

9 Diatoms as indicators of environmental change near arctic and alpine treeline

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Introduction

Timber line represents the most prominent ecotone in mountainous and arctic regions. It is characterized by the transition from closed forest to the most advanced solitary trees (i.e., timber line), to single tree islands (i.e., treeline), and eventually to unforested vegetation. This biological boundary can vary in width between tens of meters and many kilometers. In northern Europe it is formed by deciduous trees (*Betula*, *Alnus*, *Populus*), whereas coniferous trees (*Pinus*, *Picea*, *Larix*) form treeline in the Alps, northern North America and Eurasia.

Treeline is primarily related to cold temperatures but a complex set of different climatic factors, as well as the specific adaptation of trees, actually defines the forest limit (e.g., Tranquillini, 1979). This is evident from the decrease in altitude of treeline from subtropical to arctic regions and, on a smaller scale, by the higher forest limit on southern slopes compared to northern slopes (Ellenberg, 1986). In the Alps, timber line represents the transition between the subalpine and the alpine belts (Ozenda, 1985; Ellenberg, 1986). The lower boundary of the alpine belt, however, is difficult to locate as human impact, grazing and climatic oscillations have lowered natural tree limit by several hundred meters in the last millennia (e.g., Lang, 1994; Tinner *et al.*, 1996).

In the north, physical and biotic features are sufficiently distinct to unequivocally separate 'arctic' from 'boreal' regions. However, great disparity exists among definitions as to where the Boreal region ends and the Arctic region begins (Larsen, 1989). The zone of transition between the two, the so-called 'forest-tundra' transition, or ecotone, can be identified with a certain degree of accuracy, but the drawing of lines on maps to delineate Arctic, transitional, and Boreal zones remains controversial. The Arctic as a geographical concept has been most usefully defined either as the area north of polar treeline or as the region north of the July mean daily isotherm of 10 °C (Hustich, 1979). The most pragmatic way to delimit the southern margin of the Arctic is to take the boundary of wooded vegetation that can be observed on aerial photographs or satellite images.

Aquatic habitats suitable for diatoms at these altitudes and latitudes are many-fold. The lakes are characterized by special limnological features, and

are usually only ice free during a short period in summer, with cold water temperatures prevailing. Furthermore, light availability in the water column is strongly restricted by ice and snow cover as well as by the polar winter. During summer, however, the light conditions change significantly, especially at high latitude lakes: the photoperiod is long and the angle of the sun is high. The resulting UV (ultraviolet) radiation may have an inhibitory effect on periphytic littoral algae, such as *Achnanthes minutissima* Kützing, if dissolved organic matter is at low concentrations (e.g., Vinebrooke & Leavitt, 1996). Lakes that are influenced by glacial meltwater are turbid with high concentration of silt and clay. In the absence of glaciers, such lakes have either a high water transparency or, if mires are present in their catchment, the input of humic acids will result in dystrophic conditions.

Lakes on opposite sides of treeline exhibit striking differences in water chemistry and physical conditions (Pienitz *et al.*, 1997a,b; Vincent & Pienitz, 1996; Sommaruga & Psenner, 1997), which are reflected by abrupt changes in diatom community structure and composition. For example, differences in lake mixing regimes, nutrients, and lakewater transparency are most apparent at this ecotonal boundary marked by sharp changes in abiotic (e.g., changes in albedo and permafrost) and biotic variables (e.g., atmospheric deposition of macronutrients by pollen; Doskey & Ugoagwu, 1989; Lee *et al.*, 1996). Furthermore, sediment accumulation rates may change drastically across this ecotone: accumulation rates above treeline are often up to an order of magnitude lower than in comparable boreal or temperate lake basins.

The dearth of alpine and northern treeline diatom studies is primarily related to logistic problems. Nevertheless, early diatom studies from high altitude and high latitude regions usually provide extended taxon lists (e.g., Cleve-Euler, 1934; Krasske, 1932; Hustedt, 1942, 1943; Foged, 1955) and often classify taxa according to their plant-geographical distribution (e.g., nordic-alpine).

Freshwater diatoms, like most algae, are usually not considered sensitive indicators of temperature (e.g., Battarbee, 1991), even though clear latitudinal patterns in their distributions are apparent (Foged, 1964), and classifications according to their thermal requirements (Backman & Cleve-Euler, 1922; Hustedt, 1939, 1956) have long existed. Several experimental studies (e.g., Eppley, 1977; Patrick, 1971, 1977; Hartig & Wallen, 1986; Dauta *et al.*, 1990) indicate a temperature dependency of diatom growth and community composition. Under natural conditions, Stoermer & Ladewski (1976) and Kingston *et al.* (1983) found a relationship between temperature and the occurrence of certain diatoms. Kilham *et al.* (1996), however, associate the climatic distribution of diatoms with resource-related competitive interactions.

Diatoms as paleoenvironmental indicators at treeline

Treeline vegetation will be strongly impacted by future climatic warming (Houghton *et al.*, 1990; Smith *et al.*, 1992; Monserud *et al.*, 1993; Grabherr *et al.*,

1994; Kupfer & Cairns, 1996). However, aquatic environments and ecosystems, water supplies and fisheries will also be affected (Houghton *et al.*, 1996; Watson *et al.*, 1996). Global warming will result in increased heat uptake of lakes which, in turn, will lead to earlier break-up of ice and, consequently, to changes in stratification and oxygen regimes (Robertson & Ragotzkie, 1990; Hondzo & Stefan, 1993; Schindler *et al.*, 1990, 1996a,b; Sommaruga-Wögrath *et al.*, 1997; Livingstone, 1998).

Because the location of northern treeline results from and influences the mean position of major atmospheric boundaries (i.e., the Polar Front; Bryson, 1966; Pielke & Vidale, 1995), it is important to understand the linkages between climate and vegetation along the northern edge of the boreal forests. The sensitivity of arctic treeline position to climatic factors makes this ecotone an ideal location for investigating the effects and timing of climatic change. Paleocological records provide a means of reconstructing the impact of past climatic variations on treeline vegetation, thereby allowing a better understanding of the causes and dynamics of past and future climatic change. Moreover, latitudinal changes in the position of the Polar Front through time provide important boundary conditions that may be used in testing and evaluating Global Circulation Models.

Paleolimnological data on past climatic changes in treeline regions are particularly important, as many of the more traditional, terrestrial-based paleocological techniques, such as palynology, may reach their methodological limits at sites above treeline (e.g., Lang, 1994; Gajewski *et al.*, 1995; Smol *et al.*, 1995). These restrictions do not apply to diatoms. They are extremely abundant and ecologically diverse. Their short lifespan and fast migration rates enable them to respond quickly to environmental changes. Their potential as paleo-indicators mostly relies on their good preservation in lake sediments.

Many variables affect the size and species composition of diatom communities. Studies using diatom records to infer past climates have generally yielded qualitative results rather than quantitative paleoclimate estimates. Climate either directly (e.g., via changes in lake water temperature, mixing regime) or indirectly influences diatoms by controlling, for example, habitat availability, catchment and aquatic vegetation, water colour and transparency, or nutrient supply (e.g., Moser *et al.*, 1996).

Diatom studies in alpine, boreal, and arctic lakes (e.g., Hustedt, 1942; Cleve-Euler, 1951–1955; Sabelina *et al.*, 1951; Florin, 1957; Foged 1964, 1981; Mölder & Tynni, 1967–1975; Tynni, 1975, 1976; Koivo & Ritchie, 1978; Arzet, 1987; Niederhauser & Schanz, 1993) have shown relationships between diatom assemblages and aspects of water chemistry. These surveys also illustrated the need for more precise, quantitative diatom autecological data to refine or replace the classifications introduced by Kolbe (1927) and Hustedt (1939, 1956).

