5. ALGAL INDICATORS OF ENVIRONMENTAL CHANGE IN ARCTIC AND ANTARCTIC LAKES AND PONDS

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Introduction

High latitude regions have been repeatedly identified as important reference areas for the study of long-term ecosystem change, as arctic and antarctic ecosystems are expected to show the first signs of environmental shifts (such as climatic warming). In addition, due to positive feedback mechanisms, circumpolar ecosystems are affected more strongly by environmental changes (both natural and anthropogenic) than temperate and tropical regions. Long-term monitoring data, however, are noticeably lacking for almost all high latitude regions, and so indirect proxy methods must be used to reconstruct past environmental trajectories. As shown by the chapters in this volume, paleolimnological approaches (i.e., the study of lake and pond histories from the physical, chemical, and biological information preserved in sediment profiles) have played a leading role in providing these missing data sets. Using these long-term records, natural and anthropogenic forcing factors can be examined, natural variability can be assessed, and episodic events can be identified and studied (Smol 2002; Cohen 2003). Such data are required to help track the causes and consequences of environmental change, to better understand the natural modes of environmental change, and to make more effective decisions regarding environmental management issues.

A characteristic feature of high latitude regions is the thousands of ponds and lakes that, along with wetlands, dominate most circumpolar landscapes. The sediments that accumulate in these systems archive a diverse "library" of information that can be used by paleolimnologists to reconstruct past environments. Algal indicators play a leading role in many of these long-term assessments.

Although the word "algae" has no formal taxonomic meaning, the word is commonly used to describe a diverse group consisting of primarily aquatic, photosynthetic protists and prokaryotes (i.e, cyanoprokaryotes, which are now often referred to as cyanobacteria or blue-green algae) that contain chlorophyll-a (Chl-a) as their primary photosynthetic pigment and have simple reproductive structures. As a group, they exhibit tremendous diversity in life forms, morphological features, as well as reproductive and physiological strategies.

Other chapters in this volume provide details on the application of algal indicators (especially diatoms) to paleolimnological reconstructions in different high latitude regions (Chapters 9 to 15). The reader is also referred to seven recent reviews that are relevant to algal-based paleolimnological reconstructions in high latitude regions. Douglas and Smol (1999), Lotter et al. (1999) and Spaulding and McKnight (1999) recently reviewed the applications of diatoms to high arctic, subarctic, and antarctic paleolimnology, respectively. Smol and Douglas (1996) summarized the potential applicability of using changes in algal assemblages as part of arctic biomonitoring programs. Moser et al. (2000) discussed the ways that diatoms can be used to track paleohydrology in arctic regions, whereas Pienitz (2001) provided an overview of the use of diatoms in northern peatlands. In addition, Smol and Cumming (2000) reviewed the application of algae to paleoclimatic reconstructions in general, which included examples from high latitude regions. Many chapters in this book provide more recent examples of algal-based paleolimnology, and so only a brief overview is provided here of how algal indicators have been used to track long-term environmental change in arctic and antarctic regions. We begin with a summary of some of the key historical studies on the taxonomy, distribution, and ecology of algal assemblages from high

latitudes. We then discuss the current approaches that are typically employed, and provide a survey of some of the major types of questions that can be addressed using algal remains in paleolimnological studies.

Historical overview of algal research in the Arctic and Antarctic[1]

The first surveys

The first algae studies from polar regions were published in the mid-19th century with Joseph Dalton Hooker's (1847) records from marine antarctic waters and Christian Gottfried Ehrenberg's (1843, 1844, 1853) observations from Alaska, Spitsbergen (Svalbard), and the Antarctic Ocean. Even during this early period of discovery, both Hooker and Ehrenberg were pondering about micro-organism habitat selectivity and species biogeographic distributions. The observations of Hooker (1847) from his Antarctic Voyage of H.M. Discovery ships Erebus and Terror, and Sutherland (1852) during the search for the missing crew of these ships from Baffin Bay and Barrow Straits (1850-1851), make specific reference to the brown and green colours of the bottom ice and pore water. Hooker more specifically says "The Water and the Ice to the South Polar ocean were alike found to abound with microscopic vegetables", while Sutherland at the opposite pole described the algae as a "green slimy-looking substance" in the bottom ice representing "infusory animalcules" and "minute vegetable forms of exquisite beauty" (Horner 1985). Following these early observations, the studies of freshwater and marine microbes multiplied quickly from across the Arctic, with many publications documenting the diatom floras (e.g., Cleve 1867, 1873, 1883, 1896, 1898, 1900; Lagerstedt 1873; Cleve and Grunow 1880; Dickie 1880; Grunow 1884; Østrup 1895, 1897a,b), whereas more limited diatom work was done in the subantarctic and antarctic ecozones (e.g., Castracane 1886; Reinsch 1890).

   Cleve (1896) was the first to observe the similarity of diatom distributions across the Arctic and states "The great resemblance between diatoms found in the ice at Cape Wankarema, between Franz Josefs Land and Novaja Semlja, and at the east coast of Greenland and those observed in the Labrador-stream, tends to show that the ice-flakes are drifted from Behring strait to the north of Greenland, where one portion of them continues to drift along the east-coast of Greenland and another along the Labrador-stream". Fridtjof Nansen (1897, 1906) was probably the first arctic researcher to use a simple "multi-proxy" approach to scientifically examine the drift theory using diatoms (identified by Cleve), Ciliata and Flagellata "germs" (documented by Nansen). Through this research, which included documenting the similarity of marine and freshwater diatoms and microbes in meltwater pools from the Bering Strait and Greenland, Nansen proposed that drift ice could pass across the North Pole.

   Marine and freshwater floristic surveys at both poles continued during the early 20th century. In the Antarctic, the studies varied from diatoms (Holmboe 1902), general freshwater algae (e.g., Wille 1902, 1924; Gain 1911, 1912; West and West 1911; Carlson 1913), to marine taxa (Petit 1908; Van Heurck 1909; Peragallo 1921; Heiden and Kolbe 1928), whilst arctic surveys were also expanding into both freshwater and

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[1] Appendix 1 lists the location of historical algal collections from polar phycologists.

marine diatom floristic studies (e.g., Østrup 1901, 1910, 1920; Gran 1904; Petersen 1924; Palibin in Melnikow 1997). Through the research publications of Cleve, Østrup, Lagerstedt and Petersen, many new taxa were identified and preliminary diatom distributions across the Arctic were documented.

Arctic research (1920-1990)

Two Canadian expeditions, the *1913-1918 Canadian Arctic Expedition of the Western Arctic* and the *1938-1939 Canadian Arctic Expedition of the Eastern Arctic*, provided a more complete biogeographical understanding of brackish and freshwater algae from the Canadian Arctic Archipelago. Lowe (1923) studied the algae of small brackish ponds in both Alaska and the Northwest Territories. Lowe's diatom flora is brief and he does not provide illustrations or discuss ecology in any detail. A second Canadian Arctic Expedition was undertaken in 1938-1939, with a focus on the Eastern Arctic, including several high arctic sites. Diatom identifications were delayed by World War II, but completed when Ross (1947) published descriptions of 192 freshwater taxa. Wheldon (1947) documented other freshwater algae. Between 1950 and 1990, most of the algal studies were ecologically or ecosystem-based (for a review see Hamilton et al. 2001).

Friedrich Hustedt (1942), using diatoms collected from Swedish Lapland, was probably the first to make a concerted effort to link environmental variables to diatom ecology. Throughout his career, Hustedt established the foundations for the first simple transfer functions relating diatom autecology to pH and general water quality. Meanwhile, the prominent Danish phycologist, Niels Foged, appreciated the significance of Hustedt's work and proceeded, whenever possible, to link environmental conditions, especially pH and temperature, with geological regions and diatom community composition, especially in Greenland (1953, 1955, 1958, 1972, 1973, 1977), Iceland (1974), Spitsbergen (1964), and Alaska (1981). Foged (1972, 1977, 1989) was one of the first researchers to use diatoms from arctic postglacial deposits to reconstruct isostatic processes, marine-lacustrine transitions, and emerging lake patterns after the last glaciation.

A milestone for North American work was the monograph by Patrick and Freese (1961), which described freshwater diatoms from northern Alaska. Meanwhile, Croasdale (1973) described and illustrated 225 freshwater algal taxa (exclusive of diatoms) from northern Ellesmere Island in the Canadian High Arctic. The first detailed paleolimnological study of a high arctic lake was completed by Smol (1983), who used diatom and chrysophyte microfossils to infer paleoclimatic trends from a small lake on eastern-central Ellesmere Island.

Antarctic research (1920-1990)

As summarized by Spaulding and McKnight (1999), the earliest phycological work in the antarctic regions was from expeditions to more accessible sites, such as the subantarctic Kerguelen and South Georgia islands (Reinsch 1890; Carlson 1913). Before 1960, limnological research on continental Antarctica was almost non-existent

(< 10 publications). However, in the following two decades, over 100 taxonomic or floristic papers on algae were completed (Prescott 1979). Over 70 investigations on limnology and terrestrial ecology were also published, with a diversity of studies ranging from algal-soil interactions (primarily cyanobacteria), to salinity and nutrient dynamics in permanently frozen lakes. Diatom research during this time was not extensive, but researchers such as Fukushima (1962a,b, 1963, 1964, 1966, 1969, 1970), Fukushima et al. (1973, 1974, 1975) and Kobayashi (1962a,b, 1963a,b,c, 1965a,b) published regional floras and taxonomic treatises. These floristic studies were further complemented by the work of other researchers, including Bourrelly and Manguin (1954), Aleshinskaja and Bardin (1965), Opalinski (1972a,b, 1974), and Seaburg et al. (1979) from many other sectors across the antarctic region. One significant finding was the observation that the number of antarctic algal taxa decreased with latitude (Hirano 1965; Fukushima 1970). Similar in timing to research developments in the Arctic, Brady (1982) used diatoms from sediments to infer climatic conditions through the Late Cenozoic, and Burckle et al. (1988) examined diatoms in ice cores to interpret aspects of the glacial history of Antarctica.

