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## Historical Changes in Arctic Freshwater Ecosystems

Various types of ecosystem-based climate proxies have been used to assess past arctic change. Although lotic records are relatively poor because of the constant reworking of riverine material, high-quality lentic data have been assembled back to the end of the Pleistocene and deglaciation of the circumpolar Arctic. In general, climatic variations in the Holocene, partly due to changes in the shrinking effect of glacier coverage, produced significant temporal and spatial variations in arctic hydrology and freshwater ecosystems. Of particular note were the vast expansions of northern peatlands during major protracted periods of wetting. More recent lake biota and sedimentological data reflect the general warming trend that has occurred over the last one to two centuries and indicate major changes to freshwater characteristics such as ice-cover duration and thermal stratification. Such data provide an excellent baseline against which future effects of climate change can be both projected and measured.

### INTRODUCTION

Analysis of the stability, sensitivity, rate, and mode of the response of freshwater ecosystems to past climate change has proven to be a valuable tool for determining the scope of potential responses to future climate changes. Preserved records of ecosystem variations (e.g., trees, fossils, and sedimentary deposits), combined with dating techniques such as carbon-14, lead-210, or ring/varve counting, have been a primary source of information for unraveling past environmental changes that pre-date the age of scientific monitoring and instrumental records. The application of climate change proxies in paleoclimatic analysis has traditionally relied on identification of systematic shifts in ecosystem patterns known from modern analogues or by comparison with independent instrumental or proxy climate records to determine perturbations in climate-driven environmental conditions such as growing-season length, solar insolation, temperature, humidity, ice-cover extent and duration, or hydrologic balance. Such ecosystem-based climate proxies may include the presence, distribution, or diversity of terrestrial, aquatic, or wetland species or assemblages; changes in water or nutrient balances recorded by chemical or isotopic changes; changes in growth rates or characteristics of individual plants and animals; or changes in physical environments (e.g., lake levels, dissolved oxygen content) that are known to be linked to the productivity and health of freshwater ecosystems.

The reliability of and confidence in these ecosystem indicators of climate change has been enhanced through development of spatial networks of paleoclimatic data, by comparison with instrumental climate records where available, and through concurrent examination of abiotic climate change proxies in nearby locations. Such abiotic proxy records include shifts in the isotopic composition of glacial deposits (and to some extent permafrost or pore water), which provide regional information about changes in origin, air-mass evolution, and condensation temperature of precipitation (or recharge); changes in summer melt characteristics of glacial deposits or sedimentary and geomorphological evidence such as the presence of laminated lake sediments (varves), the latter of which are indicative of water depths great enough to produce stratified water columns and meromixis; and variations in varve thicknesses in lakes and fining/coarsening sequences or paleo-shoreline mapping that can be used to reconstruct shifts in lake or sea levels.

### ECOSYSTEM MEMORY OF CLIMATE CHANGE

The accumulation of ecosystem records of environmental change relies on the preservation of historical signals in ice caps, terrestrial deposits (soils, vegetation, permafrost), and aquatic deposits (wetlands, rivers, lakes, ice), coupled with methods for reconstructing the timing of deposition. As continuity of deposition and preservation potential are not equal in all environments, there is a systematic bias in the paleoclimatic record toward well preserved lentic environments, and to a lesser extent wetlands, as compared to lotic systems. The following sections describe common archives and the basis of key memory mechanisms.

#### Lentic Archives

Biological indicators of environmental change that are preserved in lake sediments include pollen and spores, plant macrofossils, charcoal, cyanobacteria, algae including diatoms, chrysophyte scales and cysts and other siliceous microfossils, biogenic silica content, algal morphological indicators, fossil pigments, bacteria, and invertebrate fossils such as Cladocera, chironomids and related Diptera, ostracods, and fish (1). In general, the best biological indicators are those with good preservation potential, for example, siliceous, chitinized, or (under neutral to alkaline pH conditions) carbonaceous body parts. They also must be readily identifiable in the sedimentary record, and exist within assemblages that have well-defined ecosystem optima or tolerances. Lentic records commonly

extend back 6000 to 11000 years to the time of deglaciation in the circumpolar Arctic.