Considerable progress has recently been made in the development of inferential statistics useful for inferring past conditions from paleocological data. Surface sediment calibration sets (see Charles & Smol, 1994) are currently widely used to estimate environmental optima and tolerances of diatoms and

for the development of diatom-based transfer functions (see Hall & Smol, this volume). These transfer functions allow quantitative reconstructions of past limnological conditions, using a range of numerical regression and calibration techniques (Birks, 1995). Although only a few calibration sets are available for treeline regions (e.g., Pienitz & Smol, 1993; Pienitz *et al.*, 1995a; Wunsam *et al.*, 1995; Allaire, 1996; Rühland, 1996; Lotter *et al.*, 1997; Weckström *et al.*, 1997a), many more are currently being completed in different regions (Fig. 9.1).

The Arctic

NORTH AMERICA

Having studied modern diatom assemblages along a transect crossing three vegetation zones in northwestern Canada (Fig. 9.1-A), Pienitz *et al.* (1995a) found that summer surface water temperature and lake depth were the two best predictors of diatom distribution. Their weighted-averaging (WA) model for diatom-temperature relationships predicted temperatures that closely approximated the actual observed values (Fig. 9.2), with the final inference model yielding a bootstrapped root mean squared error of prediction (RMSEP) of 1.8 to 2.0 °C. The WA optima ranged from 15.4 °C (*Stauroneis smithii* var. *minima* Haworth) to 21.5 °C (*Synedra radians* Kützing). Planktonic diatoms generally displayed optima at the higher end of the temperature range, whereas small benthic taxa with 'nordic-alpine' affinities were positioned at the lower end of the temperature gradient. Variance partitioning tests showed that there was a statistically significant component of variation in the diatom data that was explained by temperature independent of chemistry, thus suggesting that fossil diatom data could be used to reconstruct temperature changes. Such reconstructions, however, are related to water rather than air temperature. Although these two variables are closely related, the timing and extent of stratification (which is dependent on the timing of ice break-up), atmospheric circulation and lake depth also affect water temperature and must be considered in any extrapolation to air temperature (Pienitz *et al.*, 1995a; Livingstone & Lotter, 1998).

The inclusion of an altitudinal gradient in the Pienitz *et al.* (1995a) calibration set revealed some similarities between alpine lakes and lakes located in arctic tundra regions, thereby indicating the potential of diatoms as paleoclimate proxies in alpine regions (Pienitz, 1993).

By studying oligotrophic lakes that spanned boreal forest, forest-tundra and arctic tundra in the central Northwest Territories (Fig. 9.1-C), Pienitz and Smol (1993) demonstrated that dissolved inorganic carbon (DIC) and dissolved organic carbon (DOC) concentrations explained significant variation in the diatom distributions. WA regression and calibration techniques were used to develop transfer functions relating diatom distributions to measured DIC and DOC. These transfer functions were later applied to fossil diatoms from two

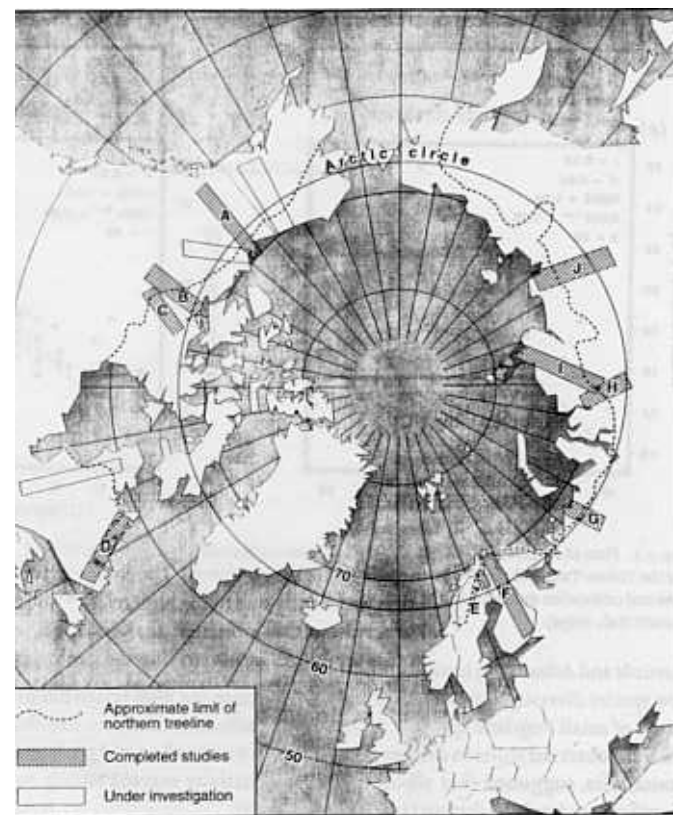


Fig. 9.1. Map showing diatom study regions at northern treeline.

treeline lakes. Diatom-inferred DIC and DOC and diatom concentrations revealed rapid increases in lake productivity associated with climate warming at ca. 5000 yrs BP and a contemporaneous shift from tundra to forest-tundra vegetation (MacDonald *et al.*, 1993; Pienitz, 1993; Pienitz *et al.*, 1999). Because lakewater DOC closely tracks the abundance of coniferous trees in a drainage basin (Pienitz *et al.*, 1997a,b; Vincent & Pienitz, 1996), diatom-based reconstructions of DOC can be used as a proxy for past vegetation shifts (Pienitz, 1993; Pienitz & Smol, 1993; Pienitz *et al.*, 1999).

Rühland's (1996) calibration set from the Canadian Northwest Territories (Fig. 9.1-B) similarly revealed distinct differences in diatom assemblages from boreal forest and arctic tundra sites. The most apparent trend was a shift from communities dominated by centric diatoms (e.g., *Cyclotella* spp.) in boreal forest lakes to those dominated by small, benthic, pennate taxa (e.g., *Fragilaria*,

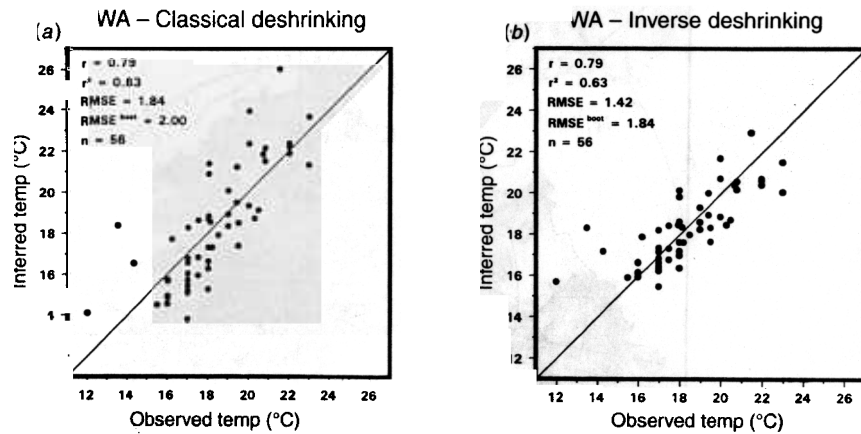


Fig. 9.2. Plots of observed vs. diatom-inferred summer surface water temperature (Temp) for the Yukon-Tuktoyaktuk Peninsula calibration set, based on weighted-averaging regression and calibration models using (a) classical deshrinking and (b) inverse deshrinking (after Pienitz *et al.*, 1995a).

Navicula and *Achnanthes*) in arctic tundra regions (Fig. 9.3). The comparatively low species diversity at tundra sites was mostly due to the high relative abundance of small *Fragilaria* spp. The results of the ordination analyses, together with the observed shifts in diatom assemblages across treeline and geological boundaries, suggested that alkalinity and conductivity exerted strong and significant controls on diatom taxa (Rühland, 1996).