High latitude studies (1991- present)

Over the last ca. 15 years, research using algae (and especially diatoms) from both polar regions has increased exponentially (reviewed in Douglas and Smol 1999; Lotter et al. 1999; Spaulding and McKnight 1999). As summarized by the chapters in this volume, the development of algal-based research from primarily descriptive floristic studies to their application in elucidating patterns of global environmental significance has been striking.

Algal indicators

Algae are often the dominant primary producers in lakes and ponds, and are found in virtually every water body where there is sufficient light for photosynthesis. Algae are important bioindicators of environmental conditions for a variety of reasons (Stevenson and Smol 2003). First, they are typically abundant and diverse, and reflect all the major habitats present in aquatic systems. Algae have rapid dispersal rates, short life cycles, and respond quickly to environmental changes. Importantly, many taxa have well-defined environmental optima and tolerances (Birks 1998) to important limnological variables, and so, as described later in this chapter, species assemblage data can be used to characterize environmental conditions. As many taxa leave reliable morphological and biogeochemical records in lake and pond sediments, they can be used by paleolimnologists to reconstruct past environments.

   Below, we first describe the major algal indicators that are used by paleolimnologists. We then summarize some of the definitions typically used in algal assessments of environmental change. Finally, we describe some of the main types of applications that have been undertaken using algal-based paleolimnological techniques.
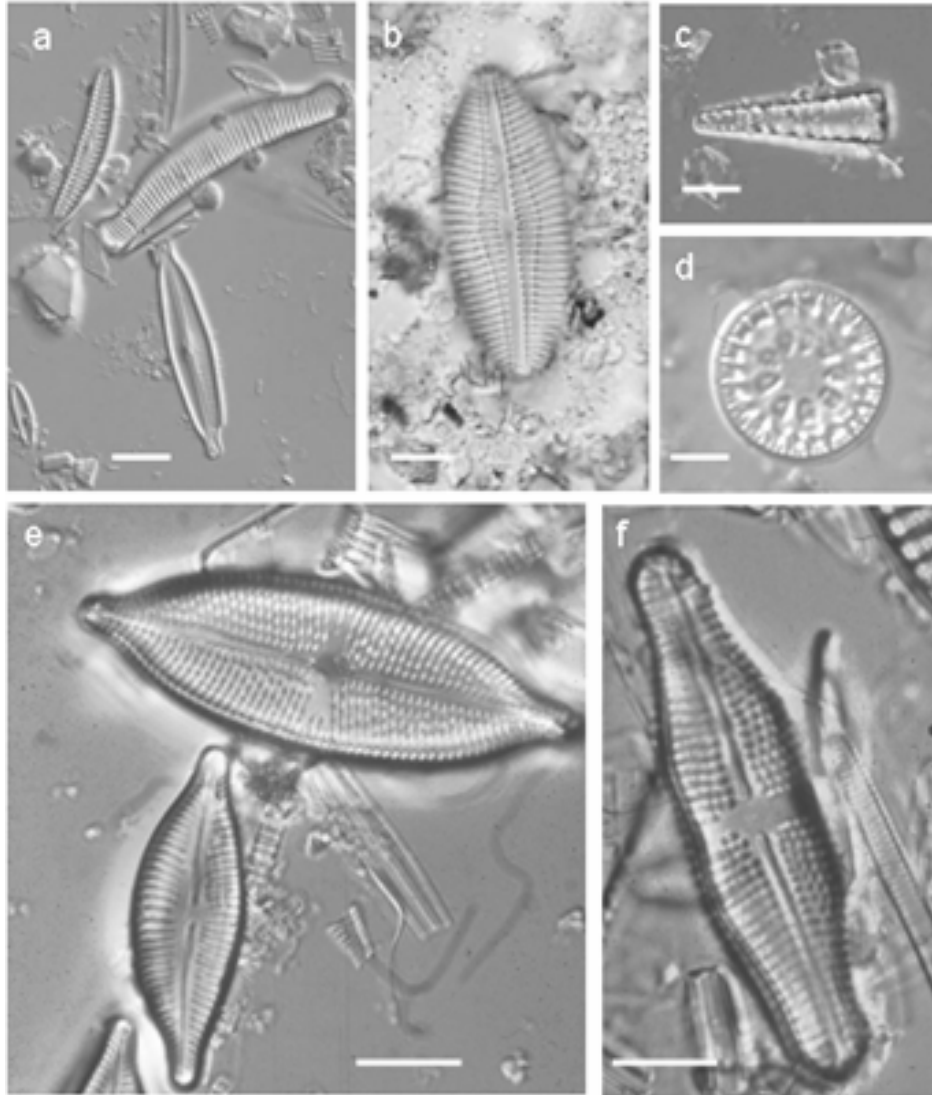
Figure 1. Light micrographs (DIC: differential interference contrast) of diatoms from Ellesmere Island, Canadian High Arctic. (a) Left to right: *Cymbella botellus* (Lagerstedt) A. Schmidt, *Eunotia praerupta* Ehrenberg, *Encyonopsis* sp.; (b) *Diploneis* sp.; (c) Complete clavate frustule in girdle view of *Meridion circulare* (Greville) Agardh.; (d) *Cyclotella antiqua* W. Smith.; (e) top to bottom: *Aneumastus tusculus* Ehrenberg Mann and Stickle (synonym *Navicula tuscula* Ehrenberg) and *Cymbopleura designata* Krammer (synonym *Cymbella designata* Krammer). (f) Raphe valve of *Achnanthes coarctata* (Brébisson) Grunow. Scale bar represents 10 μm.

Diatoms (class Bacillariophyceae)

The most commonly used biological indicators of past limnological conditions are diatoms, considered by many to be the most successful group of algae. Round et al. (1990) describe many aspects of the biology and taxonomy of diatoms, whereas Stoermer and Smol (1999) have provided a series of review chapters describing the many ways that diatoms can be used in environmental assessments.

Diatoms have many characteristics that make them ideal biomonitors of environmental change in high latitude systems where they are especially common in benthic, shallow water habitats. Diatoms are an extremely diverse group of algae, with global estimates ranging from 10,000 to 100,000 or more taxa (Mann and Droop 1996). Many species have well defined optima to important environmental variables, such as lake water pH, nutrients, salinity, and climate-related variables, and are therefore reliable indicators of environmental conditions (Stoermer and Smol 1999). The taxonomy of diatoms is based primarily on the size, shape, and ornamentation of their siliceous cell walls (called frustules), each composed of two valves (Figure 1). As these siliceous valves are typically well preserved in lake and pond sediments, they can be used by paleolimnologists to track environmental changes.

Because of their small size (many less than 30 μm in diameter or length), high-resolution light microscopy, as well as transmission and scanning electron microscopy, are typically required for critical taxonomic assessments (Round et al. 1990). Diatom valves can easily be separated from the sediment matrix using standard digestion techniques, which are well established and documented (Battarbee et al. 2001). Under most circumstances, no special preparation techniques are required for arctic and antarctic assemblages.

Chrysophytes (classes Chrysophyceae and Synurophyceae)

Although used less commonly than diatoms, chrysophyte algae hold considerable potential in paleolimnological studies. Sandgren et al. (1995) provided a series of review chapters dealing with many aspects of chrysophyte biology, including chapters detailing ecological (Siver 1995) and paleolimnological (Smol 1995) applications.
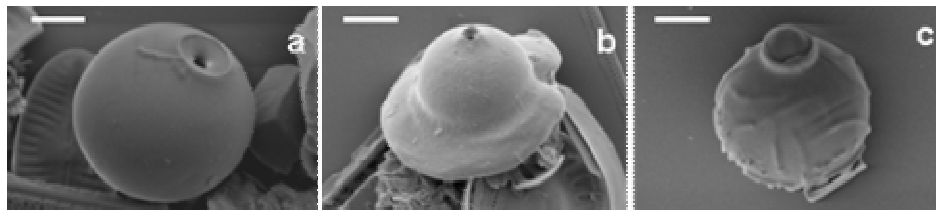

Figure 2. Scanning electron micrographs of chrysophycean cysts from Greenland lake sediments. Cyst morphotypes numbers follow Duff et al. (1995) and Wilkinson et al. (2001). (a) Stomatocyst #11. (b) Stomatocyst #337. (c) Stomatocyst #374. Scale bar represents 2 μm. Images courtesy of Sergi Pla.
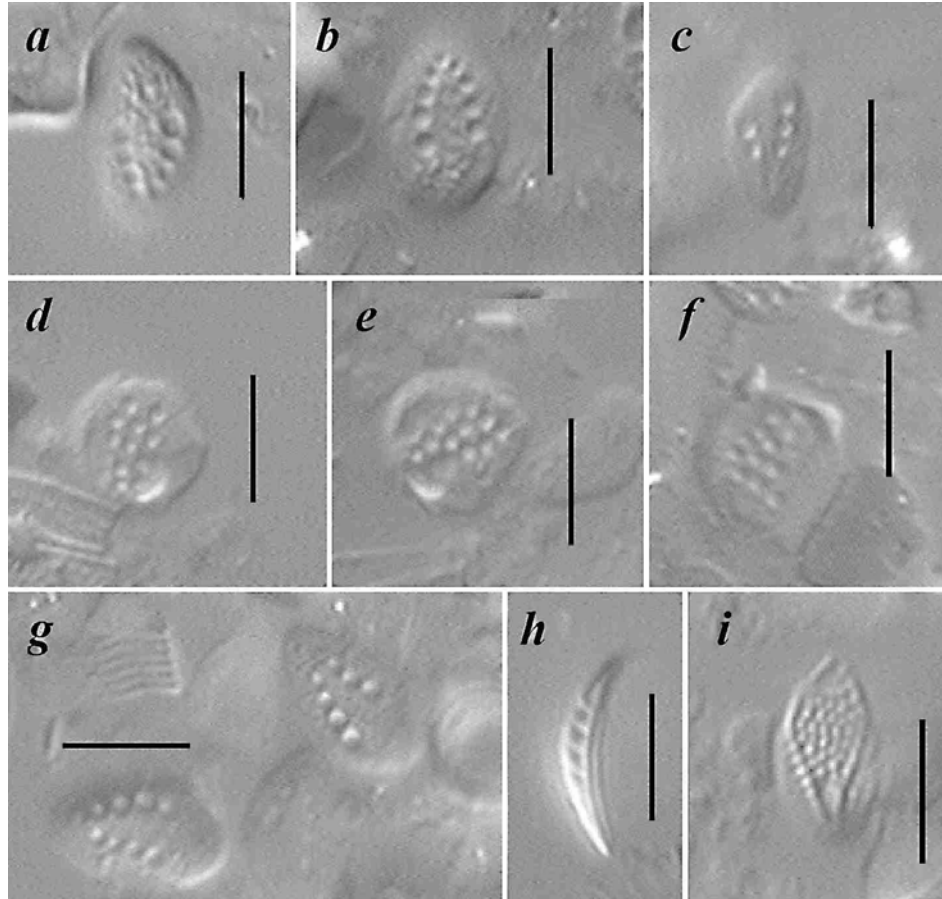
Figure 3. Light micrographs (DIC: differential interference contrast) of disarticulated scales of the chrysophyte *Mallomonas* from the sediments of Kekerturnak Lake, eastern Baffin Island, Nunavut. Scales of *M. allorgei-lychenensis* (a-g); *M. pseudocoronata* (h-i). Both of these taxa were restricted to the lake's most recent sediments. Scale bars are 5 μm. From Wolfe and Perren (2001); used with permission.

