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Diatoms as indicators of environmental change in subarctic and alpine regions

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12.1 Introduction

Subarctic and mountain regions are characterized by strong gradients that make their terrestrial and aquatic ecosystems very sensitive to environmental change. The terrestrial Arctic can be delimited by the northern tree line, the 10 °C July isotherm, or the southern extent of discontinuous permafrost which, in the eastern Canadian Arctic for example, currently extends to the southern end of Hudson Bay. In this chapter, we focus on the subarctic region, which, depending on local climates, roughly falls between 50° N and 70° N latitude and includes the transition from boreal forest (taiga) in the south to tundra landscapes in the north, whereas the chapter by Douglas and Smol (this volume) discusses diatom-based studies from the High Arctic. In mountain regions the same steep climatic and environmental gradients are present but over much shorter distances, with the timber line also representing the most prominent ecotone. 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. tree line), and eventually to open, unforested vegetation. This biological boundary can vary in width from tens of meters in mountain regions to many kilometers in the Subarctic. In northern Europe it is formed by deciduous trees such as *Betula*, *Alnus*, and *Populus*, whereas coniferous trees (e.g. *Pinus*, *Picea*, *Larix*, *Juniperus*) form the tree line in the European Alps, northern North America, and Eurasia. This ecotone is primarily related to cold temperatures with a complex set of different microclimatic factors, as well as the specific adaptation of trees, defining the forest limit (e.g. Tranquillini, 1979). In the European Alps, for instance, the timber line represents the transition between the subalpine and the alpine elevational belts (Ozenda, 1985). The lower boundary of the alpine belt, however, is difficult to

locate as human impact, grazing, and climatic oscillations have lowered the natural tree limit by several hundred meters, at least during the past three to four millennia (e.g. Tinner *et al.*, 1996).

Aquatic habitats suitable for diatoms at these latitudes and altitudes are manifold. High-latitude and high-altitude lakes and rivers are characterized by special limnological features and are usually ice free for only a short period in summer, with cold water temperatures prevailing (Battarbee *et al.*, 2002b). Lakes influenced by glacial meltwaters are turbid with high concentrations of silt and clay, whereas in the absence of glaciers, water transparency is either high or, if mires are present in the catchment, the input of humic acids will result in brown water (dystrophic) conditions. Furthermore, light availability in the water column is strongly restricted by ice and snow cover, and at high latitudes also by the polar winter. During summer, however, the light conditions change significantly, especially in high-latitude lakes: the photoperiod is long and the angle of the sun is higher.

Climatic control of ultraviolet (UV) radiation and underwater UV exposure have been identified as important factors regulating lake production and algal community composition in high-altitude and high-latitude lakes (e.g. Pienitz and Vincent, 2000). For example, UV 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 and Leavitt, 1996). There are many mechanisms linking UV exposure to climate in the aquatic environment: some are caused by climate-induced changes in the stratosphere, while many are associated with temperature-related effects on the main UV-attenuating components of natural waters, notably changes in snow and ice cover, and in chromophoric (colored) dissolved organic matter (CDOM) associated with shifts in terrestrial vegetation in the catchment of lakes. There are

also a variety of hydrological effects of climate with major implications for underwater UV such as changes in snow and rainfall (with runoff, vegetation, and albedo effects), evaporation and cloud cover, pathways of runoff, and degree of interaction between soil and water. Finally, there are more subtle effects such as changes in wind-induced mixing and climate-induced shifts in species composition towards more or less UV-tolerant species. Many of these effects are especially pronounced in high-latitude and high-altitude aquatic ecosystems where there is a precarious balance between freezing and melting throughout summer, and where small changes in CDOM concentrations can have large effects on UV transparency.

Lakes on opposite sides of the tree line exhibit striking differences in water chemistry and physical conditions (Pienitz et al., 1997a, 1997b; Sommaruga and Psenner, 1997; Fallu and Pienitz, 1999; Rühland et al., 2003), which are reflected by abrupt changes in diatom-community structure and composition. For example, differences in lake mixing regimes, nutrients, and lake-water 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; see Lee et al., 1996). Furthermore, sediment accumulation rates may change drastically across this ecotone: accumulation rates in lakes above the tree line without glacial melt-water influx are often up to an order of magnitude lower than in comparable boreal or temperate lake basins (Laing et al., 2002). The dearth of alpine and northern-tree-line diatom studies is primarily related to logistical problems. Nevertheless, early diatom studies from high-altitude and high-latitude regions usually provided extended taxon lists (e.g. Krasske, 1932; Cleve-Euler, 1934; Hustedt, 1943, 1942; Foged, 1955) and often classified taxa according to their plant-geographical distribution (e.g. nordic-alpine). Freshwater diatoms, like most algae, are usually not considered sensitive indicators of temperature directly (e.g. Battarbee, 1991; Anderson, 2000), even though clear latitudinal and altitudinal patterns in their distributions are apparent (Foged, 1964; Vyverman, 1992; Pienitz and Smol, 1993; Lotter et al., 1997), and classifications according to their thermal requirements (Backman and Cleve-Euler, 1922; Hustedt, 1939, 1956) have long existed. Several experimental studies (e.g. Patrick, 1971, 1977; Eppley, 1977; Hartig and Wallen, 1986; Dauta et al., 1990; Montagnes and Franklin, 2001) indicate a temperature dependency of diatom growth and community composition. Under natural conditions, Stoermer and Ladewski (1976) and Kingston et al. (1983) found a relationship between temperature and the occurrence of certain

diatoms. Kilham et al. (1996), however, associated the climatic distribution of diatoms with resource-related competitive interactions. The diatom-temperature relationship is a complex one, as temperature changes may have multiple, profound indirect impacts on the chemical and physical properties of the aquatic environment and available habitats, as well as on biological factors such as the competitive abilities of the biota. However, from a paleoclimatic perspective, it is not relevant if the relationship between diatoms and temperature is direct or indirect, rather how reliably the variable can be reconstructed, whether other environmental variables than climate have negligible influence (Birks, 1995), and whether the relationship between climate and indirect factors remains linear over time (Smol and Cumming, 2000). In fact, the use of diatoms as quantitative proxies of past temperatures has become common use and proved successful in several paleolimnological studies in subarctic and mountain regions of the northern hemisphere (e.g. Pienitz et al., 1999; Korhola et al., 2000; Hausmann and Lotter, 2001; Joynt and Wolfe, 2001; Bigler and Hall, 2002, 2003; Bigler et al., 2003; Schmidt et al., 2008; von Gunten et al., 2008).