A similar calibration set from Labrador (Fig. 9.1–D) showed that most diatom taxa were distributed along alkalinity and water colour gradients (Allaire, 1996), which together explained 30% of the total variance. Lake depth explained an additional 13% of the variation in the species data. The alkalinity optima ranged from 8.9 $\mu\text{eq/l}$ (*Eunotia paludosa* var. *trinacria* (Krasske) Nörpel) to 306.5 $\mu\text{eq/l}$ (*Cyclotella michiganiana* Skvortzow). An application of this inference model to fossil diatom data from southern Labrador revealed long-term natural acidification trends (Allaire, 1996), related to vegetational changes in the catchment.

SCANDINAVIA

Weckström *et al.* (1997a) studied the relationship between surface diatom assemblages and environmental variables in subarctic Fennoscandia (Fig. 9.1–E). Canonical Correspondence Analysis (CCA) suggested that pH, surface water temperature, conductivity, altitude, and sodium concentrations made significant contributions to explaining diatom distributions, with pH and temperature being the strongest predictor variables. Recently, this calibration set was expanded and diatom-based inference models for lakewater pH and

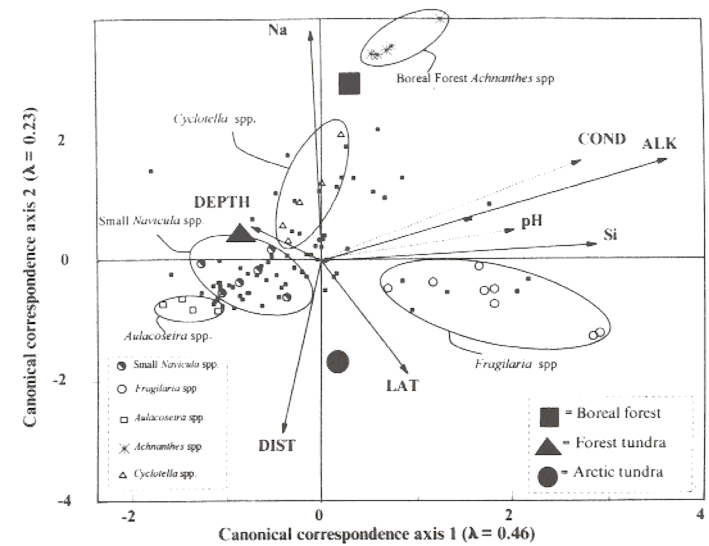


Fig. 9.3. Canonical correspondence analysis (CCA) of the Slave and Bear Province calibration set, showing general patterns in diatom distributions in relation to environmental variables (arrows) and major vegetational zones (centroids) (see Rühland, 1996).

temperature were developed (Weckström *et al.*, 1997b). The WA pH and temperature optima varied between pH 5.1 (*Tabellaria quadrisepata* Knudson) and 7.6 (*Neidium iridis* (Ehrenberg) Cleve), and between 10.3 °C (*Cyclotella rossii* Håkansson) and 14.7 °C (*Pinnularia legumen* Ehrenberg), respectively.

The diatom assemblages along a latitudinal transect extending from southern Finland to northern Norway (Fig. 9.1–F) were mainly composed of small acidophilic, periphytic taxa of boreo-alpine affinity, belonging to the genera *Achnanthes*, *Fragilaria* and *Navicula* (Pienitz *et al.*, 1995b). A regional comparison based on the biological composition of the Fennoscandian and Canadian subarctic sites showed similar trends in diatom assemblage composition with changing ecoclimatic zones.

SIBERIA

Information on freshwater diatoms from the Russian Arctic is scarce compared to its share of northern circumpolar treeline. Sabelina *et al.* (1951), Proschkina-Lavrenkov (1974), Aleksyuk & Bekman (1981), Chernyaeva (1981a,b), Antonov (1985) and Makarova (1992) published extensive reviews on freshwater diatoms from the former USSR. Besides providing information relating to diatom distributions, these references also include some ecological information. They represent the few comprehensive overviews of Russian diatoms, and are useful

for identifying taxa commonly found in Siberia, the Kola Peninsula, Novaya Zemlya, and other arctic regions.

Recent research has focused on three areas spanning treeline in northern Siberia (Fig. 9.1). A first transect is located close to Norilsk near the Taymyr Peninsula (Fig. 9.1–H). Significant variables explaining the diatom distributions were conductivity, lake depth, surface water temperature, silica and DIC. *Pinnularia balfouriana* Grunow and *Thalassiosira pseudonana* Hasle & Heimdal were more abundant in tundra lakes, while *Stauroneis anceps* Ehrenberg was more commonly found in boreal forest lakes (Laing *et al.*, unpublished data).

A second transect in the Lena River region of north-central Siberia contains 31 oligotrophic lakes (Fig. 9.1–J). Multivariate techniques indicated that lake depth, DOC, particulate organic carbon (POC) and chloride were ecologically significant for diatoms. In particular, assemblages in forest lakes separated from tundra lakes along a combined depth and DOC gradient. Forest lakes were generally deeper, with higher DOC (Laing *et al.*, unpublished data).

Another 27 lakes spanning treeline in the Pechora River region have been sampled as a third Russian treeline transect (Fig. 9.1–G), but these analyses are still in progress (T. Laing, pers. comm.). Overall, these three transects indicate that forest lakes as compared to tundra lakes are associated with higher nutrient concentrations. Compiling all three Russian transects into one calibration set indicated that diatom assemblages were regionally distinct, reflecting local differences in geology, pollution and other factors. In general, however, the most common diatom taxa were similar to those found in northern Canada and Fennoscandia (Laing *et al.*, unpublished data).

Two sediment cores, both from lakes currently located in the tundra zone, were examined for changes in the fossil diatom assemblages (T. Laing, unpublished data). The abundance of *Picea* and *Larix* macrofossils and higher arboreal pollen values in the lower part of a sediment core taken northwest of Norilsk (between 4400 and 4000 yrs BP), as well as the presence of fossil rooted stumps within the catchment, revealed that trees were once locally present. Diatom assemblages showed a minor shift to taxa characteristic of cooler conditions (e.g., *Amphora pediculus* (Kützing) Grunow) concurrent with the disappearance of trees (T. Laing, unpublished data). The second sediment core taken in the Lena River region showed that trees existed in the area between 7500 and 3500 yrs BP. The major change in diatom assemblages occurred concurrently with the period of treeline advance, with their dominant taxa (e.g., *Achnanthes minutissima*) probably reflecting increases in lake productivity (T. Laing, unpublished data).

Several long sediment cores were sampled from lakes located along a 1400 km transect spanning forest-tundra (near Norilsk) through polar desert environments on the islands of Severnaya Zemlya (Fig. 9.1–I). Preliminary results from Lama Lake (east of Norilsk) show marked changes in community structure during the Holocene, especially with respect to ratios of planktonic/benthic taxa. The strong fluctuations observed within the planktonic taxa may be due to climate-induced variations in the thermal

regime (e.g., a transition from dimictic to cold-monomictic conditions) of Lama Lake (Kienel, unpublished data).

The Alps

A STEEP ALTITUDINAL GRADIENT

Recent studies in mountainous regions have demonstrated a zonation of diatom assemblages along altitudinal gradients, which also incorporate gradients of water temperature (Servant-Wildary, 1982; Vyverman, 1992; Vyverman & Sabbe, 1995). Direct influences of temperature on the physiology of algal growth have been presented by, e.g., Raven & Geider (1988), whereas indirect effects due to prolonged ice-cover and changes in turbulent mixing have been discussed by Smol (1988) and Smol *et al.* (1991).

Sixty-eight Swiss lakes (Fig. 9.4) spanning an altitudinal gradient from 330 to 2350 m a.s.l. and a summer air temperature gradient of 7 to 21 °C demonstrate the importance of climate to diatoms and other aquatic organisms (chironomids, cladocera, chrysophytes), and have been used to develop multiproxy temperature inference models (Lotter *et al.*, 1997). The power of reconstructing past climate change may be amplified by the use of several independent lines of evidence.

As air temperatures most closely correspond to surface water temperatures during summer (Livingstone & Lotter, 1998), instrumental air temperature time series have been used as a basis for the July temperature inference models. Only hardwater lakes with pH values well above 7 were chosen to rule out the strong influence of acid waters on the composition of aquatic organisms.