Chrysophytes often dominate the plankton of high latitude lakes and ponds (e.g., Sheath 1986), and recent work suggests that many periphytic forms are also common (Douglas and Smol 1995a; Wilkinson et al. 1997). Chrysophytes are represented in the fossil record primarily by their endogenous resting stages (Figure 2) known as stomatocysts (also called statospores in the older literature). Similar to diatoms, stomatocysts are siliceous and well preserved in sediments, and can be studied using similar techniques developed for diatoms (Zeeb and Smol 2001). Different taxa produce cysts that are believed to be species-specific. Relatively few cyst morphotypes have been linked to the taxa that produce them; however, well-defined taxonomic guidelines

have been developed for describing cyst morphotypes using electron and light microscopy (Duff et al. 1995; Pla 2001; Wilkinson et al. 2001). Although many cysts are now simply identified as numbered morphotypes, work continues on linking cysts to the taxa that produced them. Nonetheless, from a paleoecological perspective, numbered cyst morphotypes can still be used in paleolimnological assessments, provided that the ecological characteristics of morphotypes can be determined using surface sediment calibration sets, as described below. Compared to other geographic regions (e.g., Duff et al. 1997), a moderate number of studies have been completed for chrysophyte cysts in arctic and subarctic regions (e.g., Duff and Smol 1988, 1989; Duff et al. 1992; Pienitz et al. 1992; Brown et al. 1994, 1997; Gilbert et al. 1997; Wilkinson et al. 1997). Studies on cyst morphotypes from subantarctic regions have also been initiated (e.g., Van de Vijver and Beyens 1997a,b, 2000).

   In addition to stomatocysts, the siliceous scales and bristles of taxa in the classes Synurophyceae and Chrysophyceae (which include important genera such as *Mallomonas*, *Synura*, *Spinifermonas*, *Paraphysomonas*, and *Chrysosphaerella*) are species-specific and typically well preserved in sediments (Zeeb and Smol 2001). Scaled chrysophytes are rare or absent in many high latitude settings, however they are present in some lakes and ponds (e.g., Kristiansen 2001), and have been used by paleolimnologists to track recent environmental changes (Figure 3; Wolfe and Perren 2001).

Other morphological indicators

Although siliceous microfossils, such as diatom valves and, to a lesser extent, chrysophyte scales and cysts are the most commonly used algal indicators in paleolimnological studies, lake and pond sediments also preserve a diverse array of other morphological fossils. Many of these have yet to be explored in high latitude environments.

   As summarized by van Geel (2001) and Jankovská and Komárek (2000), many green (Chlorophyta), dinoflagellate (Pyrrhophyta) and blue-green algae (Cyanoprokaryotes or often referred to as Cyanobacteria) leave some morphological fossils. Probably the most commonly reported non-siliceous remains used by paleoecologists are colonies of the green alga *Pediastrum* (Komárek and Jankovská 2001), which are counted by palynologists as *Pediastrum* colonies often survive the sediment preparation techniques used for pollen (Bennett and Willis 2001). Although some of the earliest paleolimnological work in the Arctic considered algal remains such as *Pediastrum* and *Botryococcus* colonies (e.g., Fredskild 1983), the abundances of these microfossils are still rarely reported. Given the low temperatures that characterize high latitude lakes and ponds, it is likely that many other morphological algal remains are preserved in these deposits, and represent a potentially valuable and as yet untapped source of paleoenvironmental information. For example, filamentous and sheet-forming Cyanobacteria are often very common in many polar lakes and ponds (Figure 4). Their reproductive and resting structures, such as akinetes, are well preserved in some temperate deposits (e.g., van Geel et al. 1994). Stratigraphic analyses of these morphological remains should provide important information on ecosystem development.

Figure 4. Filamentous and sheet-forming Cyanobacteria (blue green algae) are common in many polar lakes and ponds.

Biogeochemical indicators

Not all algal groups leave morphological fossils. However, a suite of biogeochemical indicators can often be used to characterize essentially all algal groups, at least in a general way. Foremost amongst these biogeochemical indicators are fossil pigments (i.e., chlorophylls and carotenoids, the latter represented by carotenes and xanthophylls). As described by Leavitt and Hodgson (2001), fossil pigment analyses can provide important information on past algal and cyanobacterial populations, as many groups have specific pigment compositions. For example, alloxanthin is specific to cryptophytes, whereas oscillaxanthin is only produced by some Cyanobacteria (see Table I in Leavitt and Hodgson 2001). There is clearly considerable potential for using fossil pigment analyses in high latitude paleolimnology, although little work has been completed thus far. Paleo-pigment analyses also hold considerable potential for tracking past ultra-violet (UV) light penetration (e.g., Leavitt et al. 1997, 2003a,b; Hodgson et al., this volume), which is a major concern in high latitude regions (Vincent et al. 1998). Furthermore, blue-green algae are often important primary producers in many high latitude lakes and ponds (Vincent 2000). Although akinetes and other morphological fossils are occasionally recovered from sediments (van Geel 2001), fossil pigments may provide more reliable estimates of past populations in arctic and antarctic ecosystems. Given that high latitude systems are cold and dark for long periods of time, potential problems of pigment diagenesis may be lessened in these environments. Clearly, considerable potential remains for applying these techniques to future studies.

The field of organic biogeochemistry is developing rapidly, with many new potential indicators and applications. Some examples of these include biomarker hydrocarbons (e.g., alkanes, lignins, phenols), ratios of various elements, such as carbon to nitrogen, as well as many other biomarkers which may potentially be related, at least in an indirect way, to past algal populations. Meyers and Teranes (2001) summarized many of these relatively new approaches and applications; however, most freshwater applications are still from temperate regions.

Biogenic silica

Estimates of past population sizes are possible by calculating absolute abundances of microfossils (either as concentration data or correcting these data for changing sedimentation rates, to provide accumulation data). However, biogeochemical techniques can also be used to estimate past shifts in total population sizes of past diatom (and other siliceous algal) assemblages. For example, biogenic silica analysis (Conley and Schelske 2001) uses a timed chemical digestion technique to estimate the total amount of silica (SiO_2) in sediments that is derived from biogenic sources. As climatic conditions, such as changes in ice and snow cover on lakes (Smol 1983, 1988), may pose important limitations on past overall primary production, biogenic silica analyses can provide a proxy of production of siliceous algae, and therefore also climatic conditions. For example, Willemse and Törnqvist (1999) used biogenic silica levels, as well as other paleolimnological data, to track past primary production in western Greenland lake sediment records, and correlated these changes to climatic shifts, as inferred from isotope data gathered from the Greenland Ice Core Project. Similarly, Wolfe (2003) used biogenic silica to explore the relationship between past siliceous algal production and climate in the Canadian Arctic.

Ecological classifications of algae

Habitat classification

Different algal taxa often characterize specific aquatic habitats. As the availability of these habitats is often closely related to climatic and other environmental conditions in polar regions, documenting the nature and degree of algal habitat specificity has important paleolimnological implications (Smol 1988; Douglas and Smol 1999; Pienitz 2001). For example, certain taxa are characteristic of open water assemblages, while other species are adapted to attached (periphytic) shallow water habitats.

The term phytoplankton refers to a diverse group of algae that characterize the open water regions of lakes and ponds. Phytoplanktonic organisms have little control over their position in the water column, and are largely dependent on currents. However, some taxa (such as cryptophytes and many chrysophytes) are flagellated and therefore have some mobility. For example, during periods of low light penetration (such as under ice cover) these algae may move to the surface of the water column and take advantage of any light for photosynthesis that may penetrate the snow and ice cover.

The second major functional group of algae is the periphyton, which includes taxa that characterize a suite of shallow, littoral zone habitats. Periphytic algae, which include many different phyla (using the most recent guidelines from the Botanical Code, algae are now classified into phyla, whereas previously the taxonomic category of division was used), are further differentiated by the type of substrates that they exploit. For example, the epilithon are algae attached to rocks, the epiphyton attached to plants, the epipsammon attached to sand grains, and the epipelon living on the sediment surface. Given that many high latitude lakes have extended snow and ice covers (thus precluding extensive phytoplankton growth), benthic algae often dominate these systems.

Some taxa are found in both planktonic and periphytic habitats due to entrainment into the water column by wind and water current action. These are often referred to as the tychoplankton.