In general, fossil pollen and spores, plant macrofossils, and charcoal are used to determine temporal shifts in terrestrial ecosystem boundaries, notably past fluctuations in northern treeline and fire history. Pollen and spores from emergent plants may also be useful indicators for the presence and extent of shallow-water environments. Preserved remains of aquatic organisms, such as algae and macrophytes, provide additional information on aquatic ecosystem characteristics and lake-level status. Such indicators, which are used to reconstruct ecological optima and tolerances for past conditions, are normally applied in conjunction with surface-sediment calibration datasets to quantitatively compare present-day ecosystem variables or assemblages with those preserved in the sediment record (1–3). Douglas and Smol (4) provide details on the application of diatoms as environmental indicators in the high Arctic, and Smol and Cumming (5) provided a general treatment of all algal indicators of climate change. Biological indicators useful for lake-level reconstructions include the ratio of planktonic to littoral Cladocera as an index of the relative size of the littoral zone or water depth of northern lakes (6, 7). Chironomids and diatoms may be used in a similar manner. While such information allows for quantitative reconstruction of lake levels, errors in projecting lake water depth from Cladocera, chironomids, and diatoms may be large (8, 9; see also 7). Cladoceran remains may also provide evidence of changes in species trophic structure, including fish (10–12), and chironomids may be used to reconstruct changes in conductivity mediated by variations in runoff and evaporation (13).

Due to their small volume and minimal capacity to buffer climate-driven changes, the shallow lakes and ponds characteristic of large parts of the Arctic may be well suited for hydrological and climate reconstructions. Past shifts in diatom assemblages have been used to track habitat availability for aquatic vegetation, the extent of open-water conditions, shifts in physical and chemical characteristics, and water levels (9).

Isotopic analysis (e.g.,  $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$ ,  $\delta^{15}\text{N}$ ) of fossil material, bulk organic sediments, or components such as cellulose or lignin can provide additional quantitative information. For example, carbon and oxygen isotope analysis of sediment cellulose has been applied in many parts of the circumpolar Arctic (7). It relies on the key assumptions that fine-grained cellulose in offshore sediments (excluding woody material, etc.) is derived from aquatic plants or algae and that the cellulose–water fractionation is constant (14). Often the source of material (aquatic versus terrestrial) can be confirmed from other tests such as carbon–nitrogen ratios (14), although these two assumptions may not be applicable in all arctic systems (15). Under ideal conditions, the  $\delta^{18}\text{O}$  signals in aquatic cellulose are exclusively inherited from the lake water and therefore record shifts in the water balance of the lake (i.e., input, through-flow, residency, and catchment runoff characteristics; 16). Studies of ice cores from Greenland and arctic islands support the interpretation of  $\delta^{18}\text{O}$  signals and other climate proxies across the circumpolar Arctic (5). Ice-core records of past precipitation ( $\delta^{18}\text{O}$ ,  $\delta^2\text{H}$ ) can help to distinguish climatically and hydrologically driven changes observed in lake sediment records.

Stratigraphic reconstructions using  $\delta^{13}\text{C}$ ,  $\delta^{14}\text{C}$ , or  $\delta^{15}\text{N}$  measured in aquatic cellulose and fossil material can likewise be used to examine changes in ecosystem carbon and nitrogen cycles and ecosystem productivity. Trends in chemical parameters such as dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), and total nitrogen can also be reconstructed from fossil diatom assemblages as demonstrated

for lakes in the treeline region of the central Canadian Arctic (17), Fennoscandia (18), and elsewhere.

While lakes are nearly ideal preservation environments, lake sediment records may not always offer unambiguous evidence of climate-induced ecosystem changes. Other factors not driven by climate, including selective preservation of some organisms (19), erosion or deepening of outlets, damming by peat accumulation, or subsequent permafrost development, can alter lake records (20). Such problems are overcome to some extent by using multi-proxy approaches, by comparing multiple lake records, and by using spatial networks of archives. Further research on modern ecosystems, especially processes controlling the preservation and modification of proxy records, is still required in many cases to reconcile present and past conditions.