CCA of this calibration set showed that catchment (14.6%; geology, land use, vegetation type), climate (13.4%; temperature, precipitation), and limnological variables (11.5%; water depth, surface area, catchment area) had the largest, statistically significant independent explanatory powers, whereas water chemistry (conductivity, pH, alkalinity, DOC, nutrients, metals) explained also a large (14.6%) but not significant part of the total variance. A weighted averaging partial least squares model for diatoms and July temperature provided an apparent $r^2 = 0.96$, a jack-knifed $r^2 = 0.80$, and a jack-knifed RMSEP = 1.6 °C. A vast majority of the diatoms (72.5%) that occurred in 20% or more of the samples showed statistically significant relationships to July temperature, either as an unimodal or a sigmoidal response.

Below elevations of 1000 m a.s.l. planktonic diatoms were dominant, whereas above 1000–1500 m a.s.l. small periphytic (in some cases probably also tycho planktonic) taxa such as *Fragilaria construens* (Ehrenberg) Grunow, *F. pinnata* Ehrenberg, *F. brevistriata* Grunow, and *Achnanthes minutissima* became more important (Fig. 9.4). There are, however, exceptions, mainly involving small centric taxa (e.g., *Cyclotella comensis*, *Thalassiosira pseudonana*). Low numbers of planktonic diatoms and increasing abundance of *Fragilaria* spp. is a



Fig. 9.4. Distribution of diatoms along an altitudinal gradient in the Swiss Alps (see Lotter *et al.*, 1997).

phenomenon often observed with increasing altitude or latitude. It may be related, on the one hand, to the fact that the growing season at these altitudes or latitudes is considerably shorter due to prolonged snow and ice-cover. As ice-melt starts at the shores, these marginal areas provide suitable habitats for the development of periphyton (Smol, 1988). Also, water transparency is generally high (Franz, 1979), thus favoring periphytic diatoms even in deeper lakes. On the other hand, alpine lakes are characterized by short-term fluctuations that may possibly favor *Fragilaria* spp. that are more adaptable and competitive.

Another diatom-temperature training set from the Alps, based exclusively on *Cyclotella* species, yielded an apparent $r^2 = 0.62$, with a bootstrap RMSEP = 1.3 °C (Wunsam *et al.*, 1995). Species temperature optima and tolerances were estimated by a WA model with *C. comensis* at the higher end (19.7 °C) and *C. styriaca* Hustedt at the lower end (11.9 °C) of the gradient. The enormous variability, especially within the small *Cyclotella* taxa, calls for more autecological studies of the various morphotypes.

Two calibration sets for nutrients (see also Hall & Smol, this volume), in particular, total phosphorus (TP), are also available from the Alps (Wunsam & Schmidt, 1995; Wunsam *et al.*, 1995; Lotter *et al.*, 1998). Yet, the majority of the calibration sites are located well below treeline. Application of these TP inference models to treeline lakes may, however, be limited by the generally low nutrient concentrations (Marchetto *et al.*, 1995; Müller *et al.*, in press) and the different diatom floras of the treeline lakes.

A CASE STUDY OF CHANGING ENVIRONMENTS: THE LATE-GLACIAL

Although many inference models have recently been developed for use with arctic/alpine diatom assemblages, few of these have been applied as yet. Paleoenvironmental records from the Alps illustrate how the application of these models may help to better understand environmental changes at the end of the last Ice-Age.

Multidisciplinary paleolimnological techniques (Schmidt *et al.*, 1998) were applied to a long sediment core from Längsee (548 m a.s.l.), a small, meromictic kettle-hole lake situated in the southeastern Alps (Carinthia, Austria). Due to its location at the southern slope of the Alps, close to the Würm pleniglacial ice margin, the lake became ice-free early, probably already more than 18 000 years ago. Transfer functions (Wunsam & Schmidt, 1995; Wunsam *et al.*, 1995) have been applied to infer total phosphorus concentrations and summer lake surface temperature. Before 15 500 yr BP (Fig. 9.5), climatic warming after deglaciation allowed the immigration and expansion of shrubs (e.g., *Juniperus*) into the lake's catchment. Increase in lake temperature enhanced the development of the diatom plankton (*Cyclotella ocellata* Pantocsek, *C. comensis*, *C. cyclopuncta* Håkansson & Carter, *C. distinguenda* var. *unipunctata* (Hustedt) Håkansson & Carter, *Stephanodiscus alpinus*). For this phase a mean surface

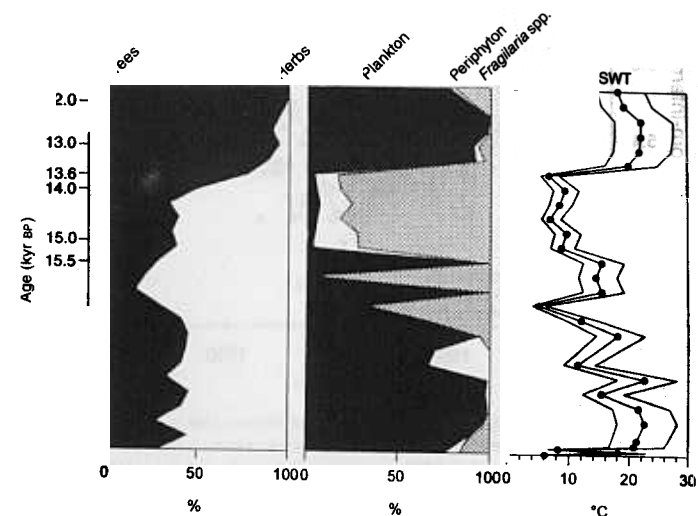


Fig. 9.5. Multidisciplinary paleolimnological approach to a late-glacial core section of Längsee (548 m a.s.l., Austria). Pollen percentages of trees and herbs, percentages of diatom life forms, and diatom-inferred summer surface water temperature (SWT; with sample-specific error band). Time-scale according to radiocarbon dates (see Schmidt *et al.*, 1998).

water temperature of 17.3 °C was inferred, suggesting that Längsee may have begun to stratify during this time. During the following climatic cooling, lake surface water temperature declined. Lower temperatures leading to prolonged ice-cover may be responsible for the low percentage of planktonic diatoms (Fig. 9.5). The change from a steppe to a tundra-like vegetation, rich in dwarf birch (*Betula nana*), and the still high amount of allochthonous material from catchment sources, indicate increasing precipitation. The contemporaneous increase in *Fragilaria* spp. (*F. construens*, including fo. *venter* (Ehrenberg) Hustedt, *F. pinnata*, all of which were more frequent in lakes with low summer surface temperature in the modern training set) explains the decrease in inferred summer water temperatures (mean inferred temperature = 10.7 °C). About 13 600 yr BP, reforestation by *Pinus cembra* began, which is also indicated by an increase in the amount of tree pollen and organic carbon content of the sediment. Diatom-inferred summer water temperatures increased at the same time towards modern levels (Fig. 9.5).