Environmental optima and tolerances

For many decades, limnologists have been attempting to classify aquatic ecosystems based on the algal assemblages characterizing these environments (for a historical review, see Stevenson and Smol 2003). For example, Hustedt (1937-1939) divided the diatom taxa he identified in Sumatra, Bali and Java based on pH categories, namely acidobiontic (occurring at pH values < 7, optimum distribution at pH = 5.5 and under), acidophilous (occurring at pH of about 7, and most common at pH < 7), indifferent (equal occurrences on both sides of pH 7), and alkaliphilous (occurring at pH values of about 7, and most common at pH > 7). Subsequent researchers added the category circumneutral to designate taxa that are most commonly found near pH 7. Although these terms are still used today, data derived from surface sediment calibration sets (discussed below) have largely supplanted these categories.

Surface sediment calibration sets or training sets

Over the last ca. 20 years, paleolimnologists have been cataloguing the ecological optima and, to some extent, tolerances of algal (especially diatom) assemblages employing more quantifiable approaches by using surface sediment calibration sets or training sets and appropriate multivariate statistics. The overall approach is straight-forward, and has been reviewed in Charles and Smol (1995) and Smol (2002), with a synopsis of the major statistical techniques summarized in Birks (1998). Briefly, a paleolimnologist chooses an appropriate set of calibration lakes and ponds (typically about 50 in number) that encompasses the major environmental gradients characterizing the study region. Limnological and other environmental data are gathered for the lake set. It is desirable to have several years of limnological data for a training set, but in high latitude regions, where logistical constraints often override scientific aspirations, environmental data from a single sampling date are often the only available measurements. However, given that the open water period is usually very short for many circumpolar lakes, and if an appropriate and consistent time window is used to collect the environmental data, ecologically relevant data can still be collected from a

single sampling date. The limnological data collected as part of a calibration set typically includes chemical variables such as pH, specific conductivity, nutrient concentrations, dissolved organic carbon (DOC), as well as physical variables such as morphometric data and temperature, and occasionally biological data, such as grazers and the distributions and types of plant substrates (e.g., mosses). This information comprises the first data matrix used in the calibration set, namely the measured environmental variables characterizing the lake set.

The second matrix of data includes the indicators (typically expressed as relative abundance data) collected for the calibration lakes and ponds. In order to provide a temporally and spatially integrated sample of indicators, paleolimnologists collect the surface (e.g., top 0.5 cm or top 1 cm) of sediment from each calibration site. This surface sediment sample contains the preserved remains of diatoms, chrysophytes, and other indicators that lived in the lake over the last few years, and so provides the "response variables" for the calibration set. Using a variety of statistical approaches (Birks 1998), the ecological optima and tolerances of taxa can then be estimated, and transfer functions can be constructed that allow environmental conditions to be inferred from fossil assemblage data.

Although surface sediments are routinely used for training sets, arctic paleolimnologists have employed similar calibration approaches to describe the environmental optima and tolerances of periphytic diatoms, such as those attached to mosses or rocks (e.g., Douglas and Smol 1995b; Vinocur and Pizarro 2000; Michelutti et al. 2003a). As habitat specificity is an important ecological variable in paleolimnological reconstructions, these biological data can be used to reconstruct past climatic and other environmental conditions.

Paleolimnological reconstructions

Algal assemblages as indicators of past climatic change

Although long-term monitoring data are rarely available, fortunately many algal taxa provide direct or indirect proxy data of climatically relevant variables. Given that many of the traditional paleoclimate indicators, such as pollen grains or tree ring sequences, are more difficult or impossible to use in polar regions (e.g., absence of trees), and that lakes and ponds are often characteristic features of these landscapes, fossil algal assemblages are now being used routinely in many paleoclimatic studies.

Lake ice and snow cover, and related limnological variables

An overriding factor influencing the physical, chemical, and biological characteristics of high latitude aquatic systems is the extent and duration of ice and snow cover, which itself is closely related to prevailing climatic conditions. In the first detailed high arctic paleolimnological study using diatoms and chrysophytes, Smol (1983) proposed that the extent of snow and ice cover on an Ellesmere Island lake was a dominant factor influencing algal assemblages. As elucidated further in subsequent publications (Smol 1988; Douglas and Smol 1999), changing snow and ice cover may have an overriding influence on many physical, chemical, and biological characteristics of high latitude

lakes, and so it is not surprising that algal indicators would track, at least indirectly, past climate (Figure 5).

Ice and snow cover on lakes and ponds is influenced by several climatic factors. Certainly air temperature is a critical variable, but other factors, such as wind, precipitation, and local morphometric and topographic characteristics are also important (Douglas and Smol 1999). In most arctic regions, lakes and ponds are totally frozen by September and only begin to thaw in June or July. In some high arctic and antarctic lakes, persistent ice cover during the summer is common (e.g., an ice thickness of over 5 m has been recorded in August on Ellesmere Island; Blake 1989), with only a shallow moat of ice-free water in the lake's littoral zone. Although some algae still persist under an ice cover, the concentration and community composition are markedly affected (Smol 1983, 1988; Douglas and Smol 1999). During warmer years, ice and snow cover is reduced, and progressively larger portions of the lake system are more amenable to the growth of different algal communities (Figure 5). As summarized by Douglas and Smol (1999), changes in ice cover have a cascading effect throughout the aquatic ecosystem, affecting the length of the growing season, the percentage of plankton, the development of substrates such as mosses, diversity, pH, nutrient levels, and other physical, chemical and biological factors. As diatoms and other indicators track these limnological changes, shifts in past algal assemblages can be used to estimate past climatic and other environmental changes.

Smaller water bodies, particularly in the High Arctic, may be expected to be even more responsive to environmental changes (Rouse et al. 1997). In polar regions, ponds are often defined as water bodies that freeze completely in winter. These shallow sites, many of them less than 0.5 m in depth, often represent the dominant type of surface waters in high latitude ecosystems. Given their small volumes, ponds should be especially sensitive bellwethers of environmental shifts related to climate change (Douglas and Smol 1994). The first paleolimnological studies from shallow arctic ponds revealed striking successional changes beginning in the 19th century that appeared to be related to climatic warming (Douglas et al. 1994). As summarized by numerous examples in this volume, many other researchers have used similar approaches to track climatic changes in a diverse range of lakes and ponds (see the chapter by Wolfe and Smith for a thorough review).

Although ice cover is an important limnological variable in all high latitude ecosystems, related environmental variables will also influence algal assemblages. Lakes in high polar regions are rarely thermally stratified, but as one moves farther from the poles, shifts in thermal stratification may also affect algal assemblages. For example, Sorvari and Korhola (1998) and Sorvari et al. (2002) recorded marked diatom changes in sediment cores from several Finish Lapland lakes. In deeper lakes, they reported synchronous increases in small planktonic *Cyclotella* diatoms in the more recent sediments, with concurrent relative decreases in benthic taxa. They interpreted these stratigraphic changes as evidence of longer ice-free periods and enhanced thermal stratification. Similarly, Rühland et al. (2003) recorded increases in a planktonic *Cyclotella* taxon in the 19th century sediments of a lake in subarctic Canada, which they suspected may have been at least indirectly related to enhanced thermal stratification with climate warming.
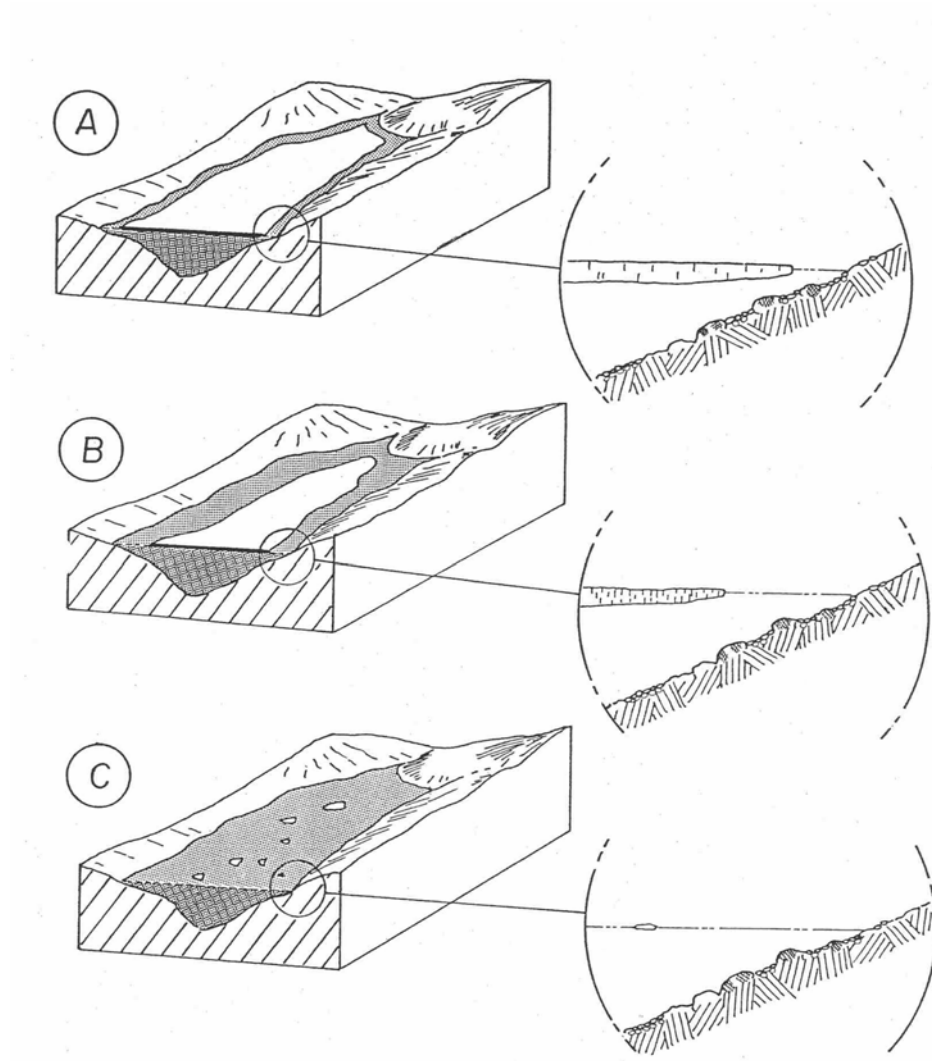
Figure 5. Although a variety of climate-related factors influence the limnological characteristics (and hence the biota) of high latitude lakes, changes in ice and snow cover are often overriding variables. This schematic diagram shows ice and snow conditions on a polar lake during relatively cold (A), moderate (B), and warm (C) conditions. A permanent float of ice and snow may persist throughout the summer during colder years (A), precluding the development of large populations of planktonic algae, and restricting much of the primary production to the shallow, open water moat. Many other physical, chemical and biological changes occur in lakes that are either directly or indirectly affected by snow and ice cover (Douglas and Smol 1999). From Smol (1988); used with permission.

