	0.16	0.11
Saan	0.00	0.04	0.02	0.03	0.00	0.00	0.28	0.17	0.11	0.43	0.12	0.12	0.28	0.06	0.05	0.59	0.30	0.26
Teri	0.20	0.00	0.00	0.16	0.01	0.02	0.00	0.00	0.06	0.08	0.05	0.01	0.16	0.02	0.00	0.05	0.01	0.07

critical role in aquatic ecosystems as an important link in the cycling of energy resources among trophic levels (Korhola & Rautio, 2001). Many cladoceran species appear to be adapted to a broad range of (seasonal) temperature changes (Meijering, 1983). However, their optimum temperatures are usually at the higher side of the tolerance range. Their reproduction and growth have been shown to be slower in cold water (Allan, 1976; Allan & Goulden, 1980; Goss & Bunting, 1983; Frey & Hann, 1985; Moore et al., 1996), while temperature also seems be critical to the broad-scale community dynamics and body size of cladocerans (Gillooly & Dodson, 2000). In addition, temperature has been shown to be of importance to zooplankton biomass (e.g., George & Harris, 1985) and diversity (e.g., Patalas, 1990; Stemberger et al., 1996).

Harmsworth (1968) classified the European cladoceran species as ‘arctic’, sub-arctic’, ‘north temperate’, and ‘south temperate’ according to their latitudinal affinities, whereas DeCosta (1964) reports a clear distributional pattern among Cladocera over a latitudinal temperature range of 17 °C. Sandøy and Nilssen (1986), Rautio (1998) and Korhola (1999) found altitude, either directly (dispersal and colonization abilities) or indirectly (temperature, amount of aquatic vegetation), to be the main factor controlling crustacean species compositions in lakes and ponds in Norway and Finnish Lapland.

Lotter et al. (1997) and Korhola (1999) have made the first attempts to quantify the relationship between climate and cladoceran assemblages. They first found physical factors, including, for example, water depth, temperature, to contribute statistically significantly to the distributional patterns of cladoceran taxa in alpine and arctic lakes sampled along steep ecoclimatic gradients. Quantitative inference models for mean summer air temperature were then developed for both planktonic and benthic life-forms of Cladocera, using weighted averaging partial least squares (WA-PLS) and linear-based partial least squares (PLS) regression. The first applications of the alpine Cladocera-temperature transfer functions to late-glacial sequences of Gerzensee in Switzerland (Lotter et al., 2000) and Kråkenes lake in Norway (Duigan & Birks, 2000) are promising.

Despite this promise the response amongst the MOLAR lakes (Table 10) is quite weak or entirely lacking. The highest r^2 value of 0.39 is for Øvre Neådalsvatn for PCA axis 1 scores and mean annual temperature. Cladoceran analyses were not carried out at Terianske and the number of individuals found in the Hagelseewli core was too small for reliable estimates of species composition to be made. These findings suggest that the lakes selected in this study were not sufficiently close to important ecological boundaries for Cladocera or that cladoceran composition is not sensitive to climate change within the range of change embraced by this study. A further possibility is that cladoceran communities may respond to climatic changes with a time lag that is undetected by our regression with LOESS smoothed data. For example, in Saanajärvi, the cladoceran community was extremely scarce until the 1930’s, after which there was a distinct increase especially in the population of *Daphnia longispina* (Rautio et al., 2000; Korhola et al., this issue). The low number of the other cladoceran species makes reasonable quantification difficult, yet the concentrations of *Bosmina longispina* as well as some chydorid taxa such as *Alona affinis*, *A. excisa*, *A. quadrangularis*, *Acroperus elongatus*, *Alonella nana*, *Chydorus sphaericus*, and *Eurycercus lamellatus* also increased (Rautio et al., 2000). This change in the compositional structure of the Cladoceran community cannot be connected to a recovery from acidification or water-level oscillations, since there is no evidence in Saanajärvi for either of these events. The cladoceran record at Saanajärvi is probably therefore a reflection of complex climate forcing of lake