12.2 Diatoms as paleoenvironmental indicators at the tree line

Tree-line vegetation will be strongly impacted by future climatic warming (ACIA, 2004; IPCC, 2007). Furthermore, aquatic environments and ecosystems, water supplies, and fisheries will likewise be affected (Wrona et al., 2006). Global warming will result in increased heat uptake of lakes which, in turn, will lead to earlier break-up and later onset of ice cover and, consequently, to changes in stratification and oxygen regimes (e.g. Schindler et al., 1996; Livingstone, 1997; Sommaruga-Wögrath et al., 1997; Catalan et al., 2002a; Vincent et al., 2008). Ultra-sensitive lakes, i.e. those which are colder than can be expected from air temperatures, will warm up distinctly during global warming (Thompson et al., 2005a). Moreover, thawing of permafrost catchment soils will have an impact on nutrient, CDOM, and heavy-metal concentrations in such lakes (e.g. Smol, 2002; Baron et al., 2005; Kamenik et al., 2005).

Because the location of the northern tree line results from and also influences the mean position of major atmospheric boundaries (i.e. the Polar Front; Pielke and Vidale, 1995), it is important to understand the linkages between climate and vegetation along the northern edge of the boreal forests. The sensitivity of the arctic and alpine tree-line position to climatic factors makes this ecotone an ideal location for investigating the effects and the timing of climatic change (e.g. Pienitz and Smol,

1993; Lotter, 2005; Tinner and Ammann, 2005). Paleocological records provide a means of reconstructing the impact of past climatic variations on tree-line 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 tree-line regions are particularly important, as many of the more traditional, terrestrial-based paleoecological techniques, such as palynology, may reach their methodological limits at sites above the tree line (e.g. Gajewski et al., 1995; Smol et al., 1995). These restrictions do not apply to diatoms or other aquatic organisms, which are extremely abundant and ecologically diverse. Their short lifespan and fast migration rates enable them to respond quickly to environmental changes. Their potential as paleoindicators mostly relies on their good preservation and abundance in lake sediments.

Many variables affect the abundance of diatoms 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, length of ice cover) or indirectly influences diatoms by controlling, for example, habitat availability and quality, catchment and aquatic vegetation, water color and transparency, or nutrient supply (e.g. Moser et al., 1996).

Diatom-temperature transfer functions were applied on the fossil record preserved in the sediments of Lake Tsuolbmajävi (northern Finland, 68° 41' N, 22° 05' E), a shallow, well-mixed water body with a mean July surface-water temperature of c. 14° C (Korhola et al., 2000). The diatom-inferred mean July water temperatures revealed a detailed paleoclimate record with variations within the range of 2 °C during the lake's history (Figure 12.1), including the mid-Holocene "thermal maximum" (c. 8–5 ka BP), the Medieval Warm Period, as well as the Little Ice Age (LIA) cooling event. Diatoms also suggest a water temperature increase of c. 1.5 °C since the termination of the LIA, which corresponds to estimates of post-LIA air-temperature increases (Overpeck et al., 1997) for arctic regions in general. Because of the very close positive correlation between summer air and water temperature in Finnish Lapland it was not surprising that the obtained water-temperature curve closely tracked the air-temperature reconstruction for the same lake sediment record (Figure 12.1; see Korhola and Weckström, 2004).

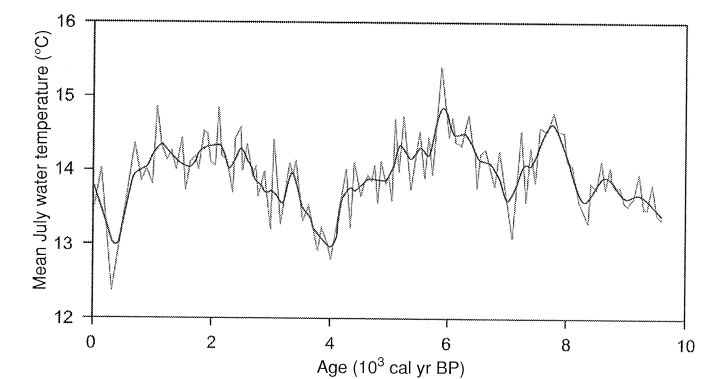


Figure 12.1 Holocene mean July water temperature reconstructions based on a fossil diatom record from Lake Tsuolbmajävi, Finnish Lapland. The bold line represents a LOESS smoother (span 0.05). (Modified after Korhola and Weckström, 2004.)

A striking and common feature of the Holocene sedimentary records of subarctic and alpine lakes is the dominance of pioneering benthic *Fragilaria* species (now grouped within the genera *Pseudostaurosira*, *Staurosira*, and *Staurosirella*) in initial diatom communities, sometimes making up more than 80% of the diatom flora (Pienitz et al., 1991; Lotter et al., 1997; Seppä and Weckström, 1999; Bigler et al., 2002; Solovieva and Jones, 2002; Rosén et al., 2004). *Fragilaria* spp. are commonly associated with high environmental instability and are known to tolerate broad environmental gradients (from brackish to freshwater) and poor light conditions (Haworth, 1976; Smol, 1988; Denys, 1990). The ability of small *Fragilaria* species to quickly reproduce and adapt to short-term environmental fluctuations makes them very competitive, which is of vital benefit especially in unstable limnological conditions such as the ones prevailing during the early Holocene.

Diatom studies in alpine, boreal, and subarctic lakes have shown relationships between the composition of diatom assemblages and water chemistry (e.g. Tynni, 1976; Koivo and Ritchie, 1978; Niederhauser and Schanz, 1993; Lotter et al., 1998). These surveys also illustrate the need for more precise, quantitative diatom autecological data to refine or replace the traditional classification schemes first introduced by Kolbe (1927), Hustedt (1939, 1956), and Cholnoky (1968).

Over the past two decades, multivariate analyses of modern diatom assemblages preserved in surface lake sediments have been used to develop regional empirical models (transfer functions or surface-sediment calibration data sets; see Birks, this volume) based on the relationships between the present-day species composition and environmental conditions (e.g. Rühland and Smol, 2002; Bloom et al., 2003; Schmidt et al.,

2004b). Application of these models to fossil diatom assemblages in long sedimentary sequences (cores) allows quantitative reconstructions of past lake conditions over centuries to millennia, such as air and lake-water temperature (e.g. Pienitz et al., 1995; Wunsam et al., 1995; Lotter et al., 1997; Rosén et al., 2000; Bigler and Hall, 2003), length of ice-cover (Thompson et al., 2005b), mixing dates (Schmidt et al., 2004a), pH (Weckström et al., 1997; Rosén et al., 2000), total phosphorus (e.g. Wunsam and Schmidt, 1995; Lotter et al., 1998; Kauppila et al., 2002), dissolved organic matter (DOC) and total organic matter (TOC) content (e.g. Pienitz and Smol, 1993; Fallu and Pienitz, 1999; Rosén et al., 2000), and water color and optical regime (e.g. Pienitz and Vincent, 2000; Dixit et al., 2001; Fallu et al., 2002).