   Undertaking detailed paleolimnological studies of sediment cores is time-consuming, and so it is often difficult, due to practical and logistical reasons, to attain regional assessments of environmental change. Detailed, contiguous sampling of lake sediment cores certainly provides much information on the timing and trajectories of environmental changes. However, if a large number of lakes and ponds need to be studied, and if the overall research question can be restricted to simply asking "Are recent algal assemblages similar to those present before the period of major human impacts, such as from the early 1800s?", then paleolimnologists can still provide 'snapshots' of past environmental change by using the so-called "top-bottom" or "before and after" paleolimnological approach (Smol 2002). The top-bottom approach is fairly simple. Paleolimnologists remove sediment cores spanning the last ca. 200 years from the study lakes, as they would in a typical stratigraphic study. However, instead of analysing many sediment sections from each core, they only analyse indicators, such as diatoms or chrysophytes, from the surface centimetre of sediment (representing recent algal assemblages, the "top" sediment sample) and from a sediment slice that represents the time period known to pre-date significant anthropogenic activities (the "bottom" sediment sample). Comparing algal assemblages from these two time periods allows the paleolimnologist to estimate if change has occurred in an ecosystem. This approach is an approximation, and certainly does not provide the same answers attainable from a detailed paleolimnological investigation. However, it is a practical and reasonable approach where regional questions are posed. For example, Rühland et al. (2003) used the top-bottom approach to track overall patterns in diatom assemblage changes from 50 lakes across the Canadian arctic treeline ecosystem. Similar to the studies noted earlier, they showed that *Cyclotella* taxa percentages increased in almost every study lake, at the expense of benthic diatom taxa, with the greatest change occurring in the deeper lakes. They interpreted this regional assemblage shift as indicative of climate warming, resulting in a shorter duration of ice cover, a longer growing season, and/or stronger thermal stratification. Similarly, Betts-Piper et al. (2004) used a top-bottom approach to track marked changes in chrysophyte cyst assemblages in a suite of Svalbard lakes.

   Perhaps some of the most striking evidence of environmental change was first documented from shallow ponds on eastern-central Ellesmere Island, Canada. Paleolimnological analyses from several sites at Cape Herschel showed an unprecedented shift in diatom assemblages beginning ca. AD 1850 (Douglas et al. 1994). At this time there was an almost complete shift from an assemblage consisting mainly of benthic *Fragilaria construens-pinnata* taxa (now positioned in the genera *Staurosira* and *Staurosirella*, respectively) to one of much greater diversity. The authors concluded that a lengthening in the growing season, due to climate warming, had been responsible for this marked change in the paleolimnological record. Further work by Overpeck et al. (1997) supported these findings. In their study, a high resolution 400-year climate record was examined using various proxy records (i.e., ice cores, dendrochronology etc.) demonstrating that, starting ca. 1845, climate forcing factors such as volcanism, solar radiation, and other variables had combined to influence warming at high latitudes. As described in subsequent chapters, many other studies have since reported similar findings throughout the Arctic. The timing of the shifts in algal assemblage varies, reflecting the heterogeneity of climate across the Arctic, as well as the sensitivity of small shallow ponds versus larger lakes, which have a greater thermal inertia and hence respond more slowly (Michelutti et al. 2003b). Comparing studies

between regions emphasizes the diverse limnological responses occurring at different latitudes. For example, in high arctic regions, shallow sites typically record the most pronounced changes, whereas in subarctic regions (where thermal stratification may be a factor), deeper lakes generally track the most striking changes. Moreover, regions that were not expected to have warmed (e.g., parts of northern Québec and Labrador; Laing et al. 2002; Ponader et al. 2002; Paterson et al. 2003) have recorded relatively complacent sedimentary algal profiles.

Dissolved organic carbon (DOC) reconstructions at northern treeline
Lakes located at or near the treeline boundary in the vast boreal forest region of the northern hemisphere are receiving considerable attention because of their sensitivity to climatic change. Reconstructing the past position of the arctic treeline boundary has important implications, as it corresponds fairly closely to the mean summer position of the Arctic Front and, in particular, to the 10°C July isotherm (Bryson 1966; Larsen 1989; Finney et al., this volume; Pienitz et al., this volume). In addition, lakes and ponds located along latitudinal and ecotonal transects that include steep climate and vegetation gradients show profound changes in water chemistry and physical properties. These changes are reflected in the highly variable algal community compositions across northern treeline (e.g., Pienitz and Smol 1993; Pienitz et al. 1995a,b; Korsman and Birks 1996; Korsman and Segerström 1998; Fallu and Pienitz 1999; Gregory-Eaves et al. 1999; Lotter et al. 1999; Fallu et al. 2002; Rühland and Smol 2002). Two major gradients emerge from algal (mostly diatom) distributional studies across the treeline ecotone (based on lake surface sediment studies). First, the concentration of lake water dissolved organic carbon (DOC, which is primarily controlled by external inputs of humic and fulvic acids from the catchment vegetation and the position of treeline) and related variables (water colour and transparency, which affect the underwater optical conditions in the water column). Second, temperature (surface water and air temperature), which affects many other lake properties, such as the intensity and duration of water column stratification. As discussed later in this chapter, as well as elsewhere in this volume, transfer functions have been constructed to infer both lake water DOC concentrations and temperature (e.g., Pienitz et al. 1999; Seppä and Weckström 1999; Korhola et al. 2000; Rosén et al. 2000; Saulnier-Talbot et al. 2003; Chapters 9-13, this volume).

Tracking past changes in ultraviolet (UV) radiation
Paleolimnological reconstructions of past irradiance regimes can contribute to a better understanding of the scales, causes and consequences of temporal variability in ultraviolet radiation (UVR). Using microfossil remains, such as diatoms (e.g., Pienitz et al. 1999), retrospective analyses permit reconstructions of concentrations of UVR-absorbing dissolved organic carbon (DOC) or its correlate chromophoric dissolved organic matter (CDOM), which can act as natural sunscreens. Important optical properties of water bodies include spectral irradiance regimes (UVR/photosynthetic active radiation (PAR) ratios) and water transparency (depth of UVR penetration), as well as algal responses to variable UVR flux in freshwater ecosystems. Diatom-based paleolimnological approaches have shown that climatically-induced changes in the

export of terrestrial (allochthonous) DOC to lakes near treeline is up to 100-fold more effective than modern stratospheric ozone depletion at altering biological exposure to UVR (Pienitz and Vincent 2000). Furthermore, paleolimnological studies have also shown that historical variability in UVR exposure has been high during the Holocene (Pienitz and Vincent 2000; Saulnier-Talbot et al. 2003).

To address the potential impact of long-term climate change relative to that of ozone depletion, Pienitz and Vincent (2000) combined paleolimnological analyses of diatom assemblages with bio-optical models based on present-day conditions in northern Canadian lakes. This new paleo-optical approach allowed them to estimate 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 treeline (Queen's Lake; 64°07'N, 110°34'W) in the central Northwest Territories, Canada. Analysis of fossil pollen records indicated that regional vegetation cover was sparse and tundra-like following deglaciation ca. 8000 yr BP and persisted until trees colonized the catchment ca. 5000 years ago (MacDonald et al. 1993). Diatom community structure and inferred DOC levels (Pienitz et al. 1999) showed three distinct and abrupt changes during the history of Queen's Lake. Both diatom biomass and inferred DOC concentrations were low (< 2 mg DOC l^{-1}) during the initial lake phase, with particularly few fossils recovered from sediments older than 5000 yr BP. This initial period of lake development was followed by major and rapid shifts in species composition and inferred chemical conditions ca. 5000 yr BP, with increased ratios of periphytic/planktonic taxa to > 70% of the total diatom assemblage. This second period of forest advance also corresponded to a major increase in algal production, recorded as the sediment mass-specific concentration of diatom valves, as well as a three-fold increase in inferred DOC levels. Based on fossil pollen analyses, Pienitz and Vincent (2000) argued that changes in lake chemistry and production resulted from climatic warming that stimulated treeline advance and increased forest density for about 2000 years. Finally, diatom-based reconstructions indicated that DOC concentrations declined more than 85% after 3000 yr BP, concomitant with the onset of Neoglacial climatic cooling and a southward retreat of treeline (MacDonald et al. 1993; Pienitz et al. 1999).

The large and rapid changes in DOC suggested that Queen's Lake experienced major shifts in the underwater optical environment over the last 6000 years as a consequence of climate-induced variation in forest development (Pienitz et al. 1999). Consistent with this hypothesis, application of bio-optical models derived from measurements in high-latitude waters (Vincent et al. 1998) showed that the inferred DOC shifts were equivalent to a decrease in exposure of two orders of magnitude of biologically-effective UVR during the mid-Holocene vegetation maximum between ca. 5000 and 3000 yr BP. In contrast, the most recent 3000 years were characterized by a > 50-fold increase in levels of damaging UVR, with recent inferences agreeing closely with present-day estimates of UVR exposure. Overall, changes in DOC concentrations arising from climatic variability increased exposure to photosynthetically damaging UVR several orders of magnitude more than did the relatively moderate (30%) decline in stratospheric ozone levels (Pienitz and Vincent 2000).