Table 10. Cladocera PCA axis 1 vs. climate

	Summer1 temperature			Summer2 temperature			Autumn temperature			Winter temperature			Continentality index			Annual temperature		
Span	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05
Gks	0.00	0.01	0.00	0.01	0.01	0.00	0.12	0.00	0.01	0.19	0.19	0.011	0.20	0.22	0.11	0.07	0.01	0.02
Ledv	0.00	0.04	0.09	0.01	0.03	0.08	0.07	0.00	0.00	0.03	0.00	0.01	0.01	0.01	0.01	0.02	0.01	0.02
Ovne	0.21	0.02	0.00	0.12	0.06	0.04	0.31	0.17	0.18	0.35	0.21	0.12	0.34	0.21	0.11	0.39	0.23	0.18
Redo	0.02	0.00	0.00	0.06	0.02	0.03	0.06	0.06	0.10	0.00	0.00	0.00	0.02	0.00	0.00	0.03	0.01	0.01
Saan	0.00	0.05	0.01	0.00	0.00	0.01	0.05	0.05	0.08	0.01	0.05	0.03	0.01	0.01	0.01	0.00	0.08	0.03

ecosystems via the structure of the food-web. Cladocerans are predators, which are resource limited. The apparent 20–30-year time lag in response to the most distinct warming in Saanajärvi suggests that the temperature rise may have been sufficient enough to create changes first in the composition and production of the phytoplankton community, and thereafter an increase in Cladocera production via improved food availability and 'bottom-up' trophic cascades. This delayed response if true, however, contrasts markedly with the much more immediate response of the diatom and chrysophyte populations (see above).

Chironomids

Chironomids are versatile midges, whose aquatic larvae are abundant and taxon rich in most lakes. The heavily chitinised larval head capsules usually preserve well in lake sediments and can be readily identified, at least to the generic level. Chironomid species are known to differ significantly in their temperature tolerances. For example, Brundin (1949) showed that oligostenothermic chironomid assemblages change their vertical distribution in relation to temperature. They occur above the thermocline in arctic and subarctic conditions but occur below the thermocline in temperate areas. Moreover, changes in temperature can have a direct effect on chironomid pupation, emergence, growth, flight, feeding and hatching (Smol et al., 1991).

The importance of temperature for the distribution, abundance, survival, and composition of chironomid assemblages is now widely accepted by palaeolimnologists, and the value of chironomids as proxy indicators of climate change has been manifested by a number of studies (reviewed by Walker, 1995; Battarbee, 2000; Korhola et al., 2001). Subsequently, several regional chironomid–temperature calibration functions have been generated during the recent years in North America (e.g., Walker et al., 1991, 1997; Wilson et al., 1993) and Europe (Lotter et al., 1997; Olander et al., 1997, 1999; Brooks & Birks, 2000a,b, 2001; Vasko et al., 2000; Rosén et al., 2001). The existing chironomid–temperature transfer functions have been used to quantify climates during late-glacial times in the Atlantic Canada and Europe with promising results (Levesque et al., 1993, 1994, 1997; Brooks & Birks, 2000a, 2001). For example, Brooks and Birks (2000a) demonstrated the close parallelism between late-glacial chironomid-based July air temperature reconstructions for a site in Scotland and the GRIP oxygen-isotope record. They argue that this close parallelism shows 'the potential of fossil chironomid assemblages and associated modern calibration functions to derive fine-resolution quantitative palaeoclimatic reconstructions'.

However, until now only a few chironomid-inferred temperature reconstructions have been attempted for the Holocene (see however, Brooks & Birks, 2000b, 2001; Rosén et al., 2001; Korhola et al., submitted). The amplitude of temperature variation is much smaller during the Holocene, and at the MOLAR sites in this study only Hagelseewli and Redó show a clear relationship between chironomid changes and temperature (Table 11). At other sites the relationship is quite weak and at Saanajärvi there were insufficient head capsules present in the sediment cores to analyse in any statistically valid way. The apparently weak response of chironomids at some of these sites may not necessarily be related to a lack of sensitivity but to the extreme climate situations of the lakes and their distance from important temperature thresholds.