The impact of the steep climatic and vegetation gradients associated with the northern-tree-line ecotone on lake-water chemistry, in particular alkalinity, dissolved inorganic carbon (DIC), conductivity, and related parameters was also evidenced by changing diatom distributions in calibration studies. Substantial differences in lakes from the boreal forest biome to the arctic tundra were observed, with usually decreasing ionic concentrations from south to north (Pienitz et al., 1997a, 1997b; Rühland and Smol, 1998; Fallu and Pienitz, 1999; Gregory-Eaves et al., 2000; Fallu et al., 2002; Rühland et al., 2003). This aspect is of particular interest within the context of arctic warming, as accelerated permafrost melting results in major changes in hydrological processes and external inputs into lakes from rapidly eroding catchment soils.

In the following sections, we shall provide some examples of case studies that showcase the potential of applied diatom studies for addressing important questions in research on climate and global environmental-change impacts in subarctic and alpine regions.

12.3 The Subarctic

The pronounced impacts of past displacements (migration) of the northern tree line as a result of changes in Holocene climate have been documented for subarctic Canada (e.g. Pienitz et al., 1999; MacDonald et al., 2000) and Eurasia (e.g. Laing et al., 1999). For example, following deglaciation about 8 ka BP the advance and subsequent retreat of the northern tree line in the central Canadian Subarctic in response to shifts in the mean summer position of the Arctic frontal zone was accompanied by profound limnological and hydrological changes (MacDonald et al., 1993; Wolfe et al., 1996). Consequently, changes in the composition of fossil diatom assemblages

(in particular in the proportion of periphytic versus planktonic taxa), diatom concentrations, and diatom-inferred DOC concentrations showed three distinct and abrupt successional shifts in the history of Queen's Lake (Pienitz et al., 1999).

12.3.1 Effects of landscape and climate change on underwater light exposure

To address the potential impact of long-term climate change relative to that of stratospheric ozone depletion, Pienitz and Vincent (2000) combined paleolimnological analyses with bio-optical models based on present-day conditions in subarctic lakes of northern Canada. This new paleo-optical approach allowed estimating past underwater light conditions from DOC concentrations that were inferred from fossil diatom assemblages preserved in Holocene sedimentary deposits from a lake near the northern tree line in the central Northwest Territories (Canada). Saulnier-Talbot et al. (2003) used a similar diatom-based paleo-optical approach to estimate past depths of UV penetration in coastal Lake Kachishayoot (northwestern Québec, Canada; 55° 20' N, 77° 37.4' W; 102 m above sea level, a.s.l.) after its isolation from the marine waters. Studies of optical environments in coastal systems have revealed that shifts from marine to freshwater conditions are accompanied by increased DOC, changes in UV radiation attenuation, and declines in UV penetration (Conde et al., 2000). Consistent with these modern observations, Saulnier-Talbot et al.'s (2003) multiproxy investigation revealed abrupt increases in diatom-inferred DOC concentrations and water color that coincided with the retreat of post-glacial marine waters (induced by isostatic rebound) and the arrival of spruce trees in the landscape and the catchment of the study site (Figure 12.2). Their investigation also revealed large changes in the underwater irradiance environment over the course of the Holocene, from extremely high UV exposure following the initial formation of the lake and its isolation from the sea, to an order-of-magnitude lower exposure associated with the development of spruce forests in the catchment. Furthermore, the analysis of plant macrofossils revealed that UV penetration remained low even following forest retreat due to the development of alternative DOC sources in the catchment, such as moss-dominated wetlands (e.g. *Sphagnum*; Figure 12.2). Many freshwater ecosystems presently located in ecotonal regions of the Subarctic will likely experience similar important shifts in underwater spectral irradiance through the effects of climate change on catchment vegetation and organic matter loading. Moreover, the results of Saulnier-Talbot et al. (2003) show that major shifts in the physical and chemical lake conditions are likely to

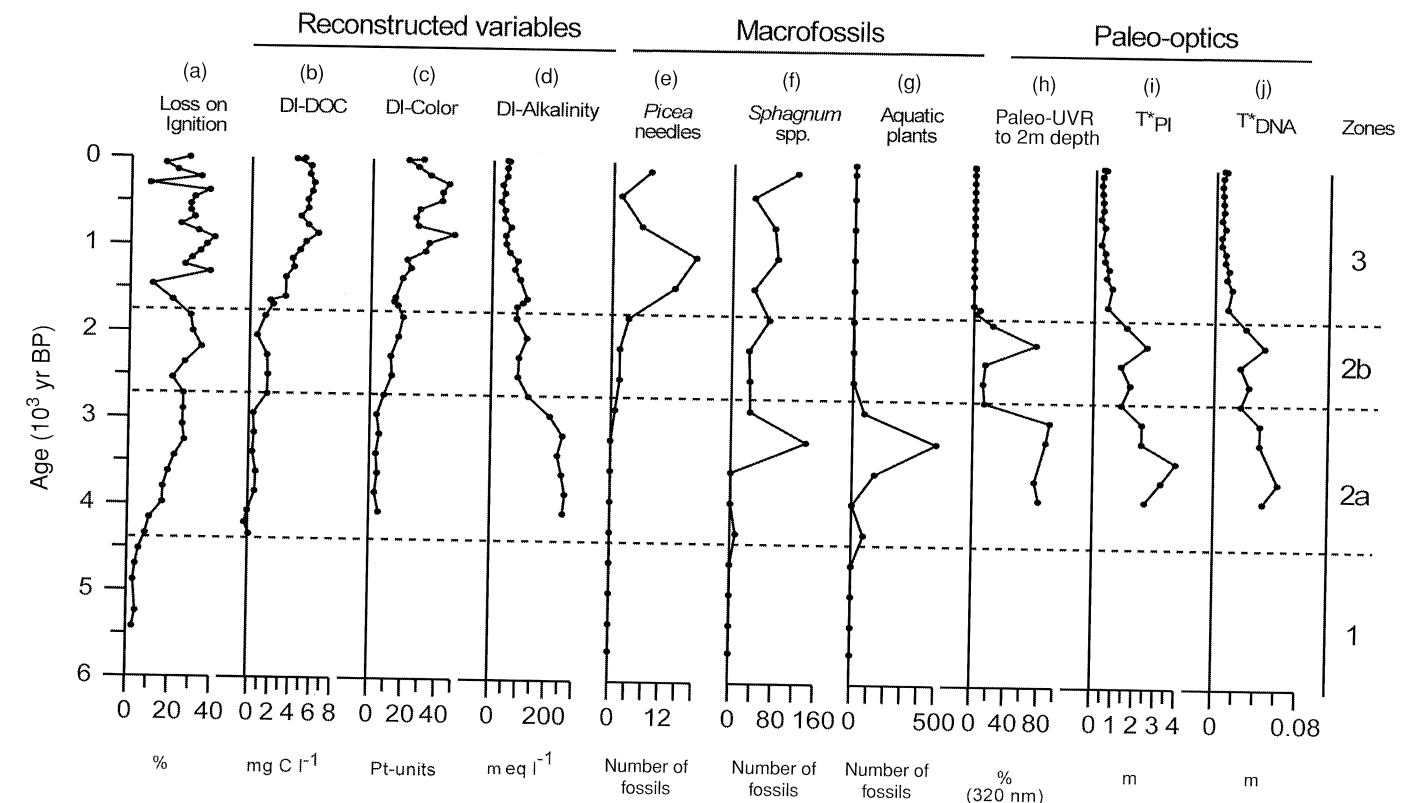


Figure 12.2 Changes in the catchment vegetation and limnological properties of Lake Kachishayoot (subarctic Québec, Canada) over the 5000 years following deglaciation. Concomitant with the gradual development of organic soils (a) and the invasion and establishment of spruce (*Picea*) (e) there was a rise in diatom-inferred DOC (b) and lake-water color (c), and a sharp decrease in underwater UV radiation (depth of paleo-UVR) (h) and biological transparency weighted for UV-photoinhibition, T^*_{PI} (i), or for UV-photo-damage of DNA, T^*_{DNA} (j). (Modified after Saulnier-Talbot et al., 2003.)