Saulnier-Talbot et al. (2003) used a diatom-based paleo-optical approach to estimate past depths of UV penetration in coastal Lake Kachishayoot (northwestern Québec, Canada; 55°20'N, 77°37'W; 102 m a.s.l.) following its isolation from the marine waters due to glacio-isostatic rebound of the Hudson Bay lowlands. Their multi-proxy

investigation revealed abrupt increases in diatom-inferred DOC concentrations and water colour that coincided with the retreat of postglacial marine waters and the arrival of spruce trees to the lake's catchment. They also tracked large changes in the underwater irradiance environment over the course of the postglacial period, 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 establishment of spruce forests in the lake's catchment. The use of additional macrofossil markers revealed that UVR penetration remained low even following forest retreat due to the development of alternate DOC sources, such as *Sphagnum* mats.

In another investigation of a lake chronoseries from Glacier Bay, Alaska, Engstrom et al. (2000) demonstrated that DOC concentrations were low for at least the first century following lake formation and that this initially high UVR exposure can structure biotic communities (Fritz and Engstrom 1995; Williamson et al. 2001). Finally, the observations that diatoms are particularly sensitive to changes in UVR exposure (e.g., Vinebrooke and Leavitt 1998; Watkins et al. 2001), and that these organisms are rare in early postglacial sediments (Pienitz et al. 1999), provide evidence that extreme UVR transparency is a mechanism directing the early development of glacial lake ecosystems in high latitude regions.

In addition to the type of studies described above, fossil pigment analyses also provide important insights on past trajectories of UV penetration in lakes and ponds (e.g., Leavitt et al. 1997, 2003a,b). Hodgson et al. (this volume) summarize some of the ongoing studies in antarctic regions.

Although further research is required to validate fossil interpretations, paleoecological analyses of lake sedimentary records can provide valuable insights into the history of UVR exposure and its potential impacts on freshwater ecosystems. For example, when used in combination with long-term environmental monitoring (e.g., Schindler et al. 1996), historical reconstructions may be valuable at identifying the importance of UVR relative to other stressors in regulating lake structure and function.

Climate-related changes in lake water pH
A number of within-lake and catchment processes may link lake water pH to a variety of climate-related variables, such as temperature (Psenner and Schmidt 1992). Using these relationships, paleolimnological studies from soft-water alpine lakes have suggested diatom-inferred pH changes may be linked to climate (e.g., Sommaruga-Wögrath et al. 1997; Koinig et al. 1998). Similar processes may be occurring in polar lakes. For example, Wolfe (2002) used diatom-inferred pH to estimate past climate-related changes in two Baffin Island (Nunavut) lakes over the last ca. 5000 years. Recently, Antoniades (2004) applied similar approaches to two high arctic lakes.

Temperature inferences
As noted throughout this review, most attempts at inferring past climatic changes use algae to track some limnological variable that is indirectly related to temperature (e.g., pH, salinity, habitat availability, etc.). Using fossil algal assemblages, such as diatoms, to directly track temperature is neither a straightforward subject, nor one without controversy. As discussed by Smol and Cumming (2000), from a paleoclimatic

perspective, it does not matter if the relationships between algal indicators and temperature are direct or indirect, only how reliably the variable can be reconstructed and whether the relationship between climate and indirect factor(s) remains linear over time. For example, Pienitz et al. (1995a) found that water depth and summer temperature were strongly related to diatom species assemblage data from northern Canadian (Yukon and Northwest Territories) lakes. The authors acknowledged that the relationship may not be a simple one, and that lake water temperature may be the measured environmental variable that simply captured most of the variance. A number of temperature transfer functions have since been developed and applied for other arctic regions (e.g., Weckström et al. 1997; Rosén et al. 2000; Joynt and Wolfe 2001; Bigler and Hall 2002; Wolfe 2003).

Athalassic lakes are systems known to occur in the semi-arid polar and subpolar regions of both hemispheres, yet remain relatively untapped sources of paleoclimatic information. The sediments of these saline lakes potentially contain high-resolution records of past climates and hydrological regimes (Pienitz et al. 1992; Fritz et al. 1999), as brine concentrations and lake-levels are governed, to a large extent, by the balance between precipitation and evaporation (or effective moisture). Because lake water salinity concentration and composition have a strong influence on algal distributions that can be quantified (e.g., Wilson et al. 1994; Zeeb and Smol 1995), past changes in climatic and hydrologic conditions can be reconstructed from the algal microfossils preserved in the paleolimnological records of these northern lakes. Using this approach, Pienitz et al. (2000) provided sub-centennial scale evidence for ca. 1500-year cyclic changes in paleosalinity and paleoproductivity from a climate-sensitive saline basin in the central Yukon, Canada (62°45'N, 136°38'W). This study demonstrated the potential of these high latitude saline sites as recorders of paleoclimatic shifts. Paleolimnological work has recently been initiated on saline lake systems in Greenland (Anderson et al., this volume), and similar types of studies can be undertaken with antarctic lakes (e.g., Roberts et al. 2001). For example, a number of researchers working on continental antarctic lakes have recently combined their data sets and developed diatom-based transfer functions to infer lake water salinity and water depth, from which past changes in moisture balance can potentially be deduced (Verleyen et al. 2003).

Tracking past river flow

Paleolimnological studies of river systems may be challenging, as rivers are high-energy systems and typically have the opposite characteristics that paleolimnologists rely upon to attain reliable archives of environmental change (Smol 2002). Nonetheless, under certain conditions, diatoms and other paleolimnological information pertaining to rivers (e.g., past river inflow, which may be an important climatic indicator) can be archived in arctic lake sediments. For example, Ludlam et al. (1996) and Antoniades and Douglas (2002) noted that certain diatoms (e.g., *Meridion circulare* and *Hannaea arcus*) were commonly associated with fluvial habitats in northern Ellesmere Island and Cornwallis Island rivers, respectively, than with nearby lake environments. Using these relationships, Ludlam et al. (1996) proposed a Lotic Index, which was simply calculated as the ratio of the relative abundances of *Hannaea* and *Meridion* diatoms, divided by the total number of pennate diatoms. Using this index, they reconstructed past river

discharge using diatoms preserved in the varved sediments of a downstream lake on northern Ellesmere Island. They interpreted the diatom changes over the last two centuries as indicating a decline in runoff beginning ca. AD 1800 until the late 1800s, followed by increased runoff until the mid-20th century. These types of studies hold considerable promise for other high latitude regions. For example, Potapova (1996) noted that flow regime was the measured environmental variable that best described the species composition of stream and river epilithic diatom communities from northeastern Siberia. Diatoms are also important components of antarctic rivers (e.g., Kawecka and Olech 1993), and so these approaches may well be applicable in the southern hemisphere as well.

River diatoms can also be used to study river flow in much more complex arctic river systems, although the approaches are somewhat different. As it is generally recognized that the current state of the Arctic Ocean and its influence on global climate is at least partly dependent on the freshwater input from the discharge of large circumpolar rivers (currently estimated at about 10% of the global freshwater runoff), there is considerable interest in tracking past river inflow. Perhaps the most promising approach to estimate past river inflow from these large complex deltas is to track diatoms and other paleolimnological indicators in sediment cores collected from the delta floodplain lakes.

The Mackenzie River Delta (Northwest Territories, Canada) is the second largest river delta system in the Arctic (surpassed only by the Lena River Delta in Siberia). Delta lakes are closely linked to their parent river systems, with the degree of river attachment being a prime variable determining limnological characteristics (e.g., Lesack et al. 1998). For example, delta lakes can typically be divided into three major categories along a gradient of connectivity to the parent river, namely: (1) no closure lakes, which have a continuous connection to the river; (2) low closure lakes, which flood every spring, but lose connection with the river during summer; and (3) high closure lakes, which flood only during extreme events, such as major ice jams that dam the river. Hay et al. (1997, 2000) examined the diatoms preserved in the surface sediments of 77 Mackenzie River delta lakes. Their calibration data suggested that diatoms can be used to estimate trends in past river connectivity of delta lakes. As limnological variables are strongly influenced by the amount of river input a delta lake receives (Lesack et al. 1998), these conclusions were not surprising. Michelutti et al. (2001a) subsequently used these calibration data to infer patterns of past river flow in eight Mackenzie River delta lakes.

Marine/lacustrine transgressions and sea-levels

Diatoms and other algae are excellent indicators of lake water salinity, with most taxa relatively easily differentiated between freshwater, marine, and brackish forms. Diatom analysis has been widely used at the interface of fresh and saline environments to identify lake isolation from the sea in areas of land uplift in formerly glaciated regions of the Arctic (e.g., Young and King 1989; Pienitz et al. 1991; Douglas et al. 1996; Saulnier-Talbot and Pienitz 2001) and Antarctica (e.g., Roberts and McMinn 1999) to indicate marine and brackish water transgressions. Traditional approaches mostly relied on the identification and analysis of transgressive and regressive overlaps by analysing stratigraphic boundaries between terrestrial freshwater sediments and marine littoral

facies. In these studies, diatom analysis was used to validate sea-level index points by considering changes in the composition of diatom groups of different salinity preferences. However, the potential for using diatom assemblages to quantitatively reconstruct past sea-level changes has rarely been explored, mainly because the environmental optima of individual taxa with respect to water depth are poorly documented. By determining the relationship between water depth and diatom species distributions and abundances in 74 modern sedimentary environments along the southern shores of the Beaufort Sea coast (Arctic Ocean, Canada), Campeau et al. (1998, 1999, 2000) have been able to overcome the limitations of traditional approaches and quantitatively inferred past relative sea-level changes using a diatom-based water-depth model that was applied to fossil assemblages in several long sediment cores.

Acidification and other contaminants

Algal-based paleolimnological studies have played leading roles in assessing many water quality problems (Smol 2002), and foremost amongst these has been research related to lake acidification (Battarbee et al. 1999). Based on available data, however, it appears that few high latitude regions have been acidified as a result of atmospheric deposition of strong acids, although certainly many high latitude systems are subjected to various sources of pollution (Muir and Rose, this volume). For example, the metal smelting facilities at Noril'sk (Taymyr Peninsula, Siberia, Russia) are located approximately 300 km north of the Arctic Circle, and presently represent the largest point source of sulfur dioxide emissions in the world. However, despite very high loadings of acids, Duff et al. (1999) showed that Noril'sk area lakes are still typically alkaline due to local bedrock geology and overlying glacial deposits. Not surprisingly, diatom-based paleolimnological studies in the area could not detect any acidification trends (Michelutti et al. 2001b). Similarly, Weckström et al. (2003) used diatoms in the sediments of 32 Kola Peninsula (Russia) lakes to reconstruct recent changes in lake water pH related to emissions from local industries. Signs of recent acidification could only be recorded in seven of the lakes, and they did not find evidence for any large-scale acidification in the region. Meanwhile, Moiseenko et al. (1997) noted evidence of recent lake acidification from lakes in the poorly buffered regions of Kola North, Russia.