### Lotic Archives

Sedimentary deposits in lotic systems are often poorly preserved compared to lentic systems, owing to the relatively greater reworking of most riverine deposits. However, preservation of at least partial sediment records can occur in fluvial lakes, oxbow lakes, estuaries, and artificial reservoirs. Past river discharge can also be studied by tracking the abundance of lotic diatoms in the sediments of lake basins, such as demonstrated for a lake in the high Arctic (21, 22).

### Terrestrial and Wetland Archives

Tree rings are a traditional source of climate change information, although there are obvious difficulties in applying the method to tundra environments with sparse vegetation. Conifers are, however, abundant within the circumpolar Arctic (particularly in northwestern Canada, Alaska, and Eurasia), with the northernmost conifers in the world located poleward of 72° N on the Taymir Peninsula, northern Siberia (23). Tree-ring widths increase in response to warm-season temperatures and precipitation/moisture status and have been used to reconstruct climate changes, in many cases for more than 400 years into the past (23, 24).

Diatoms, chrysophytes, and other paleolimnological indicators are also preserved in peatlands and may be used to reconstruct peatland development and related water balance and climatic driving forces (9). Records of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  from peat cellulose also provide information on climatic variability (25), although this method has not been widely applied to date in the Arctic. Selective use of pore water from within peat and permafrost has also been utilized to reconstruct the isotopic composition of past precipitation (26, 27), although dating control is often imprecise.

## RECENT WARMING: CLIMATE CHANGE AND FRESHWATER ECOSYSTEM RESPONSE DURING THE HOLOCENE

The climate of the earth has continuously varied since the maximum extent of ice sheets during the late Pleistocene (e.g., 28). The most recent climate warming trend during the industrial period overprints Holocene climate shifts that have occurred due to orbit-induced variations in solar insolation, as well as oscillations produced by local to regional shifts in sea surface temperatures, atmospheric and oceanic circulation patterns, and the extent of land-ice cover (7). During the early Holocene (10000–8000 years BP), orbital variations (the Milankovitch (29) theory of a 41000-year cycle of variation in orbital obliquity) resulted in approximately 8% higher summer insolation and 8% lower winter insolation compared to present-day values poleward of 60° N (30). This directly altered key factors controlling arctic freshwater systems, including precipitation,

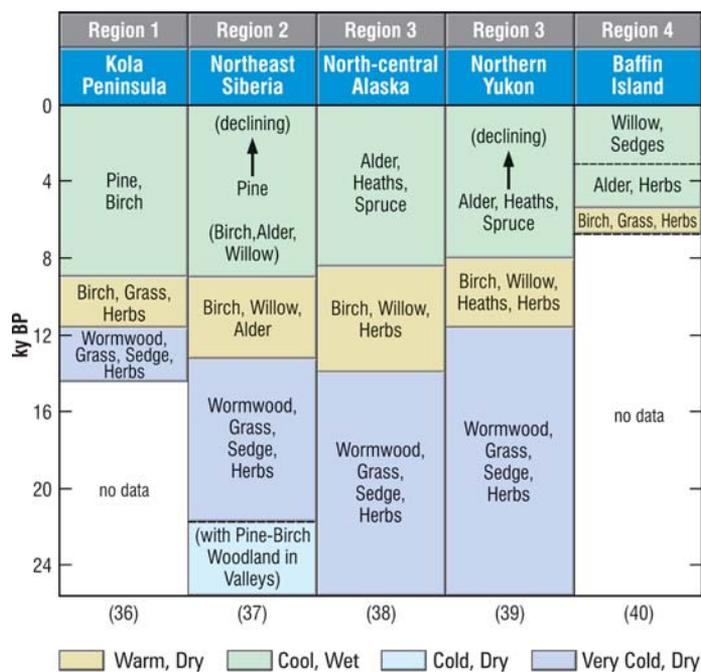


Figure 1. Pollen record of regional arctic climate change (personal communication from: I. Hutchinson, Simon Fraser University, British Columbia, 2004).

hydrology, and surface energy balance. Sea level was also 60 to 80 m below present-day levels, providing an expanded zone (up to several hundred kilometers wide) of nearshore freshwater environments.