be accompanied by profound changes in the composition of aquatic food webs, which may alter the overall structure and dynamics of these sensitive ecosystems.

12.3.2 Effects of landscape and climate change on underwater light exposure

Numerous studies of diatom records from subarctic lakes concurrently report increases in the relative abundances of small planktonic *Cyclotella* species during the past century that are accompanied by decreases of more heavily silicified, tycho-planktonic diatoms of the genus *Aulacoseira* and/or small, benthic *Fragilaria* (e.g. Sorvari and Korhola, 1998; Sorvari et al., 2002; Rühland et al., 2003; Rühland and Smol, 2005). The observed shifts in diatom community structure were speculated to be associated with the effects of intense warming in subarctic regions and were considered a "bellwether" of what

could eventually occur at more southern latitudes with continuing warming. In their comparative analysis of more than 200 paleolimnological records from arctic, alpine, and temperate ecozones throughout the northern hemisphere, Rühland et al. (2008) provided compelling evidence that ecologically important changes are already underway in temperate lakes, similar to those observed in the rapidly warming Arctic. Specifically, they examined the impact of various climate-related changes in the physical properties (e.g. length of open-water season, duration and strength of thermal stratification, timing and strength of spring thaw and resulting flooding, light availability, nutrient cycling) on the structure and dynamics of *Cyclotella*–*Aulacoseira*–*Fragilaria* diatom assemblages. Their synthesis showed remarkably similar taxon-specific shifts since the middle of the nineteenth century in non-acidified, nutrient-poor freshwater ecosystems from throughout the northern hemisphere. Aquatic ecosystem changes occurred earlier in the highly sensitive circumpolar Arctic (by about 100 years) and in the alpine lakes (by about 50 years) than in lakes in the temperate regions. Their findings suggest that many of these lakes are currently crossing or have already crossed important climate-induced ecological thresholds. For example, several circumpolar tree-line lakes including Slipper Lake (64° 35' 65" N, 110° 50' 07" W, 460 m a.s.l.), TK20 (64° 09' 00" N, 107° 49' 00" W), TK54 (64° 38' 68" N, 112° 41' 47" W) in the

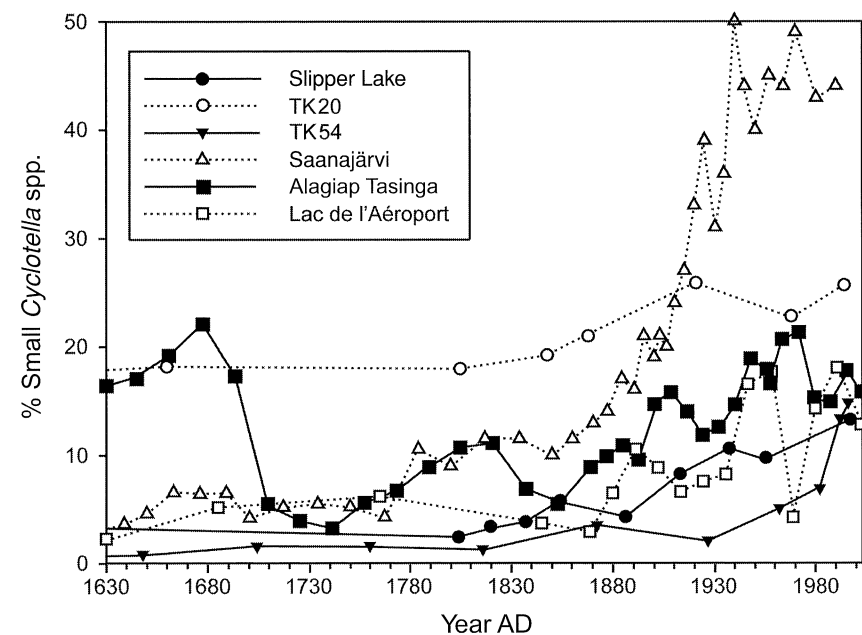


Figure 12.3 Comparison between the timing of the onset of increases in the relative abundance of small *Cyclotella* taxa (*C. stelligera*, *C. pseudostelligera*, *C. glomerata*, *C. comensis*, and *C. gordonensis*) in sedimentary records from subarctic lakes in central Canada (Slipper Lake and lakes TK20 and TK54), Finland (Lake Saanajärvi) and northern Québec (lakes Aeroport and Alagiap Tasinga). (Modified after Rühland et al., 2008.)

Canadian central subarctic region, Lake Saanajärvi (69° 05' N, 20° 52' E) in Finnish Lapland, and Lake Birgervatnet (79° 50' N, 11° 58' E) in Svalbard, recorded a marked increase in the relative abundances of planktonic *Cyclotella* taxa (including *C. stelligera* (Cleve & Grunow in Cleve) Van Heurck, *C. pseudostelligera* Hustedt, *C. glomerata* Bachmann, *C. comensis* Grunow in Van Heurck, and *C. gordonensis* Kling & Hakansson) and concomitant decreases in diatoms belonging to the genera *Aulacoseira* and *Fragilaria* (Rühland et al. 2008). More recently, diatom profiles from Lake Aeroport and Lake Alagiap Tasinga in northern Québec, Nunavik, Canada (Saulnier-Talbot and Pienitz, unpublished data) are also showing interesting trends in small planktonic *Cyclotella* taxa. These taxon-specific shifts have yielded strikingly coherent, yet geographically asynchronous, large-scale trends of ecological change (see Figure 12.3). Such shifts are explained by competitive advantages created for less-heavily silicified (lighter) planktonic cells in a thermally stratified and hence stable water column with less mixing. The common understanding from empirical studies is that these conditions, in addition to a shortened duration of ice cover and thus a longer growing season, provide favorable habitats especially for small, fast-growing planktonic *Cyclotella* spp. (Raubitschek

et al., 1999; Rautio et al., 2000; Pannard et al., 2008). In contrast, thickly silicified (heavy) planktonic *Aulacoseira* species that require turbulence-induced resuspension into the photic zone of the water column (Kilham et al., 1996) are at a disadvantage during such periods of strong stratification (Pannard et al., 2008), while small benthic *Fragilaria* species also seem to be less competitive under these conditions (Lotter and Bigler, 2000).