The sensitivity of algae to other contaminants is less well documented. For example, organochlorides, such as DDT and PCBs, are transported via atmospheric pathways or by other vectors (e.g., military installations) to high latitude regions (Muir and Rose, this volume). Paterson et al. (2003) tracked diatom and chrysophyte changes in two lakes that had been subjected to high concentrations of PCB contamination from local military facilities in Labrador, Canada. They found no noticeable influence on the algal assemblages.

Recently, Outridge et al. (2004) have documented positive correlations of mercury (Hg) concentrations with diatoms in two Canadian high arctic lakes over the last 50 to 100 years. This correlation (when diatoms were present in high numbers) indicated a close association between biology and geochemistry, and may even suggest biological feedback mechanisms that enhance some attributes of geochemical processes in polar lakes.

Local effects of eutrophication

Diatoms are widely recognized as reliable indicators of lake water nutrient levels, and so have become the mainstay of many paleolimnological investigations of eutrophication (Hall and Smol 1999). However, cultural eutrophication is not generally considered to be a major water quality issue in arctic and antarctic regions as human settlements are spaced widely apart and have low populations. There are, however, some exceptions.

   Much of what we know about high arctic eutrophication has come from work that was initiated in the late 1960s and early 1970s as part of the International Biological Programme (IBP). Two Canadian high arctic lakes in the hamlet of Resolute Bay (Cornwallis Island, Nunavut) were chosen for detailed studies of freshwater production: ultra-oligotrophic Char Lake and eutrophic Meretta Lake (Rigler 1974). Meretta Lake (72°41.75'N, 94°59.58'W) received sewage from a small number of buildings from 1949 to 1998. The Department of Transport base (referred to locally as "the North Base"), associated with the local airport, discharged its grey water and sewage through a central collecting pipe and then via an utilidor onto the land (Figure 6). Utilidors are systems of elevated horizontal, insulated pipes that transport a variety of liquids above ground to prevent them from freezing and to prevent melting of the permafrost. The utilidor outfall discharged sewage into a series of streams that ultimately drained into Meretta Lake. For almost half a century, this nutrient-rich effluent fertilized the lake. Schindler et al. (1974) summarized the limnological characteristics of Meretta Lake during the short time window of the IBP programme but, as pre-eutrophication conditions were not known, it was not possible to place current limnological conditions into a historical context. As the director of this IBP programme, Frank Rigler (1974) noted in the final report on this IBP project: "The conclusions we can draw are limited because the original condition of Meretta Lake is unknown".

   The absence of long-term monitoring data for Meretta Lake prompted Douglas and Smol (2000) to undertake a diatom-based paleolimnological study of this important reference site. Using a high-resolution sediment record, they showed that eutrophication from the "North Base" had significantly affected diatom assemblages; however the species changes were markedly different from those recorded in nutrient-enriched temperate lakes. Despite the increase in nutrients, periphytic diatoms continued to overwhelmingly dominate the assemblage, further confirming that extended ice covers, and not nutrients, were precluding the development of large concentrations of planktonic diatoms. In 1993, when the sediment core was collected, the North Base still had a moderate number of users. However, during the 1990s, the number of people using the North Base declined steadily, and in 1999 the entire utilidor system was dismantled and sewage was thereafter trucked to a designated area of the hamlet's dump. Douglas and Smol (2000) measured summer nutrient levels since 1991, and tracked the decline in eutrophication throughout the 1990s. Comparing the diatom assemblages preserved in the surface sediments of a core collected in 2000 (Michelutti et al. 2002a) with those at the surface of the 1993 core (Douglas and Smol 2000) revealed recent diatom species shifts that were consistent with nutrient reductions. These recent assemblage shifts also confirmed that there were no significant lags between environmental changes and the deposition of diatoms in the profundal zone in these largely ice-covered lakes. In addition, changes in periphytic assemblages collected

Figure 6. This utilidor, which was recently dismantled, is releasing sewage from the Resolute Bay (Cornwallis Island), North Base into a series of streams and ponds. The effluent ultimately reaches Meretta Lake, about 1.6 km downstream.

each summer since 1991 from Meretta Lake's littoral zone also tracked the recovery from eutrophication as taxa characteristic of more oligotrophic environments increased relative to more eutrophic diatoms (Michelutti et al. 2002b).As northern communities increase rapidly in size (Canadian Inuit birth rates are among the highest in the world), concerns over issues of waste disposal and other environmental problems will only escalate in the future. Paleolimnological approaches will likely become more important in water quality assessments in these remote regions, as they have been in many other parts of the world.

   Reconstructing changes in nutrient levels have other applications besides tracking the effects of cultural eutrophication. For example, nutrient levels in high latitude lakes and ponds are also indirectly linked to climatic conditions (Douglas and Smol 1999; Moser et al. 2002), and diatom-based transfer functions to infer lake water nutrient and related trophic variables are being developed for polar regions (e.g., Jones and Juggins 1995; Lim et al. 2001). In addition, wildlife, such as musk ox, caribou, and other grazers, as well as birds, marine mammals, and fish can affect nutrient concentrations, and diatoms can play important roles in tracking these sources (see sections below).

Tracking the influences of past fish and wildlife populations on freshwater systems

Recent research has suggested ways that algal assemblage data can be used, in conjunction with other paleolimnological techniques, to track past changes in ecologically and economically important animal populations. Below, we summarize three recent examples demonstrating how diatoms have been used to track past changes in sockeye salmon, caribou, and fur seal populations, although many other applications are likely possible.

Many important fish stocks are decreasing as a result of over-fishing and other human interventions (such as habitat destruction, dam construction, competition from hatchery fish, etc.). Sockeye salmon (*Oncorhyncus nerka*) is the most important commercial fish species on the Pacific west coast of North America. However, many stocks are believed to be nearing extirpation or are at least threatened, and so there is considerable interest in tracking long-term changes in salmon abundance.

Paleolimnological approaches have been developed that take advantage of the anadromous life strategy exploited by sockeye salmon. Fry of the sockeye salmon hatch in a nursery lake and then, after about one to three years, they leave the freshwater environment and migrate downstream to the Pacific Ocean. After living a further one to three years in the mid-Pacific Ocean where they accumulate over 95% of their biomass, they return with very high fidelity to their natal stream and nursery lakes, where they spawn and then die. For some lake systems, the carcasses of spawned salmon may contribute over 50% of the lake water nitrogen and phosphorus levels, and thus are an important subsidy of marine-derived nutrients for nursery lakes. As diatoms are sensitive indicators of lake water nutrient levels, stable isotope analyses (e.g., $\delta^{15}N$) can also be used to track past salmon returns. Combined paleolimnological approaches have been used to reconstruct past sockeye salmon returns for a variety of Alaskan nursery lakes (Finney et al. 2000, 2002; Gregory-Eaves et al. 2003, 2004; Holtham et al. 2004). Research is now in progress using similar approaches on nursery lakes in other arctic and subarctic regions, such as the Yukon Territory and northern British Columbia in Canada (D. Selbie and J.P. Smol, unpublished data).

The effects of land-based mammals can also be examined using paleophycological approaches. For example, the world's largest caribou herd in the Rivière George region of northern Québec was known to have undergone a large population increase since the 1950s, which was accompanied by pronounced impacts on vegetation cover, soil erosion, and other terrestrial disturbances. Laing et al. (2002) used diatom-based paleolimnological techniques to assess the effects of wildlife fluctuations on several northern lake ecosystems. They found no evidence of marked changes in lake conditions as a result of the fluctuating herd populations. The results of the Laing et al. (2002) study confirm that, in order to be registered in the diatom record, a perturbation must be sustained and significantly outside baseline natural variability for a lake. While this is often evident for anthropogenic impacts on water quality, evaluating the relative importance of natural factors as influences on limnological conditions is more complicated.

In the southern hemisphere, diatoms have been used to assist conservation managers determine the effects of increasing fur seal (*Arctocephalus gazella*) populations on coastal antarctic lakes. Although seals were almost extirpated by over-hunting in the 19th century, the cessation of sealing in 1912, coupled with the intensification of the

South Georgian whaling industry between 1902 and 1965 (baleen whales being the principal competitors of seals for food), has resulted in a striking increase in fur seal populations on some of the South Orkney Islands. Using a variety of paleoindicators, including preserved seal hairs, diatom assemblages, and other data, paleolimnologists were able to ascertain that historical sealing and whaling activities have affected fur seal populations, which in turn have impacted the ecology of coastal lakes (Hodgson and Johnston 1997; Hodgson et al. 1998). Higher seal populations, and therefore higher loading of nutrients from seal excrements (which can be tracked using diatom assemblages; Jones and Juggins 1995), have led to lake eutrophication, which in turn has raised conservation and management concerns.

Complementing archeological investigations

It is now well documented that high latitude ecosystems have been affected by long-range transport of atmospheric pollutants (Muir and Rose, this volume). However, it is generally assumed that high arctic lakes and ponds have been unaffected by direct local human activities before the arrival of Europeans, as most native peoples were primarily nomadic with relatively low population densities, and had un-intrusive hunting and gathering technologies and customs. Using similar techniques to those developed for the previously described salmon research, Douglas et al. (2004) combined archeological and paleolimnological approaches to challenge some of these assumptions.