INDIRECT EFFECTS: A TEMPERATURE-PH RELATIONSHIP IN ALPINE LAKES

High altitude areas in the Alps are affected by precipitation with pH values between 4.8 and 5.2 and consequently acidification of crystalline bedrock sites has been reported. In these areas soil and vegetation have less influence on

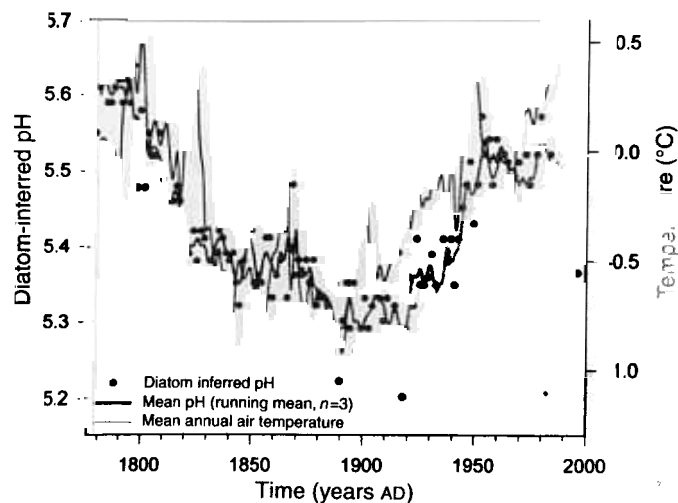


Fig. 9.6. Diatom-inferred pH history of Schwarzsee ob Sölden (2796 m a.s.l., Austria), during the last centuries, compared with the Austrian temperature curve (after Koinig *et al.*, 1997). The chronology is based on ^{210}Pb (constant rate of supply model) and ^{137}Cs dating (see Koinig, 1994; Koinig *et al.*, 1997; Sommaruga-Wögerth *et al.*, 1997).

biogenic acidification, because only a small fraction of the drainage area is covered by soil. High mountain lakes therefore react very sensitively to climatic and hydrological changes as well as to increasing acidity of precipitation (Arzet, 1987; Niederhauser, 1993; see also Battarbee *et al.*, this volume).

Paleolimnological investigations in Schwarzsee ob Sölden (2796 m a.s.l., Tyrol, Austria) showed a diatom-inferred pH decline from 6 to 5 (Arzet, 1987). Using a WA model based on a regional Alpine calibration set (Marchetto & Schmidt, 1993), the diatom-inferred pH changes in a core from Schwarzsee dating back to the eighteenth century were predominantly due to changes in abundances of the dominant *Aulacoseira* species (*A. alpigena* (Grunow) Krammer, *A. nygaardii* Camburn & Kingston, *A. distans*, including var. *nivalis* (W. Smith) Haworth, *A. perglabra* (Oestrup) Haworth; see Koinig, 1994 and Koinig *et al.*, 1997). The lowest inferred pH values occurred between 1880 and 1920. Towards 1970, the inferred pH values increased again to 5.55. A comparison of these pH reconstructions with the mean Austrian air temperature showed a strong correlation throughout the past 200 years (Fig. 9.6). These findings support the idea of a climate-driven pH control in high-alpine lakes (Psenner & Schmidt, 1992), i.e., that climatic cooling may cause decreases in pH, and rising temperatures increases in pH. The pH decline started at the onset of the Little Ice-Age, with glacier readvances in the Alps culminating around 1850. Koinig *et al.* (1997, 1998) and Sommaruga-Wögerth *et al.* (1997) suggested that pH increases during warm episodes may be a result of enhanced weather-

ing rates, increased in-lake alkalinity production, longer water retention times, and larger amounts of dust deposition from the surroundings (see also Marchetto *et al.*, 1995). However, the hypothesis that the influence of modern acidification is counteracted by recent climatic warming is not valid for all lakes. At Lake Rassas (2682 m a.s.l., Southern Tyrol, Italy) the onset of anthropogenically derived acid precipitation at the beginning of the twentieth century (Schmidt & Psenner, 1992; Psenner & Schmidt, 1992) led to a decoupling of the temperature – pH relationship, and thus to lake acidification that could be traced by diatoms.

Common features to arctic and alpine diatom assemblages

Many of the above-mentioned calibration sets have revealed interesting similarities in diatom assemblage composition across the treeline, namely the presence of assemblages composed of large benthic and planktonic taxa in the more nutrient-enriched forest lakes, and assemblages dominated by small benthic taxa in the more dilute lakes above treeline. This distinct trend in diatom community structure and cell size with changing latitude and altitude, in patterns unrelated to water depth, may be related to differences in the physico-thermal properties of the lakes and the length of the growing season (Pienitz, 1993). For example, there is evidence that climatic warming, with its likely consequences of a longer ice-free season and enhanced thermal stratification, would give a competitive advantage to planktonic forms, keeping these diatoms in suspension in the photic zone for longer periods of time (Smol, 1988; Fee *et al.*, 1992).

The differences observed between diatom cell size in lakes below and above the treeline could be related to nutrient availability, length of growing season, and diatom growth rates. The maximum specific growth rates in algae decrease with increasing cell size (Raven & Geider 1988), and the high surface-to-volume ratio of small cells provides them with a competitive advantage under low nutrient conditions. According to Denys (1988), small benthic *Fragilaria* spp. fit into the classic model of organisms favored by *r*-selection (i.e., small size, high reproductive rate, large ecological amplitude). Because of their higher turnover rates, these opportunistic, small-celled diatoms may quickly form blooms and (temporarily) outcompete larger diatom species with slower growth rates during the brief growing season in tundra lakes (Pienitz, 1993).

With respect to patterns observed in planktonic/benthic forms and diatom cell size, availability of silica may also play an important role. As some of the studies revealed, silica concentrations explained a significant proportion of the variance in diatom distribution. Diatoms assimilate large quantities of silica, thereby modifying the flux rates of silica in freshwater ecosystems (e.g., Hutchinson, 1967; Wetzel, 1983; Schelske, this volume). Silica concentrations, on the other hand, are known to affect diatom growth rates, as well as the

succession and composition of diatom communities (e.g., Lund, 1964; Servant-Vildary *et al.*, 1992). The small number of planktonic taxa observed in lakes above treeline may also be related to silica deficiency, which is a crucial factor especially for the growth of freshwater planktonic diatoms (e.g., Jørgensen, 1957; Kilham, 1971).

Summary

Diatoms in treeline regions are important and sensitive indicators of environmental change. The arctic and alpine treeline are important ecotones. Their present-day, past, and future positions depend largely on climatic factors. Climatic fluctuations at this ecotone either directly or indirectly influence diatom communities through alterations in physical and chemical limnetic properties. Therefore, diatoms have great potential as environmental indicators and contribute to and complement paleoecological studies in treeline regions. Reconstructing changes in past treeline position provides essential boundary conditions for Global Circulation Models to hindcast past or predict future climate change.

In all studies involving diatom calibration sets, pH or pH-related variables (e.g., alkalinity, ANC, DIC, Ca) have been shown to influence significantly diatom distributions. Apart from the predominant control exerted by pH and related variables, two major gradients appear to emerge from these studies: the concentration of lakewater DOC (which is related to catchment vegetation and treeline), and surface-water temperature (which is related to latitude and/or altitude). Temperature is a complex variable that is highly correlated with other characteristics of the environment, such as mixing regime and duration of ice-cover. The distinct influence exerted by the temperature gradient on diatom distribution as shown in the studies from northwestern Canada, Fennoscandia and the Alps, is of ecological and paleoecological significance as it strengthens the assumption that the relationship between organisms and climate is clearest at ecotonal boundaries, and, consequently, ecotones are optimal areas for studying climatic change (e.g., Smol *et al.*, 1991).

The potential for inferring past DOC levels from paleolimnological records combined with recent advances in bio-optical modelling in northern lakes (e.g., Laurion *et al.*, 1997), leads to the exciting prospect of reconstructing past underwater light regimes. Such analyses could include estimates of euphotic depth and spectral attenuation across the ultraviolet waveband. This new theme in paleolimnology ('lake paleo-optics') offers opportunities for integrating studies of the present-day with historical properties of lakes (Vincent & Pienitz, 1996). This approach is of special interest for lakes in treeline regions, since lakes above treeline may be more sensitive to small changes in DOC and rising UV-B (ultraviolet B) radiation associated with stratospheric ozone depletion than lakes of the boreal forest (Vincent & Pienitz, 1996).

Lake depth generally emerged as an important predictor for diatom com-

munities, especially in arctic treeline regions. Its importance is known from many investigations and seems to support Smol's (1988) hypothesis that microhabitat availability significantly influences diatom assemblage composition (i.e., the relative percentage of planktonic and benthic taxa). Moreover, in paleoclimatological studies, lake depth becomes an important indicator with respect to lake-level changes (see Wolin & Duthie, this volume), e.g., through changes in atmospheric circulation patterns.