During the Holocene, rapidly melting ice sheets presented a shrinking barrier to major airflows, and variations in insolation altered the spatial distribution of atmospheric heating (7). Several climate heating episodes between 11000 and 7700 years BP are attributed to the catastrophic drainage of Lake Agassiz and the Laurentide glacial lakes in North America. Paleogeographic data from this interval suggest that the Laurentide Ice Sheet was almost completely gone, with the possible exception of residual ice masses in northern Québec. In general, most of the Arctic experienced summers 1 to 2 °C warmer than today during the early to middle Holocene (24). A common assumption is that decreases in summer insolation resulted in cooler summers in the late Holocene, which culminated in the Little Ice Age (ca. 1600). This cooling trend ended sometime in the 18th century. Detailed reconstructions of climate and ecosystems in North America at 6000 years BP (28) confirm that the Holocene was also a time of increased moisture, resulting in the spread of peatlands. In the European Arctic, combined evidence from oxygen isotope and pollen inferred precipitation records, cladoceran-inferred lake levels, diatom-inferred lake-water ionic strength, and elemental flux records of erosion intensity into lakes, all suggest more oceanic conditions in the region during the early part of the Holocene than today, with a shift towards drier conditions between approximately 6000 and 4500 years BP (31, 34). In the late Holocene, there has been a general tendency towards increased moisture, resulting in more effective peat formation (32).

Despite pervasive orbit-driven forcings, climate changes during the Holocene varied significantly between regions of the Arctic due to differences in moisture sources (24). In general, arctic Europe, eastern Greenland, the Russian European North, and the North Atlantic were dominated by Atlantic moisture sources; Siberia was dominated by Nordic Seas moisture; Chukotka, the Bering Sea region, Alaska, and the western Canadian Arctic were dominated by Pacific moisture; and northeastern Canada, the Labrador Sea and Davis Strait regions, and western Greenland were dominated by Labrador Sea and Atlantic moisture. The following sections

describe significant regional differences in climate and ecosystem evolution during the Holocene (Fig. 1). Much of the subsequent discussion focuses on historical changes in hydroclimatology (e.g., atmospheric moisture sources) and terrestrial landscape features (e.g., vegetation) in the context of their primary control over the water cycle affecting freshwater ecosystems. More details about these changes can be found in (33, 34).

### Region 1: Arctic Europe, Eastern Greenland, the Russian European North, and the North Atlantic

The present-day climate in northern Fennoscandia is dominated by westerly airflow that brings cyclonic rains to the area, especially during winter (46). The Scandes Mountains of mid-central Sweden mark the boundary between oceanic climate conditions to the west and more continental conditions to the east, especially in northern Finland and Russia, which are strongly influenced by the Siberian high-pressure cell that allows easterly air flow into northern Fennoscandia during winter. Climate and freshwater ecosystem changes during the Holocene have been attributed largely to fluctuations in the prevailing air circulation patterns in the region. Pollen, diatom, chironomid, and oxygen isotope records from lake sediments have been used to reconstruct climate conditions and ecosystem responses during the Holocene (e.g., 42–46). These studies suggest that northern Fennoscandia was a sparse, treeless tundra environment following final disintegration of the Scandinavian Ice Sheet (10000–9000 years BP) until birch (*Betula* spp.) forests spread to the shores of the Arctic Ocean and to an altitude of at least 400 m in the mountains between 9600 and 8300 years BP [see (34) for discussion of changes in terrestrial vegetation]. Increased moisture during this period has been attributed to strengthening of the Siberian High which may have enhanced sea-level pressure gradients between the continent and the Atlantic Ocean, strengthened the Icelandic Low, and produced greater penetration of westerly winter storms and increased snowfall over western Fennoscandia (see also 47). Associated strengthening of westerlies and northward shifts in the Atlantic storm tracks may also have produced higher snowfall in Greenland during this period (7).

The decline of birch forests was accompanied by rapid increases in pine (*Pinus* spp.) forests between 9200 to 8000 years BP in the extreme northeast and 7900 to 5500 years BP in the western and southwestern parts of the region, signaling a shift toward drier summers and increased seasonality (46). Pollen evidence suggests that the late-Holocene treeline retreat in northern Norway and Finland started about 5000 years BP, and included southward retreat of treeline species of both pine and birch, which were subsequently replaced by tundra vegetation. This retreat has been attributed to decreased summer insolation during the latter part of the Holocene. It has also been suggested that later snowmelt and cooler summers gradually favored birch at the expense of pine along the boreal treeline. Similar climate changes may explain peatland expansion in the late Holocene within both boreal and tundra ecozones (46).