Discussion

In this study our aim has been to assess how faithfully the sediment records of mountain lakes record recent climate change over the last 200 years compared to instrumental records and to evaluate, thereby, the extent to which different proxy methods might be reliably used to reconstruct climate change over longer time

Table 11. Chironomids PCA axis 1 vs. climate

	Summer1 temperature			Summer2 temperature			Autumn temperature			Winter temperature			Continentality index			Annual temperature		
Span	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05	0.5	0.1	0.05
Gks	0.01	0.03	0.17	0.00	0.02	0.09	0.08	0.04	0.01	0.02	0.01	0.01	0.03	0.05	0.14	0.00	0.00	0.02
Hage	0.15	0.06	0.03	0.43	0.04	0.04	0.52	0.21	0.09	0.51	0.27	0.15	0.41	0.11	0.04	0.65	0.53	0.22
Ledv	0.01	0.00	0.00	0.00	0.01	0.02	0.03	0.00	0.00	0.20	0.03	0.03	0.17	0.01	0.01	0.02	0.00	0.01
Ovne	0.03	0.02	0.01	0.14	0.02	0.02	0.16	0.18	0.17	0.26	0.16	0.21	0.21	0.16	0.19	0.30	0.17	0.25
Redo	0.35	0.17	0.19	0.26	0.16	0.14	0.27	0.20	0.09	0.17	0.06	0.07	0.01	0.06	0.04	0.34	0.18	0.20
Teri	0.10	0.06	0.07	0.15	0.13	0.19	0.00	0.01	0.01	0.03	0.06	0.03	0.02	0.12	0.09	0.06	0.03	0.04

periods. As far as possible the study sites were selected to be as free from disturbance by human activity as possible. Sites were above the local timber line, their catchments were free from obvious recreational or other human use, and they were either distant from atmospherically transported pollutants or, in the case of Alpine and Eastern European sites, they were assumed to be insensitive to the impacts of acid deposition.

On the other hand the lakes were all different in their physical charactersitics, principally in size, depth and climatic setting and in some cases substantially different in their water chemistry with some sites e.g., Hagelseewli and Jezero v. Ledvici situated on base-rich rocks. Consequently, it was anticipated at the outset that each site would respond to climate in an individualistic way and that the sensitivity and accuracy of the different proxy methods in recording climate change would also differ between sites and thus provide a test of the range over which the methods are useful.

Our approach has been to make direct comparisons between the proxy data and the instrumental temperature modelled statistically for each study site. For the instrumental data this procedure has involved combining and homogenising temperature records from meteorological stations and adjusting the data for altitudinal differences using lapse-rate corrections. The accuracy of the procedure was assessed by comparison with on-site automatic weather station data. The results suggest that this is a relatively accurate procedure and one that can thereby be further used to reconstruct past surface water temperature and ice cover for the same time period with reasonable confidence. For the proxy data there are greater concerns associated principally with establishing accurate chronologies, being able to discount non-climate driving forces for the observed changes, and the sensitivity of the different proxies used.

Although almost all remote mountain lakes are oligotrophic and have slow sediment accumulation rates, none of the sites in this study had poor sediment records, and all sites generated good ^{210}Pb based chronologies. Assuming that there were no systematic errors in the chronologies the limitations in comparing sediment data with instrumental data are imposed mainly by the steadily increasing standard error of the ^{210}Pb dates with time, especially before 1900 when the standard error increases considerably. The uncertainty is further increased in the earliest parts of the record where the chronology from the earliest ^{210}Pb date to the beginning of the instrumental record in 1781 is based on extrapolation.

The assumption that all the changes in the proxy data were the result of climate change was challenged at several sites. At Jezero v Ledvici, the Slovenian calcareous lake, Brancelj et al. (this issue) explain several features of the sediment record due to the effects of earthquake activity and enrichment from atmospherically transported nutrients. The disturbance at this site is consequently sufficient to question whether any of the stratigraphic changes could be due to climate change.

At Terianske, despite its relatively high alkalinity, acid deposition cannot be excluded as a contributary cause for the stratigraphic changes. It is in an area of high acid deposition and the spheroidal carbonaceous particle record reflects this. On the other hand, whilst evidence of acid deposition and air pollution is present at all other sites, levels are probably too low to account for changes in the biostratigraphic record. There are also concerns at Gossenköllesee that past land-use change in the lake catchment may have had an impact on the nutrient status of the lake (Kamenik et al., 2000) although changes in the intensity of animal grazing in the past may have been promoted by climate.

Making allowances for these possible anthropogenic influences it could be argued that most if not all of the stratigraphic changes at most sites in the recent sediment record might be expected to be the result of climate change over the last 200 years. On the assumption that the sediment chronology at each site is accurate we have carried out statistical comparisons between the instrumental record and the proxy record using LOESS smoothers and regression techniques.