The results obtained from diatom studies in treeline regions seem to confirm a general relationship between the distribution of diatoms and ecoclimatic or vegetational zones. Despite the extremely high degree of floristic diversity that characterizes oligotrophic boreal lakes compared with lakes in temperate regions (e.g., Lange-Bertalot & Metzeltin, 1996), a surprisingly high degree of floristic similarity could be observed among calibration sets from different treeline regions. These regions may be floristically similar enough to allow the development of supra-regional data sets. A recently launched joint research initiative, the Circumpolar Treeline Diatom Database (CTDD), aims at expanding and improving existing diatom calibration sets by combining the existing data sets from North America, Scandinavia and Siberia into one large data set for the whole of circumpolar, northern hemispheric treeline regions. Nevertheless, all transfer function approaches have to be assessed critically (see, e.g., Birks, 1995) before using their results for hindcasting past environmental change at the arctic or alpine ecotone.

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References

- Aleksyuk, G. V., & Bekman, M. Y. (1981). Fitoplankton Putoranskikh ozer iusloviya ego razvitiya. In *Ozera Severo-Zapada Sibirskoj platformy*, ed. G. J. Galaziy & Y. P. Paramuzin, pp. 110-118. Novosibirsk.
- Allaire, N. (1996). *Relation entre les assemblages de diatomées et les variables environnementales de 70 lacs du Labrador, et résultats préliminaires d'une étude paléolimnologique du Lac Hope Simpson*. MA thesis, Université Laval, Québec.
- Antonov, S. E. (1985). Osobennosti fitoplanktona ozer Tajmyr, *Geografiya ozer Tajmyra*, ed. V. N. Adamenko & A. N. Egorov, pp. 128-30. Nauka, Leningrad.
- Arzet K., (1987). *Diatomeen als pH-Indikatoren in subrezentem Sedimenten von Weichwasserseen*. Dissertation Universität Innsbruck.
- Sackman, A. L., & Cleve-Euler, A. (1922). Die fossile Diatomeenflora in Österbotten. *Acta Forestalia Fennica*, 22, 5-73.
- Sattarbee, R. W. (1991). Paleolimnology and climate change. In *Evaluation of Climate Proxy*

- Data in Relation to the European Holocene*, ed. B. Frenzel, A. Pons & B. Gläser, Paläoklimaforschung, 6, Akademie der Wissenschaften und der Literatur Mainz, pp. 149–57.
- Birks, H. J. B. (1995). Quantitative paleoenvironmental reconstructions. In *Statistical modeling of Quaternary science data*, ed. D. Maddy & J. S. Brew, Quaternary Research Association, Cambridge, pp. 161–254.
- Bryson, R. A. (1966). Air masses, streamlines, and the boreal forest. *Geographical Bulletin*, 8, 228–69.
- Charles, D. F., & Smol, J. P. (1994). Long-term chemical changes in lakes: Quantitative inferences using biotic remains in the sediment record. In *Environmental Chemistry of Lakes and Reservoirs*, ed. L. Baker, Advances in Chemistry Series, 237, pp. 3–31. American Chemical Society, Washington DC.
- Chernyaeva, G. P. (1981a). Ekologo-sistematicheskaya kharakteristika diatomej ozera Nyakshinga. In *Ozera Severo-Zapada Sibirskoj platformy*, ed. G. J. Galaziy & Y. P. Paramuzin, pp. 118–23. Novosibirsk.
- (1981b). Razpredelenie diatomej v ozadkakh I nekotorye voprosy paleogeografii ozer Agata Nizhnee I Agata Verkhnee. In *Istoriya bol'shikh ozer Tsentral'noj Subarktiki*, ed. G. J. Galaziy & Y. P. Paramuzin, pp. 122–30. Novosibirsk.
- Cleve-Euler, A. (1934). The diatoms of Finnish Lapland. *Societas Scientiarum Fennica Commentationes Biologicae*, IV, 14, 1–154.
- (1951–1955). Die Diatomeen von Schweden und Finnland. 1–5. *Kongliga Svenska Vetenskap Akademien Handlingar Serie 4*, 2/1, 1–163; 3/3, 1–153; 4/1, 1–158; 4/5, 1–225; 5/4, 1–232.
- Dauta, A., Devaux, J., Piquemal, F., & Boumnick, L. (1990). Growth rate of four freshwater algae in relation to light and temperature. *Hydrobiologia*, 207, 221–6.
- Denys, L. (1988). *Fragilaria* blooms in the Holocene of the western Belgian coastal plain. *Abstracts 10th International Diatom Symposium*, Joensuu, Finland.
- Doskey, P. V., & Ugoagwu, B. J. (1989). Atmospheric deposition of macronutrients by pollen at a semi-remote site in northern Wisconsin. *Atmospheric Environment*, 23, 2761–6.
- Ellenberg, H. (1986). *Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht*. Stuttgart, E. Ulmer.
- Eppley, R. W. (1977). The growth and culture of diatoms. In *The biology of diatoms*, ed. D. Werner, Botanical Monographs, 13, pp. 24–64. Oxford: Blackwell.
- Fee, E. J., Shearer, J. A., DeBruyn, E. R., & Schindler, E. U. (1992). Effects of lake size on phytoplankton photosynthesis. *Canadian Journal of Fisheries and Aquatic Sciences*, 49, 2445–59.
- Florin, M.-B. (1957). Plankton of fresh and brackish waters in the Södertälje area (Sweden). *Acta Phytogeographica Suecica*, 37, 1–93.
- Foged, N. (1955). Diatoms from Peary Island, north Greenland. *Meddelelser om Grønland*, 128, 1–90.
- (1964). Freshwater diatoms from Spitsbergen. *Tromsø Museums Skrifter*, 11, 1–205.
- (1981). *Diatoms in Alaska*. Vaduz: J. Cramer.
- Franz, H. (1979). *Ökologie der Hochgebirge*. Stuttgart: E. Ulmer.
- Gajewski, K., Garneau, M., & Bourgeois, J. C. (1995). Paleoenvironments of the Canadian High Arctic derived from pollen and plant macrofossils: Problems and potentials. *Quaternary Science Reviews*, 14, 609–29.
- Grabherr, G., Gottfried, M., & Pauli, H. (1994). Climate effects on mountain plants. *Nature*, 369, 448.
- Hartig, J. H., & Wallen, D. G. (1986). The influence of light and temperature on growth and photosynthesis of *Fragilaria crotonensis* Kitton. *Journal of Freshwater Ecology*, 3, 371–82.
- Hondzo, M., & Stefan, H. G. (1993). Regional water temperature characteristics of lakes subject to climate change. *Climate Change*, 24, 187–211.
- Houghton, J. T., Jenkins, G. J., & Ephraums, J. J. (ed.) (1990). *Climate Change: The IPCC Scientific Assessment*. Cambridge, UK: Cambridge University Press.
- Houghton, J. J., Meiro Filho, L. G., Callender, B. A., Harris, N., Kattenberg, A., & Maskell, K. (ed.) (1996). *Climate change 1995 – the science of climate change. Contribution of Working Group I to the Second Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.
- Hustedt, F. (1939). Systematische und ökologische Untersuchungen über die Diatomeen-Flora von Java, Bali und Sumatra nach dem Material der Deutschen limnologischen Sunda-Expedition. *Archiv für Hydrobiologie Beiheft II*, 16, 1–155, 274–394.
- (1942). Diatomeen aus der Umgebung von Abisko in Schwedisch-Lappland. *Archiv für Hydrobiologie*, 39, 82–174.
- (1943). Die Diatomeenflora einiger Hochgebirgsseen der Landschaft Davos in den Schweizer Alpen. *Internationale Revue der gesamten Hydrobiologie*, 43, 124–97.
- (1956). *Kieselalgen (Diatomeen)*. Stuttgart: Kosmos.
- Hustich, I. (1979). Ecological concepts and biogeographical zonation in the North: The need for a generally accepted terminology. *Holarctic Ecology*, 2, 208–17.
- Hutchinson, G. E. (1967). *A Treatise on Limnology*, vol. II, New York: John Wiley.
- Jørgensen, E. G. (1957). Diatom periodicity and silicon assimilation. *Dansk Botanisk Arkiv*, 18, 1–54.
- Kilham, P. (1971). A hypothesis concerning silica and the freshwater planktonic diatoms. *Limnology and Oceanography*, 16, 10–18.
- Kilham, S. S., Theriot, E. C., & Fritz, S. C. (1996). Linking planktonic diatoms and climate change in the large lakes of the Yellowstone ecosystem using resource theory. *Limnology and Oceanography*, 41, 1052–62.
- Kingston, J. C., Lowe, R. L., Stoermer, E. F., & Ladewski, T. B. (1983). Spatial and temporal distribution of benthic diatoms in northern Lake Michigan. *Ecology*, 64, 1566–80.
- Koinig K. A. (1994). *Die pH-Geschichte des Schwarzsees ob Sälden. Eine Rekonstruktion der letzten 200 Jahre mittels benthischer Diatomeen*. Diplomarbeit Univ. Innsbruck/Institut für Limnologie Mondsee ÖAW, 1–62.
- Koinig, K. A., Schmidt, R., & Psenner, R. (1998). Effects of air temperature changes and acid deposition on the pH history of three high alpine lakes. *Proceedings of the 14th International Diatom Symposium*. Koeltz Scientific Books, Koenigstein, 497–508.
- Koinig, K. A., Schmidt, R., Wögrath, S., Tessadri, R., & Psenner, R. (1997). Climate change as the primary cause for pH shifts in a high Alpine lake. *Water, Air and Soil Pollution*, 104, 167–80.
- Koivo, L. K., & Ritchie, J. C. (1978). Modern diatom assemblages from lake sediments in the boreal–arctic transition region near the Mackenzie Delta, N.W.T., Canada. *Canadian Journal of Botany*, 56, 1010–20.
- Kolbe, R. W. (1927). Zur Ökologie, Morphologie und Systematik der Brackwasser-Diatomeen. *Pflanzenforschung*, 7, 1–146.
- Krasske, G. (1932). Beiträge zur Kenntnis der Diatomeenflora der Alpen. *Hedwigia*, 72, 92–134.
- Kupfer, J. A., & Cairns, D. M. (1996). The suitability of montane ecotones as indicators of global climatic change. *Progress in Physical Geography*, 20, 253–72.
- Lang, G. (1994). *Quartäre Vegetationsgeschichte Europas. Methoden und Ergebnisse*. Jena: G. Fischer.
- Lange-Bertalot, H., & Metzeltin, D. (1996). Indicators of oligotrophy. 800 taxa representative of three ecologically distinct lake types. Carbonate buffered-oligo-trophic-weakly buffered soft water. *Iconographia Diatomologica*, 2, 1–390.
- Larsen, J. A. (1989). The Northern Forest Border in Canada and Alaska. *Ecological Studies*, 70, 1–255.
- Laurion, I., Vincent, W. F., & Lean, D. R. (1997). Underwater ultraviolet radiation: Development of spectral models for northern high latitude lakes. *Photochemistry and Photobiology*, 65, in press.
- Lee, E. J., Kenkel, N., & Booth, T. (1996). Atmospheric deposition of macronutrients by pollen in the boreal forest. *Écoscience*, 3, 304–9.
- Livingstone, D. M. (1998). Break-up dates of Alpine lakes as proxy data for local and regional mean surface air temperatures. *Climatic Change*, 37, 407–39.
- Livingstone, D. M., & Lotter, A. F. (1998). The relationship between air and water temperatures in lakes of the Swiss Plateau: A case study with paleolimnological implications. *Journal of Paleolimnology*, 19, 181–98.