12.4 Mountain regions: steep gradients

Studies in different mountain ranges have demonstrated a zonation of diatom assemblages along the altitudinal gradient, which also incorporates a strong gradient of water temperature (Servant-Vildary, 1982; Vyverman, 1992; Vyverman and Sabbe, 1995; Bloom et al., 2003). Direct influences of temperature on the physiology of algal growth have been presented, e.g. by Raven and Geider (1988) and Montagnes and Franklin (2001), whereas indirect effects due to prolonged ice cover and changes in turbulent mixing have been discussed by Smol (1988), Smol et al. (1991), Anderson (2000), Laing and Smol (2000), Lotter and Bigler (2000), Battarbee et al. (2002a), Catalan et al. (2002a, 2002b), Koinig et al. (2002), Lotter et al. (2002), Schmidt et al. (2004b), Karst-Riddoch et al. (2005), and Smol and Douglas (2007).

12.4.1 Himalaya

The Himalayas are characterized by steep and high (with the earth summit, Mt. Everest 8848 m a.s.l., Nepal), mainly north-west to southeast striking, mountain ranges that surround plateaus of deserts and grasslands at altitudes above 4000

meters. Major reasons for differences in vegetation between subtropical forests and deserts are the relief and the gradual influence of the Asian monsoon. The Tibetan Plateau, for example, shows a strong gradient in precipitation. Due to the decreasing influence of the Indian summer monsoon the annual precipitation ranges from c. 800 mm in the south of Tibet (28° N) to less than 50 mm, with enhanced evaporation, in the north of the Qinghai province of China (40° N). Weighted averaging (WA) and WA partial least squares (WA-PLS) regression and calibration models from diatoms of 40 freshwater to hypersaline lakes (salinity: 0.1 to 91.7 g l⁻¹) on the Tibetan Plateau show a high predictive power for conductivity (cross validated $r^2 = 0.92$, RMSEP = 0.22) and water depth (cross validated $r^2 = 0.89$, RMSEP = 0.26; Yang et al., 2003). Conductivity and chloride explained most of the variance in the diatom assemblages. Diatoms that are characteristic for the saline lakes (>1.9‰) included those typical for *Na-SO₄-Cl* lakes plus *Campylodiscus clypeus* Ehrenberg and *Surirella peisonis* Pantocsek, whereas diatom assemblages characteristic for the freshwater to slightly oligosaline lakes (<1.5‰) resembled those typical for *Ca-Mg-CO₃* lakes plus *Cyclotella ocellata* Pantocsek and *Navicula radiosa* Kützing. Most of the freshwater diatoms of this data set, at least at the species levels, are commonly distributed or known from alpine and subarctic habitats of the Holarctic region, and endemic species appear to be rare (Li et al., 2006, 2003). This is corroborated by several floristic and taxonomical studies from the Himalaya region (e.g. Mereschkowsky, 1906; Hustedt, 1922; Ioriya, 1995; Li et al., 2003, 2004, 2007). However, the recent findings of several new diatoms require further taxonomic work (e.g. Jüttner et al., 2000, 2004).

Numerous streams, differing in size, velocity, and habitats are to be found on the steep slopes of the southern mountain ranges. Their diatom assemblages along a gradient of more remote to increasingly human-impacted areas at lower altitudes are comparable with streams in other Holarctic mountain ranges (Jüttner et al., 1996, 2003; Rothfritz et al., 1997; Cantonati et al., 2001).

Long sediment sequences from lakes that used qualitative diatom analyses to trace changes in salinity and lake levels (e.g. Gasse et al., 1991, van Campo and Gasse, 1993; Fan and Gasse, 1994; Gasse, 1996; Fan et al., 1996; Li et al., 1999) suggest distinct changes in the intensity of the monsoonal climate since the end of the last ice age. In a diatom study of a peat profile in the Indian Himalayas, Rühland et al. (2006) were able to track changes in monsoon intensity and rapid melting of Himalayan glaciers at higher elevations. Recently developed diatom-based

quantitative inference models (Yang et al., 2003, 2004) provided a powerful tool to track changes in the monsoon climate for a region where the Asian monsoon provides summertime life, sustaining rains for hundreds of millions of people.

12.4.2 Alps

A combined data set of diatoms from surface-sediment samples of 106 Swiss lakes (Figure 12.4) spanning an altitudinal gradient from 334 to 2815 m a.s.l. and a July air-temperature gradient of 5 to 21.4 °C demonstrates the importance of climate to diatoms and other aquatic organisms (chironomids, cladocera, chrysophytes), and has been used to develop multi-proxy temperature and nutrient inference models (Lotter et al., 1997, 1998; Bigler et al., 2006; Hausmann and Kienast, 2006). Using several independent lines of evidence the power of reconstructing past climate change may be amplified (Lotter, 2003; Birks and Birks, 2006). Heegaard et al. (2006) analyzed the cumulative rate of compositional change along the altitudinal gradient in this data set and identified a region of major compositional change (an "aquatic ecotone") in diatom assemblages just below the alpine tree line (today between 1900 and 2000 m a.s.l.) at 1600 to 1700 m a.s.l. and a second one above the tree line at 2000 to 2100 m a.s.l.

As air temperatures most closely correspond to surface water temperatures during summer (Livingstone and Lotter, 1998; Livingstone et al., 1999), instrumental air-temperature time series have been used as a basis for the July temperature inference models. However, above a critical altitude, a decoupling between summer air and water temperatures can be observed (Livingstone et al., 2005). Canonical correspondence analysis (CCA) of the original calibration data set of Lotter et al. (1997) 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 in the diatom data. A WA-PLS model for diatoms and July air temperature provided a cross-validated r^2 of 0.80 and a RMSEP of 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 a unimodal or a sigmoidal response.