The response of aquatic ecosystems to the climate-induced changes during the Holocene has been inferred from lake-sediment and peat stratigraphic records. The very dry period corresponding to shifts from birch to pine corresponds to increasing frequency of diatom and cladoceran taxa indicating lake-level reduction and vegetation overgrowth of numerous lakes (46). Likewise, diatom and cladoceran evidence suggest dry warm summers during the period dominated by pine (~7000–3500 years BP).

There have been a variety of recent quantitative reconstructions of Holocene changes and variability in climatic and environmental variables through analysis of isotopic records and sedimentary remains of pollen, diatom assemblages, and/or chironomid head capsules from arctic and subarctic lakes in northern Sweden (42–45, 48–52). Comparative analyses revealed that the timing and scale of development of historical biotic assemblages were attributable to local geology, site-specific processes such as vegetation development, climate, hydrological setting, and in-lake biogeochemical and ecological processes. Several general climate-related trends were deduced for the region: a decrease in the average annual temperature of approximately 2.5 to 4 °C from the early Holocene to the present; summer temperatures during the early Holocene that were 1.7 to 2.3 °C above present-day measurements; winter temperatures that were 1 to 3 °C warmer than at present during the early Holocene; and a decrease in lake-water pH since the early Holocene.

Collectively, proxy records for closed-basin (i.e., a basin that has very little continuous surface outflow so that water-level variations strongly mirror changes in precipitation or moisture status) lakes suggest that water levels were high during the early Holocene, declined during the mid-Holocene dry period (~6000–4000 years BP), and rose again during the latter part of the Holocene. During the culmination of the Holocene dry period, many shallower water bodies in this region decreased greatly in size or may have dried up entirely (53).

In contrast to often quite distinct changes in physical limnology, changes in chemical limnological conditions have been relatively moderate during lake development in the Fennoscandian Arctic and on the Kola Peninsula (53, 54). Because of changing climate and successional changes in surrounding vegetation and soils, lakes close to the present treeline are typically characterized by a progressive decline in pH, alkalinity, and base cations, and a corresponding increase in DOC over the Holocene. In contrast, lakes in the barren arctic tundra at higher altitudes manifest remarkable chemical stability throughout the Holocene. Excluding the initial transient alkaline period following deglaciation evident at some sites, the long-term natural rate of pH decline in the arctic lakes of the region is estimated to be approximately 0.005 to 0.01 pH units per 100 yr. This is a generally lower rate than those of more southerly sites in boreal and temperate Fennoscandia,

where rates between 0.01 and 0.03 pH units per 100 yr have been observed. No evidence of widespread recent “industrial acidification” is apparent from extensive paleolimnological assessments in arctic Europe (53, 55–57). However, fine-resolution studies from a number of remote lakes in the region demonstrate that aquatic bio-assemblages have gone through distinct changes that parallel the post-19th century arctic temperature increase (56).

## Region 2: Siberia

Siberian climate was affected by increased summer insolation between 10000 and 8000 years BP, which probably enhanced the seasonal contrast between summer and winter insolation and strengthened the Siberian High in winter and the Siberian Low in summer (30). Following final disintegration of the Scandinavian Ice Sheet approximately 10000 to 9000 years BP, cool easterlies were replaced by predominantly westerly flows from the North Atlantic, which now could penetrate western Russia and Siberia (58). Warm, wet summers and cold, dry winters probably dominated the early to mid-Holocene, with more northerly Eurasian summer storm tracks, especially over Siberia (7). Warm periods were generally characterized by warmer, wetter summer conditions rather than by pronounced changes in winter conditions, which remained cold and dry. Pollen reconstructions from peatlands across arctic Russia suggest that temperatures were 1 to 2 °C higher than at present during the late glacial–Holocene transition, which was the warmest period during the Holocene for sites in coastal and island areas. The warmest period of the Holocene for non-coastal areas (accompanied by significantly greater precipitation) occurred between 6000 and 4500 years BP, with notable secondary warming events occurring at about 3500 and 1000 years BP (59).