The assessment of the statistical significance of the regression analysis results is difficult because serial correlation or temporal autocorrelation is a general problem in studies such as this (Ramsey & Schafer, 1997). The LOESS smoothing of the climatic variables increases these problems as the smoothing makes the predictor variables even more temporally dependent. In addition, multiple comparisons tests will create spurious statistically significant relationships (Millard & Neerchal, 2001). We have therefore not used any significance tests or reported any p-values or confidence intervals for the r^2 values. We emphasise that the reported r^2 values should be interpreted with caution due to these problems. Here we have only used the r^2 values for between-relationship comparisons.

Having allowed for the problems in making these comparisons described above, we are left with a number of relationships between the instrumental record and the sediment record that appear to be linked to climate variability. These principally include organic matter and proxies related to organic matter such as pigments and S and N, and diatoms. Chrysophytes and chironomids also appear useful at some sites, but cladoceran relationships are quite weak.

For organic matter (LOI) and proxies related to organic matter the strength of the relationship may be partly an artefact due to the coincidence of higher temperatures and better organic matter preservation in the upper layers of the cores. However, this does not account for the sub-surface variability seen at many sites, and there does indeed appear to be good evidence for a relationship between climate and LOI at many sites. This can best be explained as a result of changes in lake productivity linked to changes in nutrient, especially phosphorus, loading. However, as Catalan et al. (this issue) point out, it is not clear whether the effect of climate change is on water temperature and water column mixing that drives internal nutrient recycling or alternatively on the catchment, where an increase in the delivery of nutrients to the lake may be caused by reduced snow cover, enhanced soil development, and increased soil erosion, etc.

The diatom responses to climate change vary from site to site. Although there is little or no evidence for any pH or alkalinity-related changes in species composition (cf. Psenner & Schmidt, 1992) at any of the sites, there is a clear evidence that warmer conditions favour the development of some planktonic forms, especially *Cyclotella* taxa, either through enhanced growing conditions, e.g., at Redó, Gossenköllesee and Saanajärvi, or through the reduction in ice-cover and changes in habitat availability e.g., Hagelseewli.

The mountain lakes studied have clearly experienced significant variability in climatic conditions over the last 200 years. This is indicated by the temperature reconstructions of Agustí-Panareda and Thompson (this issue) that show decadal-scale fluctuations in mean annual temperature with an amplitude of up to 2 °C have taken place at these sites. These are sufficient to cause ecologically important changes in lake heat balance and ice-cover. However, the extent to which these climate changes are recorded by lake sediments or are unambiguously revealed by the current range of proxy methods routinely used in palaeolimnological research is open to question. Shifts in the composition of microfossil, especially diatom, assemblages linked to climate variability appear to have occurred, probably reflecting changes in seasonal conditions or habitat change rather than mean annual temperature. These changes are best shown by techniques such as principal components analysis rather than by organism-temperature transfer functions, that are unlikely to indicate accurately such relatively subtle shifts in climate modes. This conclusion has some relevance for attempts to reconstruct climate over longer time-scales. Reliance on transfer functions to capture low amplitude, high frequency climate signals over the Holocene and previous warm periods may be misplaced. More might be achieved using more ecologically sensitive, albeit less quantitative approaches (e.g., Rioual et al., 2001).

Although further work is needed to explain fully the results of this study it is apparent that the proxy methods used are not equally useful in reconstructing past climate patterns and that no single method is applicable at all sites. This indicates that the best results will be achieved where sites are carefully chosen in relation to their sensitivity to climate change and in relation to their proximity to important aquatic and/or terrestrial ecotones and where a multi-proxy analytical approach can be adopted to provide internal testing of hypotheses and a more secure interpretation of the data.

Finally, allowance needs to be made for delayed responses to climate forcing. Although the use of the low resolution smoothing adopted here allows for some lag between climate change and organism response, we are dealing with a range of taxonomic groups that have different trophic levels and positions in the food web and that can be expected to be influenced by climate in various indirect ways. Inferring climate change from apparent organism response therefore may require more complex approaches that also incorporate an understanding of species interactions and trophic dynamics (e.g., Davis et al., 1998).

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