The Thule Inuit migrated to the Canadian Arctic islands about 1000 years ago from Alaska and brought with them an effective whaling technology (e.g., seal-skin or sometimes walrus-skin boats, harpoons with toggled points, seal skin bladder floats). The Thule Inuit hunted a variety of marine mammals, but their most important prey were large bowhead whales, which provided a food staple as well as material for house construction and tools. Although nomadic during the short summer, the Thule Inuit maintained a number of winter settlements consisting of houses constructed from the bones of bowhead whales (Figure 7). The Thule Inuit abandoned most of the high arctic islands about 400 years ago. Nonetheless, the bones and other debris still present near and in the ponds adjacent to the abandoned over-wintering settlements continue to influence water chemistry (i.e., higher nutrient levels) and diatom assemblages (Douglas et al. 2004).

The highest concentrations of abandoned Thule over-wintering sites are present on south-eastern Somerset Island, Nunavut. Douglas et al. (2004) used stable isotope and diatom analyses for one such site (PaJs-13; 72'08.66°N, 94'01.50°W) to show that 13th century whaling activities markedly influenced pond ecology. Site PaJs-13 consists of 11 large semi-subterranean whalebone houses, a number of smaller, shallower sod dwellings, and a ring of 10 bowhead crania of probable ceremonial function. In addition, the adjacent beach area is strewn with several thousand bowhead bones, resulting from the flensing and caching of whales (Habu and Savelle 1994). Diatom assemblages from the pond's early history were similar to those recorded in other high arctic sites. However, at approximately AD 1200, the paleolimnological record indicated a marked shift in diatom assemblages to moss epiphytes (e.g., *Pinnularia balfouriana*), coupled with an elevated $\delta^{15}N$ ratio. This zone identified the period of nutrient enrichment from decaying whale carcasses and other refuse. Diatom

Figure 7. A Thule over-wintering site, as reconstructed by the Canadian Museum of Civilization. This whale bone house is situated at Resolute Bay, Cornwallis Island, Nunavut, which is north of the Somerset Island site described in Douglas et al. (2004). As no wood is present in the High Arctic (except possibly driftwood from more southern locations), the Thule Inuit used whale bones as the main foundations for their over-wintering houses. This structure would be covered by seal and other animal skins, and then sod for further insulation.

assemblages similarly tracked the abandonment of the site about four centuries ago, although, as noted above, the pond still has elevated nutrient levels and a somewhat distinctive diatom assemblage. The Douglas et al. (2004) Somerset Island study site possibly represents the oldest record of changes in aquatic ecology associated with human activities yet reported for any high arctic ecosystem, as well as the earliest such changes documented for a water body in Canada or the USA.

Diatoms have been used to assist archeologists in a number of applications in temperate regions (reviewed in Juggins and Cameron 1999), but have only recently been applied to polar research. Archeological sites are common throughout many arctic regions, and the patterns of settlement and abandonment of native peoples remain an area of controversy. Working collaboratively with archeologists, diatom-based paleolimnolgical techniques can potentially be used to decipher the influences of native cultures on local environments and help track the spread of different peoples throughout the Arctic.

Other applications

Paleoenvironmental information preserved in lake and pond sediments is the focus of this volume, however algae can also provide proxy data from other freshwater habitats in high latitude regions. For example, many high latitude regions (provided they are not too cold or dry) accumulate peat deposits. Incorporated in many peat profiles is a large suite of microscopic indicators, including diatoms, chrysophytes (e.g., Gilbert et al. 1997; Pienitz 2001), and other algal remains. For example, Brown et al. (1994) and Rühland et al. (2000) used diatom and chrysophyte remains in peat cores from Ellesmere Island and Siberia, respectively, to infer past climatic conditions. Diatoms have also been recovered from polar ice cores (e.g., Burckle et al. 1988; Gayley et al. 1989), where they have been used to supplement paleoenvironmental interpretations.

   Diatoms and other algal indicators have been used in a variety of forensic studies around the world (Peabody 1999). One arctic example includes Foged's (1982) examination of the eight so-called "Greenland mummies", who died ca. AD 1460 and whose mummified remains were discovered in 1972. By examining lung tissue from the bodies for diatom remains, Foged concluded that the cause of death was not drowning.

   Stoermer et al. (1988) noted similarities between the diatom assemblages they found associated with the remains of a mastodon skeleton in Michigan (USA) to those found in the littoral zones of arctic lakes and ponds (Smol 1988). Using this forensic approach, Stoermer et al. (1988) concluded that the mastodon died in a pond, similar to those currently found in arctic or periglacial environments.

Summary

Algal indicators have been used in a broad spectrum of paleolimnological applications from high latitude regions, even though most studies have only been completed over the last decade. Research has focused primarily on attempts to reconstruct climatic trends, which have included a variety of approaches, ranging from using habitat preferences of algal taxa to reconstruct past snow and ice cover on lakes, to inferring changes in lake water chemistry (e.g., DOC, pH, salinity) that are indirectly related to climatic changes. Efforts have also been made to infer temperature and past underwater light regimes from diatom assemblages, as well as distinguish riverine from lacustrine diatoms to track past river inflows. In addition, paleophycological approaches have been used to track the effects of local human disturbances (e.g., sewage inflows) and other sources of pollution, the influences of animal populations (such as anadromous fish and terrestrial mammals) on lake systems, as well as tracking marine to lacustrine transgressions in coastal systems. Collaborative work with other groups of researchers, such as archeologists, has also proved fruitful.

   Given that most studies have been published over the past decade, we believe that considerable advancements have been made in a relatively short time. However, much work remains to be done. Although a variety of morphological and biogeochemical indicators are potentially available, diatom assemblage data have overwhelmingly dominated most paleolimnological studies. More reliable inferences of past environmental conditions will be possible by employing a larger spectrum of

paleoindicators. For example, chrysophytes and blue-green algae are especially common in many high latitude lakes and ponds.

It is also becoming increasingly clear that we have only a rudimentary understanding of the limnological characteristics of high latitude systems. As the distributions and abundances of algal taxa are closely linked to environmental conditions, it is important to better understand present-day limnological processes. Fortunately, transportation and northern logistics, which have limited earlier research, are improving in many high latitude regions, and so some scientific progress is being made in these areas.

Despite these shortcomings, it is very encouraging to see the advancements made in the diversity and geographic coverage of algal-based paleolimnological studies, and the important data that this research has generated. Over a relatively short period of time, considerable progress has been made in describing, at least in a broad sense, the environmental requirements of many taxa, as well as information on the taxonomy and biogeography of indicators. As illustrated by many examples presented in subsequent chapters of this volume, paleophycological approaches have already made substantial contributions to elucidating the environmental histories of high latitude systems, and have tremendous potential for future applications.

Acknowledgements

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Appendix 1. Some polar phycologists and the locations of their algal collections of historical significance. International herbarium codes are in brackets.

Phycologist	Location of Historical Collections
Bourrelly P.	Paris Museum, Paris, France (PC)
Castracane F.	Dr. Henri Van Heurck Museum, Antwerpen, Belgium (AWH); British Museum, London, UK (BM)
Cleve P.T.	Friedrich-Hustedt-Arbeitsplatz für Diatomeenkunde, Bremerhaven, Germany (BRM); Paris Museum, Paris, France (PC); Philadelphia Academy of Natural Sciences, Philadelphia, USA (PH)
Croasdale H.	Canadian Museum of Nature, Ottawa, Canada (CANA)
Dickie G.	British Museum, London, UK (BM)
Ehrenberg C.G.	Museum für Naturkunde der Humboldt University, Berlin, Germany (BHU)
Foged N.	Botanical Museum, Copenhagen, Denmark (C)
Frenguelli J.	Museo de La Plata, Buenos Aires, Argentina (LP)
Fukushima H.	National Science Museum, Tokyo, Japan (TNS)
Gran H.H.	Oslo, Norway (not listed in Index Herbariorum, IMBB)
Grunow A.	Dr. Henri Van Heurck Museum, Antwerpen, Belgium (AWH); British Museum, London, UK (BM); Friedrich-Hustedt-Arbeitsplatz für Diatomeenkunde, Bremerhaven, Germany (BRM); Naturhistorisches Museum Wien, Austria (W)
Heiden H.	Friedrich-Hustedt-Arbeitsplatz für Diatomeenkunde, Bremerhaven, Germany (BRM)
Kobayashi T.	National Science Museum, Tokyo, Japan (TNS)
Kolbe R.W.	Swedish Museum of Natural History, Stockholm, Sweden (S-PA-k)
Hooker J.D.	British Museum, London, UK (BM)
Hustedt F.	Friedrich-Hustedt-Arbeitsplatz für Diatomeenkunde, Bremerhaven, Germany (BRM)
Lagerstedt N.G.W.	Philadelphia Academy of Natural Sciences, Philadelphia, USA (PH)
Manguin E.	Paris Museum, Paris, France (PC); Philadelphia Academy of Natural Sciences, Philadelphia, USA (PH)
Østrup E.	Botanical Museum, Copenhagen, Denmark (C)
Patrick R.	Philadelphia Academy of Natural Sciences, Philadelphia, USA (PH)
Peragallo M.	Paris Museum, Paris, France (PC); Philadelphia Academy of Natural Sciences, Philadelphia, USA (PH)
Petersen J.B.	Botanical Museum, Copenhagen, Denmark (C)
Petit P.	Dr. Henri Van Heurck Museum, Antwerpen, Belgium (AWH); Paris Museum, Paris, France (PC); Philadelphia Academy of Natural Sciences, Philadelphia, USA (PH); Swedish Museum of Natural History , Stockholm, Sweden (S)
Prescott G.W.	Farlow Herbarium, Cambridge, USA (FH); Field Museum of Natural History, Chicago, USA (F); New York Botanical Garden, New York, USA (NY)
Ross R.	British Museum, London, UK (BM); Farlow Herbarium, Cambridge, USA (FH); Canadian Museum of Nature, Ottawa, Canada (CANA)
Van Heurck H.	Dr. Henri Van Heurck Museum, Antwerpen, Belgium (AWH); British Museum, London, UK (BM); Philadelphia Academy of Natural Sciences, Philadelphia, USA (PH); Naturhistorisches Museum Wien, Austria (W)
West G.S.	British Museum, London, UK (BM)