- Lotter, A. F., Birks, H. J. B., 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.
- (1998). Modern diatom, Cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. II. Nutrients. *Journal of Paleolimnology*, **19**, 443–63.
- Lund, J. W. G. (1964). Primary production and periodicity of phytoplankton. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **15**, 37–56.
- MacDonald, G. M., Edwards, T. W. D., Moser, K. A., Pienitz, R., & Smol, J. P. (1993). Rapid response of treeline vegetation and lakes to past climate warming. *Nature*, **361**, 243–6.
- Makarova, I. W. (1992). *The Diatoms of the USSR – Fossil and Recent*, vol. II. (In Russian) Nauka, St. Petersburg.
- Marchetto, A., & R. Schmidt, (1993). A regional calibration data set to infer lakewater pH from sediment diatom assemblages in alpine lakes. *Memorie Istituto italiano di Idrobiologia*, **51**, 115–25.
- Marchetto, A., Mosello, R., Psenner, R., Bendetta, G., Boggero, A., Tait, D., & Tartari, G. A. (1995). Factors affecting water chemistry of alpine lakes. *Aquatic Sciences*, **57**, 81–9.
- Mölder, K., & Tynni, R. (1967–1975). Über Finnlands rezente und sub-fossile Diatomeen. *Bulletin of the Geological Society of Finland*, **40**, 151–70; **41**, 235–51; **42**, 129–44; **43**, 203–20; **44**, 141–59; **45**, 159–79.
- Monserud, R. A., Tchebakova, N. M., & Leemans, R. (1993). Global vegetation change predicted by the modified Budyko model. *Climatic Change*, **25**, 59–83.
- Moser, K. A., MacDonald, G. M., & Smol, J. P. (1996). Application of freshwater diatoms to geographical research. *Progress in Physical Geography*, **20**, 21–52.
- Müller, B., Lotter, A. F., Sturm, M., & Ammann, A. (1998). Influence of catchment and altitude on the water and sediment composition of 68 small lakes in Central Europe. *Aquatic Sciences*, in press.
- Niederhauser, F. (1993). *Diatomeen als Bioindikatoren zur Beurteilung der Belastung elektrolytarmer Hochgebirgsseen durch Säuren und Nährstoffe*. Dissertation, Universität Zürich.
- Niederhauser, F., & Schanz, F. (1993). Effects of nutrient (N, P, C) enrichment upon the littoral diatom community of an oligotrophic high-mountain lake. *Hydrobiologia*, **269/270**, 453–62.
- Ozenda, P. (1985). *La végétation de la chaîne alpine dans l'espace montagnard européen*. Paris: Masson.
- Patrick, R. (1971). The effects of increasing light and temperature on the structure of diatom communities. *Limnology and Oceanography*, **16**, 405–21.
- (1977). Ecology of freshwater diatoms and diatom communities. In *The Biology of Diatoms*, ed. D. Werner, Botanical Monographs, vol. **13**, pp. 284–332. Oxford: Blackwell.
- Pielke, R. A., & Vidale, P. L. (1995). The boreal forest and the polar front. *Journal of Geophysical Research*, **100**, 25755–8.
- Pienitz, R. (1993). *Paleoclimate proxy data inferred from freshwater diatoms from the Yukon and the Northwest Territories, Canada*. PhD thesis, Queen's University, Kingston (Ontario).
- Pienitz, R., & Smol, J. P. (1993). Diatom assemblages and their relationship to environmental variables in lakes from the boreal forest–tundra ecotone near Yellowknife, Northwest Territories, Canada. *Hydrobiologia*, **269/270**, 391–404.
- Pienitz, R., Smol, J. P., & Birks, H. J. B. (1995a). 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, M. S. V., Smol, J. P., Huttunen, P., & Meriläinen, J. (1995b). Diatom, chrysophyte and protozoan distributions along a latitudinal transect in Fennoscandia. *Ecography*, **18**, 429–39.
- Pienitz, R., Smol, J. P., & Lean, D. R. S. (1997a). Physical and chemical limnology of 59 lakes located between the southern Yukon and the Tuktoyaktuk Peninsula, Northwest Territories (Canada). *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 330–46.
- (1997b). Physical and chemical limnology of 24 lakes located between Yellowknife and Conroyto Lake, Northwest Territories (Canada). *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 347–58.
- Pienitz, R., Smol, J. P., & MacDonald, G. M. (1999). Paleolimnological reconstruction of Holocene climatic trends from two boreal treeline lakes, Northwest Territories, Canada. *Arctic and Alpine Research*, in press.
- Proshkina-Lavrenko, A. I. (1974). *The Diatoms of the USSR – Fossil and Recent*, vol. I. (In Russian) Nauka, Leningrad.
- Psenner, R., & R. Schmidt, (1992). Climate-driven pH control of remote alpine lakes and effects of acid deposition. *Nature*, **356**, 781–3.
- Raven, J. A., & Geider, R. J. (1988). Temperature and algal growth. *New Phytologist*, **110**, 441–61.
- Robertson, D. M., & Ragotzkie, R. A. (1990). Changes in the thermal structure of moderate to large sized lakes in response to changes in air temperature. *Aquatic Sciences*, **52**, 360–80.
- Rühland, K. (1996). *Assessing the use of diatom assemblages as paleoenvironmental proxies in the Slave and Bear geological provinces, NWT, Canada*. MSc thesis, Queen's University, Kingston (Ontario).
- Sabelina, M. M., Kisselyev, I. A., Proshkina-Lavrenko, A. I., & Sheshukova, B. C. (1951). Diatomovye vodorosli. Opredeletely presnovodnykh vodoroslei sssr, Gosudarstvennoe Izdatelystvo. *Sovetskaja Nauka*, **4**, Moscow.
- Schindler, D. W., Bayley, S. E., Parker, B. R., Beaty, K. G., Cruikshank, D. R., Fee, E. J., Schindler, E. U., & Stainton, M. P. (1996a). The effects of climatic warming on the properties of boreal lakes and streams at the Experimental Lakes Area, north-western Ontario. *Limnology and Oceanography*, **41**, 1004–17.
- Schindler, D. W., Beaty, K. G., Fee, E. J., Cruikshank, D. R., DeBruyn, E. R., Findlay, G. A., Linsey, G. A., Shearer, J. A., Stainton, M. P., & Turner, M. A. (1990). Effects of climatic warming on lakes of the central boreal forest. *Science*, **250**, 967–70.
- Schindler, D. W., Curtis, P. J., Parker, B. R., & Stainton, M. P. (1996b). Consequences of climate warming and lake acidification for UV-B penetration in North American boreal lakes. *Nature*, **379**, 705–8.
- Schmidt, R., & Psenner, R. (1992). Climate changes and anthropogenic impacts as causes for pH fluctuations in remote high alpine lakes. *Documenta Istituto Italiano Idrobiologia*, **32**, 31–57.
- Schmidt, R., Wunsam S., Brosch, U., Fott, J., Lami, A., Löffler, H., Marchetto, A., Müller, H. W., Prazakova, M., & Schwaighofer, B. (1998). Late and post-glacial history of meromictic Längsee (Austria), in respect to climate change and anthropogenic impact. *Aquatic Sciences*, **60**, 56–88.
- Servant-Vildary, S. (1982). Altitudinal zonation of mountainous diatom flora in Bolivia: Application to the study of the Quaternary. *Acta Geol. Acad. Sci. Hungaricae*, **25**, 179–210.
- Servant-Vildary, S., Melice, J. L., Sondag, F., Einarsson, A., Dickman, M., & Stewart, K. (1992). A transfer function diatom/silica displayed in Lake Myvatn (Iceland). *Abstracts 12th International Diatom Symposium*, Renesse, The Netherlands.
- Smith, T. M., Shugart, H. H., Bonan, G. B., & Smith, J. B. (1992). Modeling the potential response of vegetation to global climate change. *Advances in Ecological Research*, **22**, 93–116.
- Smol, J. P. (1988). Paleoclimate proxy from freshwater arctic diatoms. *Verhandlungen Internationale Vereinigung Limnologie*, **23**, 837–44.
- Smol, J. P., Walker, I. R., & Leavitt, P. R. (1991). Paleolimnology and hindcasting climatic trends. *Verhandlungen Internationale Vereinigung Limnologie*, **24**, 1240–6.
- Smol, J. P., Cumming, B. F., Douglas, M. S. V., & Pienitz, R. (1995). Inferring past climatic changes in Canada using paleolimnological techniques. *Geoscience Canada*, **21**, 113–8.
- Sommaruga, R., & Psenner, R. (1997). Ultraviolet radiation in a high mountain lake of the Austrian Alps: Air and underwater measurements. *Photochemistry and Photobiology*, **65**, 957–63.
- Sommaruga-Wögrath, S., Koinig, K., Schmidt, R., Sommaruga, R., Tessadri, R., & Psenner, R.