Below elevations of 1000 m a.s.l. planktonic diatoms are generally dominant, whereas above 1000–1500 m a.s.l. small periphytic (in some cases probably also tychoplanktonic) taxa

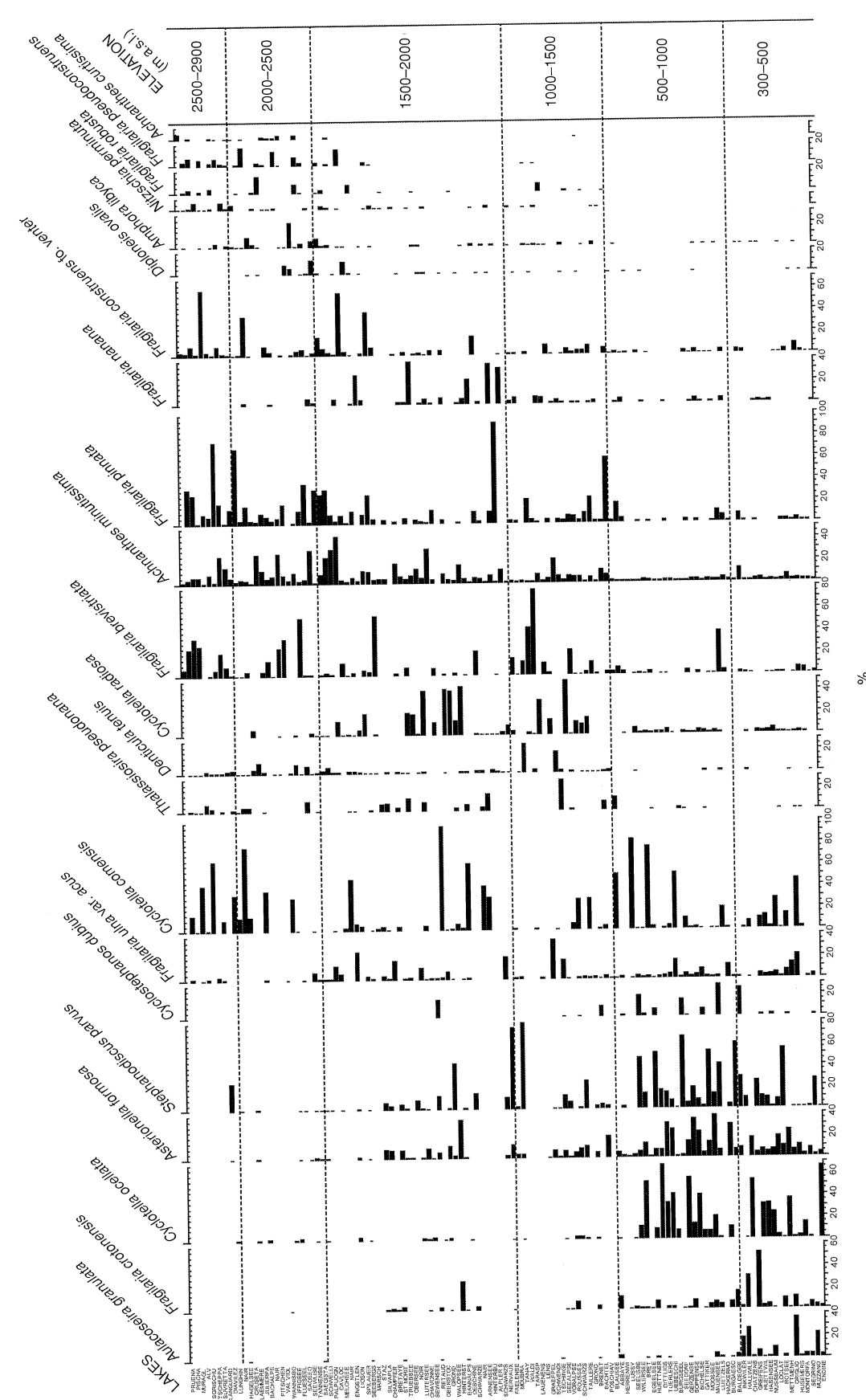


Figure 12.4 Distribution of diatoms in surficial sediments of 106 lakes along an altitudinal gradient in the Swiss Alps (only the most prominent diatoms are shown. Data combined from Lotter et al. (1997), Bigler et al. (2006), and Hausmann and Kienast (2006).

such as *Fragilaria* spp. and *Achnanthes minutissima* become more important (Figure 12.4). There are, however, exceptions, mainly involving small centric taxa (e.g. *Cyclotella comensis*, *Thalassiosira pseudonana*). Low numbers of planktonic diatoms and increasing abundances of *Fragilaria* spp. is a 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 (Lotter and Bigler, 2000). Also, water transparency is generally high, 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 of 0.62, with a cross-validated RMSEP of 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 summer-temperature gradient. The high morphological variability, especially within the small *Cyclotella* taxa, calls for molecular genetic studies, which may clarify the taxonomy of the various morphotypes that have been found to date along nutrient and temperature gradients (Wunsam et al., 1995; Hausmann and Lotter, 2001).

High seasonality, mainly caused by large temperature differences between summer and winter, is a major feature of freshwater ecosystems from the temperate zone (e.g. Wetzel, 2001), with strong impacts on alpine lakes (e.g. Ventura et al., 2000; Catalan et al., 2002a). The date of autumn mixing (in Julian days; defined as the day in autumn when the average daily temperature has declined to 4 °C) explained a statistically significant amount of variance in diatom composition from the surface sediments of 45 lakes in the Austrian Central Alps (Niedere Tauern), covering an altitudinal gradient from approximately 1500 to 2300 m a.s.l. A WA-PLS model for the date of autumn mixing yielded a cross-validated r^2 of 0.71 and a RMSEP of 0.006 \log_{10} Julian days (Schmidt et al., 2004a). The resulting diatom-inferred mixing dates, together with a chrysophyte cyst-based spring mixing model (Kamenik and Schmidt, 2005), enabled an estimation of Holocene ice-cover duration and mean seasonal air-temperature anomalies (Schmidt et al., 2007). Of all the diatoms recorded in this training set, the small diatom *Stauroneis (Fragilaria) microstriata* (Marciniak) Lange-Bertalot showed the lowest July water-temperature optimum (6.7 °C) and the

highest ice-cover-duration tolerance. However, small valve size can also be the result of lake warming. For example, in the Niedere Tauern training set the minimum valve length of *Fragilaria exiguiformis* Lange-Bertalot corresponded with the mean July water-temperature optimum (9.4 °C) of this taxon as estimated from the transfer function. Elevated temperatures may have stimulated enhanced cell division (e.g. Montagnes and Franklin, 2001), or cells did not reproduce sexually (Schmidt et al., 2004b).

Diatom-based calibration sets for nutrients (see also Hall and Smol, this volume), in particular for total phosphorus (TP), are also available from the Alps (Wunsam and Schmidt, 1995; Wunsam et al., 1995; Lotter et al., 1998; Hausmann and Kienast, 2006). Yet, the majority of the calibration sites are located below the tree line, in areas that are generally characterized by intensive agriculture and/or pasturing. With some exceptions (e.g. Hausmann et al., 2002), application of these TP inference models to tree-line lakes may, however, be limited by the generally low nutrient concentrations (Marchetto et al., 1995; Müller et al., 1998; Schmidt et al., 2004b) and the different diatom floras of the tree-line lakes.