Pollen evidence from permafrost and peat sequences suggests that boreal forest development commenced across northern Russia and Siberia by 10000 years BP, reached the current arctic coastline in most areas between 9000 and 7000 years BP, and retreated south to its present position by 4000 to 3000 years BP (60). Early forests were dominated by birch, but larch (*Larix* spp.), with some spruce (*Picea* spp.) became prevalent between 8000 and 4000 years BP. The northward expansion of the forest was facilitated by increased solar insolation at the conclusion of the Scandinavian glaciation, and by higher temperatures at the treeline due to enhanced westerly airflow (60). The eventual southward retreat of the treeline to its present-day position is likewise attributed to declining summer insolation towards the late Holocene, as well as cooler surface waters in the Norwegian, Greenland, and Barents Seas (60).

Increases in precipitation in some portions of northern Russia occurred during the interval from 9000 to 7000 years BP, followed by gradual drying to 6000 years BP (27, 59). This has been attributed to strengthening of the sea-level pressure gradients that also affected climate and ecosystems in Region 1 at this time (see 7).

Northward migration of the treeline also had a systematic impact on the ecosystem characteristics of some Siberian lakes. For a lake in the Lena River area, diatom assemblages dated prior to treeline advance were found to be dominated by small benthic *Fragilaria* species, and diatom indicators also suggest high alkalinity and low productivity at this time. Following the treeline advance, lakes shifted to stable diatom assemblages dominated by *Achnanthes* species and low alkalinity, attributed to the influence of organic runoff from a forested landscape. Re-establishment of *Fragilaria*-dominated assemblages and higher alkalinity conditions accompanied the subsequent reversion to shrub tundra. Laing et al. (61) attributed recent

## Box 1

### Northern Québec and Labrador: Long-term climate stability

Northern Québec and Labrador in the eastern Canadian Low Arctic is a landscape dominated by lakes, wetlands, and streams. Few studies have addressed the effects of recent climate change in this region, but a variety of paleolimnological studies have provided insights into long-term change.

This region is comprised of four terrestrial ecozones: “taiga shield” with bands and patches of wetland forest, forest-tundra, and lichen-woodland vegetation; “southern arctic” consisting of shrub tundra; “northern arctic” consisting of true tundra; and “arctic cordillera” (the Torngat Mountains). Major changes in the chemical and biological characteristics of lakes are associated with the transition between these different vegetation types, notably changes in alkalinity and, in particular, colored dissolved organic matter (CDOM; see 66). The darkest water color (greatest CDOM concentrations) is associated with the heavily vegetated wetland-forest catchments, while much lower values occur in lakes completely surrounded by drier lichen woodland and tundra (Fig. 2). As dissolved organic matter has a broad range of effects on high-latitude

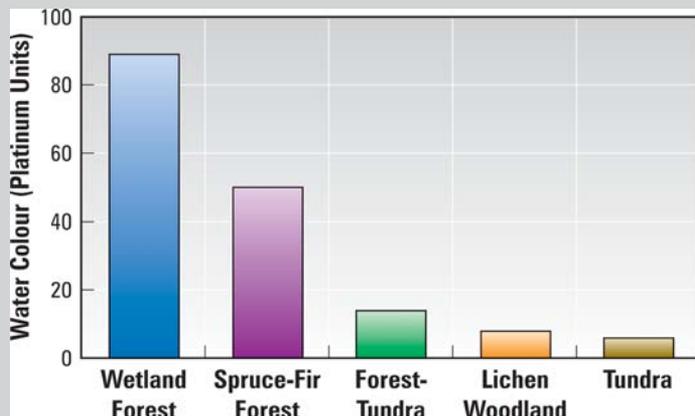


Figure 2. Colored dissolved organic matter (measured by relative water color) in lakes from different vegetation zones in Labrador. Values shown represent the mean of between 7 and 20 lakes (68).

trends over the same period (71, 72).

The paleolimnology of the region also reflects this long-term stability in climate and vegetation. Diatom assemblages in the sediment cores taken from Labrador lakes show very little change over the last 200 years, while there were major shifts in community structure elsewhere in the Arctic (73). Similarly, in a lake at the northern Québec treeline, CDOM and other inferred limnological variables remained relatively stable over the last 3000 years. For example, the mean inferred DOC concentration over this period is 5 mg/l, with a coefficient of variation for 107 strata of only 8% (74). Coastal lakes in this region exhibited major changes associated with plant succession immediately after deglaciation, and isostatic uplift causing the severing of connections with the sea, but relatively constant conditions over the last 1000 years (75–77).