- (1997). Temperature effects on the acidity of remote alpine lakes. *Nature*, **387**, 64–7.
- Stoermer, E. F., & Ladewski, T. B. (1976). Apparent optimal temperatures for the occurrence of some common phytoplankton species in southern Lake Michigan. *University of Michigan, Great Lakes Research Division Publication*, **18**.
- Tinner, W., Ammann, B., & Germann, P. (1996). Treeline fluctuations recorded for 12,500 years by soil profiles, pollen, and plant macrofossils in the Central Swiss Alps. *Arctic and Alpine Research*, **28**, 131–47.
- Tranquillini, W. (1979). *Physiological ecology of the alpine timberline*. Berlin: Springer.
- Tynni, R. (1975). Über Finnlands rezente und subfossile Diatomeen. VIII. *Bulletin Geological Survey of Finland*, **274**, 1–55.
- (1976). Über Finnlands rezente und subfossile Diatomeen. IX. *Bulletin Geological Survey of Finland*, **284**, 1–37.
- Vincent, W. F., & Pienitz, R. (1996). Sensitivity of high latitude freshwater ecosystems to global change: Temperature and solar ultraviolet radiation. *Geoscience Canada*, **23**, 231–6.
- Vinebrooke, R. D., & Leavitt, P. R. (1996). Effects of ultraviolet radiation in an alpine lake. *Limnology and Oceanography*, **41**, 1035–40.
- Vyverman, W. (1992). Altitudinal distribution of non-cosmopolitan desmids and diatoms in Papua New Guinea. *British Phycological Journal*, **27**, 49–63.
- Vyverman, W., & Sabbe, K. (1995). Diatom–temperature transfer functions based on the altitudinal zonation of diatom assemblages in Papua New Guinea: A possible tool in the reconstruction of regional paleoclimatic changes. *Journal of Paleolimnology*, **13**, 65–77.
- Watson, R. T., Zinyowera, M. C., Moss, R. H., & Dokken, D. J. (ed.) (1996). *Climate change 1995 – impacts, adaptations and mitigation of climate change: scientific-technical analyses. Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.
- Weckström, J., Korhola, A., & Blom, T. (1997a). The relationship between surface-water temperature and diatom assemblages in 30 subarctic lakes from northern Fennoscandia: a potential tool for paleotemperature reconstructions. *Arctic and Alpine Research*, **29**, 75–92.
- (1997b). Diatoms as quantitative indicators of pH and water temperature in subarctic Fennoscandian lakes. *Hydrobiologia*, **347**, 171–84.
- Wetzel, R. G. (1983). *Limnology*, 2nd edn. Saunders College Publishing.
- Wunsam, S., & Schmidt, R. (1995). A diatom–phosphorus transfer function for Alpine and prealpine lakes. *Memorie Istituto Italiano di Idrobiologia*, **53**, 85–99.
- Wunsam, S., Schmidt, R., & Klee, R. (1995). *Cyclotella*-taxa (Bacillariophyceae) in lakes of the Alpine region and their relationship to environmental variables. *Aquatic Sciences*, **57**, 360–86.