12.4.3 Changing environments: the last glacial termination
Most of the inference models that have recently been developed using arctic/alpine diatom assemblages have yet to be applied to Holocene records. 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 were used to decipher the environmental history of a long sediment core from the Längsee (548 m a.s.l.), a small, meromictic kettle-hole lake situated in the southeastern Alps (Carinthia, Austria, see Schmidt et al., 1998). Due to its location at the southern slope of the Alps, close to the Würmian pleniglacial ice margin, the lake's catchment became deglaciated as early as 19 ka ago. Diatom-based transfer functions (Wunsam and Schmidt, 1995; Wunsam et al., 1995) have been applied down-core to infer TP concentrations and summer lake surface temperatures. Recently, a mean summer epilimnetic water temperature (SEWT) inference model (cross-validated $r^2 = 0.89$, RMSEP = 1.82 °C, see Huber et al., 2010) using a locally weighted WA regression and calibration technique (Juggins, 2007) was also applied to the Längsee sediment core. The model includes water-temperature measurements from three different data sets, totalling 116 lakes from the Alps and surrounding areas (Huber et al., 2010). Although water temperature was not independent from pH, TP, and conductivity, SEWT

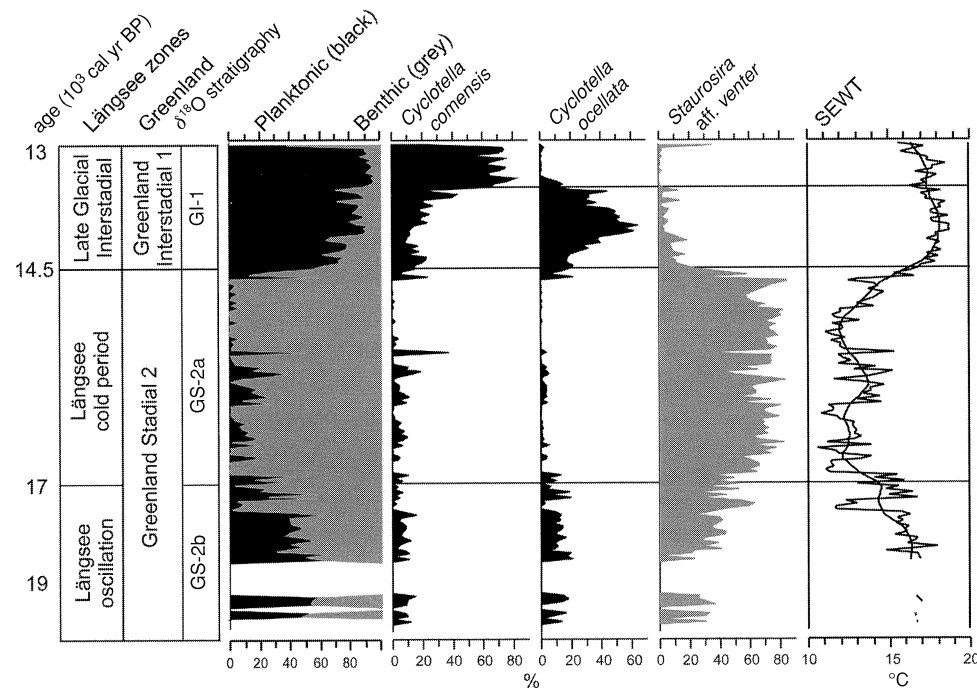


Figure 12.5 Diatom stratigraphy from a sediment core from Längsee (Austria) spanning the time between ca. 19 to 13 ka BP (modified after Huber et al., 2010). The ratio between planktonic and benthic diatoms (including Fragilariaceae), the relative abundance of selected diatoms, and the diatom-inferred mean summer epilimnetic water temperatures (SEWT) are shown. Three major phases of climate change are indicated during the Last Glacial termination and correlated with the stable oxygen isotope ($\delta^{18}\text{O}$) Greenland ice-core event stratigraphy (Walker et al., 1999).

captured most of the variance in the diatom data. A warm period between c. 19 and 17 ka BP (Längsee oscillation) favored the development of planktonic diatoms (*Cyclotella ocellata* Pantocsek, *Cyclotella comensis*, *Cyclotella distinguenda* var. *unipunctata* (Hustedt) Håkansson & Carter, *Cyclotella quadrijuncta* (Schröter) von Keissler, *Stephanodiscus alpinus* Hustedt). For this phase a SEWT range of 11.6 to 18 °C (mean 15.8 °C) was inferred. Consistent with the subsequent climatic cooling between c. 17 and 14.5 ka BP, SEWT dropped. This cool period represented in the Längsee sediment core likely corresponds to the northern hemispheric cooling, evidence of which is recorded by oxygen isotopes from Greenland ice cores (Greenland Stadial GS-2a), North Atlantic ice-rafting events (Heinrich 1), and a glacier re-advance in the Alps (Gschnitz). Lower temperatures leading to prolonged ice cover may explain the low percentage of planktonic diatoms. The contemporaneous increase in Fragilariaceae (mainly *Staurosira* aff. *venter*, which was more frequent in lakes with low SEWT in the modern training set),

explains the decrease in inferred SEWT (mean inferred temperature = 12.9 °C). Parallel with the reforestation at about 14.5 ka BP, diatom-inferred SEWT increased. For the following Late Glacial Interstadial (= Greenland Interstadial GI-1) a mean SEWT of 17.5 °C was inferred (Figure 12.5), which is c. 4 °C colder than today. Concurrent with this temperature increase Längsee became meromictic. Strong meromixis during warm and dry climate conditions likely resulted in a nutrient gradient between the phosphorus-enriched monimolimnion and the oligo- to mesotrophic conditions in the epilimnion. This phase is characterized by the dominance of *C. comensis*, a diatom with oligo- to mesotrophic affinities. However, at times of increased nutrient concentrations, either from internal loading through enhanced mixing or from external loading, coupled with increased minerogenic matter flux from catchment erosion, *C. ocellata* appeared to have been more competitive against other planktonic diatoms (Schmidt et al., 2002).

12.4.4 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 biogenic acidification, because only a small fraction of the drainage area is covered by soil. High mountain lakes are therefore very sensitive to climatic and hydrological changes as well as to

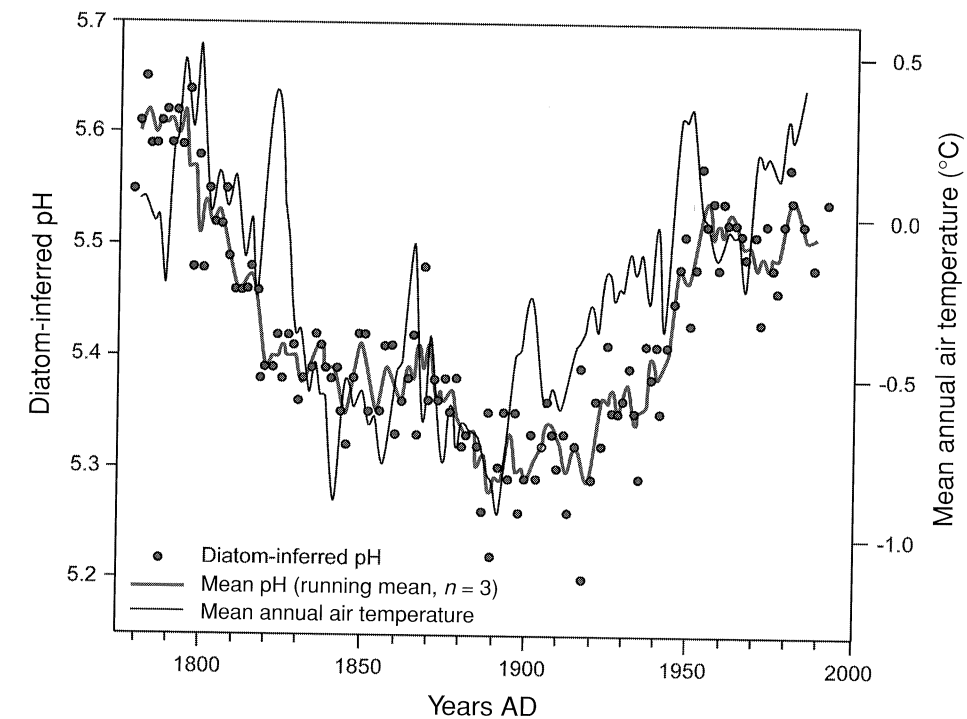


Figure 12.6 Diatom-inferred pH history of Schwarzsee ob Sölden (2796 m a.s.l., Austria) during the past two centuries, compared to the Austrian mean annual air temperatures (after Koinig et al., 1997). The chronology is based on ^{210}Pb (constant rate of supply (CRS) model) and ^{137}Cs dating (see Koinig et al., 1997; Sommaruga-Wögrath et al., 1997).

increasing acidity of precipitation (see Battarbee et al., this volume).

Paleolimnological investigations in Schwarzsee ob Sölden (2796 m a.s.l., Tyrol, Austria) showed a diatom-inferred decline from pH 6 to 5 (Arzet et al., 1986). Using a WA model based on a regional alpine calibration set (Marchetto and Schmidt, 1993), the diatom-inferred pH changes in a core from Schwarzsee dating back to the eighteenth century were predominantly due to changes in the relative abundances of the dominant *Aulacoseira* species (*Aulacoseira alpigena* (Grunow) Krammer, *Aulacoseira nygaardii* Camburn & Kingston, *Aulacoseira distans*, including var. *nivalis* (W. Smith) Haworth, *Aulacoseira perglabra* (Østrup) Haworth; see Koinig et al., 1997). The lowest inferred pH values of 5.2–5.3 occurred between AD 1880 and 1920. Towards 1970, the inferred pH values increased again to 5.5. A comparison of these pH reconstructions with the mean Austrian air temperature showed a strong correlation throughout the past ~200 years (Figure 12.6). These findings support the idea of a climate-driven pH control in high-alpine lakes (Psenner and Schmidt, 1992), implying that climatic cooling may cause decreases in pH, and rising temperatures increases in pH. The pH decline

started at the onset of the LIA, with glacier re-advances in the Alps culminating around AD 1850. Koinig et al. (1997, 1998) and Sommaruga-Wögrath et al. (1997) suggested that pH increases during warm episodes may be a result of enhanced weathering rates, increased in-lake alkalinity production, longer water retention times, and higher amounts of dust deposition (see also Marchetto et al., 1995). However, the hypothesis that recent climatic warming counteracts the influence of modern acidification is not valid for all lakes. Based on diatom assemblage changes at Lake Rassas (2682 m a.s.l., southern Tyrol, Italy), for instance, the onset of anthropogenically derived acid precipitation at the beginning of the twentieth century (Schmidt and Psenner, 1992; Psenner and Schmidt, 1992) led to a decoupling of the temperature-pH relationship, and thus to lake acidification.

12.5 Common features to subarctic and mountain lake diatom assemblages

Many of the above-mentioned calibration sets have revealed interesting similarities in diatom assemblage composition across the tree line, 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 the tree line. 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. 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 (e.g. Smol, 1988; Fee et al., 1992).

Differences observed between diatom cell size in lakes below and above the tree line 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 and Geider, 1988), and the high surface-to-volume ratio of small cells provides them with a competitive advantage under low-nutrient conditions. 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) out-compete larger diatom species with slower growth rates during the brief growing season in mountain and tundra lakes.

12.6 Summary

Diatoms in subarctic and mountain regions are important and sensitive indicators of environmental change. The subarctic–arctic and subalpine–alpine tree line is an important ecotone, with its past, present, and future position largely depending on climatic factors. Climatic fluctuations at this ecotone are either directly or indirectly influencing diatom communities through alterations in physical and chemical limnetic properties. Therefore, diatoms have great potential as environmental indicators and contribute to and complement ecological as well as paleoecological studies in tree-line regions (e.g. Lotter and Psenner, 2004). Reconstructing changes in past tree-line position provides essential boundary conditions for global circulation models to hindcast past or predict future climate change.

The potential for inferring past DOC/TOC levels from fossil diatom records combined with recent advances in bio-optical modeling in northern lakes led to the development of lake paleo-optics, which offers opportunities for integrating studies of the present day with historical properties of lakes (Pienitz and Vincent, 2000). This approach is of special interest for lakes in tree-line regions, since lakes situated above the tree line are more sensitive to small changes in DOC and rising UV radiation associated with stratospheric ozone depletion than lakes of the boreal forest (Vincent and Pienitz, 1996; Laurion et al., 1997).

In all studies involving diatom calibration data sets, pH or pH-related variables (e.g. alkalinity, 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 lake water DOC/TOC (which is related to catchment vegetation and tree line), and 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 icecover (e.g. Ohlendorf et al., 2000; Thompson et al., 2005b). The conversion of diatom-inferred mixing dates into altitude-dependent air-temperature anomalies offers opportunities to reconstruct autumn climates (Schmidt et al., 2007). The distinct influence exerted by the temperature gradient on diatom distribution as shown in the studies from subarctic regions and different mountain ranges is of ecological and paleoecological significance, as it strengthens the assumption that the relationship between organisms and climate is clearest at ecotonal boundaries; consequently, ecotones are optimal areas for studying climatic change (e.g. Smol et al., 1991; Heegaard et al., 2006). A growing number of fossil diatom records from paleolimnological studies reveal spatially coherent trends of climate-driven, taxon-specific changes across subarctic regions of the northern hemisphere, implying that freshwater ecosystems have crossed critical ecological thresholds in recent times.

The results obtained from diatom studies in tree-line regions confirm a general relationship between the zonal 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 and Metzeltin, 1996), a surprisingly high degree of floristic similarity can be observed among calibration data sets from different tree-line regions. Efforts are underway to develop supra-regional data sets for these regions within the Circumpolar Diatom Database (CDD; <http://www.cen.ulaval.ca/paleo/index.html>), which 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 regions. Nevertheless, all transfer-function approaches have to be assessed critically (see Birks, this volume) before using their results for hindcasting past environmental change at the arctic or alpine ecotone.

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