This remarkable stability at timescales of decades, centuries, and millennia suggests that northern Québec and Labrador lakes are likely to experience less short-term climate change relative to other regions of the circumpolar Arctic. Projections from the ACIA-designated climate models, however, suggest that these east–west differences in climate change will largely disappear by 2080 (see 78), by which time the lakes, rivers, and wetlands of northern Québec and Labrador will begin experiencing the climate impacts that are well advanced in other regions.

aquatic ecosystems (67), this implies that any climate-related shift in catchment vegetation is very likely to have major impacts on the limnology of these eastern Canadian lakes.

In the western Canadian subarctic, variations in climate over the last 5000 years caused large shifts in the position of the northern treeline. These shifts resulted in substantial changes in water color, the underwater light regime (including biologically damaging UV radiation exposure), and in the relative importance of benthic versus pelagic production (as indicated by their diatom communities; 64, 65, 69). In contrast, the eastern Canadian subarctic seems to have experienced relatively little change in vegetation structure at the millennial timescale. The stable forest–tundra of northern Québec and Labrador has been referred to as “an ecological museum” (70), and is partly a consequence of the extremely slow pace of northward migration and colonization by black spruce (*Picea mariana*) during periods of warming. This region also appears to be less prone to temperature change owing to the strong marine influence of the Hudson Strait and Labrador Current outflows from the Arctic. Like much of the eastern Canadian Arctic and southern Greenland, this region has shown little temperature change or even cooling from the mid-1960s to the mid-1990s, while most other sectors of the circumpolar Arctic have shown strong warming

declines in alkalinity and minor changes in diatom assemblages to the influx of humic substances from catchment peatlands.

### Region 3: Chukotka, the Bering Sea, Alaska, and Western Arctic Canada

The Laurentide Ice Sheet strongly influenced early Holocene (10000–9000 years BP) climate in northwestern North America, particularly in downwind areas. High albedos, cold surface conditions, and ice-sheet height apparently disrupted westerly airflows (or may possibly have maintained a stationary surface high-pressure cell with anticyclonic circulation), which promoted the penetration of dry, warm air from the southeast (7). Dry conditions were also prevalent at this time in unglaciated areas such as northwestern Alaska and portions of the Yukon, where a 60 to 80 m reduction in sea level increased distances to marine moisture sources by several hundred kilometers. Biological indicators from Alaskan lakes suggest dry, more productive conditions, with lower lake levels between 11000 and 8000 years BP, followed by a gradual shift to modern moisture levels by 6000 years BP (20, 62).

Terrestrial vegetation (and the northern treeline) clearly indicates a warmer-than-present early Holocene (e.g., 63). Veg-

etation shifts reconstructed mainly from fossil pollen evidence reveal the northward advance and southward retreat of the boreal forest in western North America, which has been attributed mainly to short-term changes in atmospheric circulation and associated storm tracks (i.e., shifts in the mean summer position of the Arctic Frontal Zone; 64). Higher temperatures and increased moisture during the mid-Holocene (especially between about 5000 and 3500 years BP) also produced episodes of 250 to 300 km northward advances of the treeline that are recorded in the isotopic, geochemical, diatom, and fossil-pollen records of lakes near present-day treeline in the Yellowknife area of Canada (64). Additional evidence for significant changes in diatom community structure (shifts from planktonic to benthic forms) and increased productivity is recorded in lake sediments during this mid-Holocene warming interval (ca. 6000 to 5000 years BP) in the central Canadian subarctic (14, 65). This period was also accompanied by significant increases in DOC in lakes, lower water transparency, and less exposure to photosynthetically active radiation (PAR) and UV radiation in the water column. On the Tuktoyaktuk Peninsula (near the Mackenzie Delta), forest limits were at least 70 km north of the current treeline between 9500 and 5000 years BP (e.g., 63). Permafrost zones

were also presumably located north of their present-day distribution during this period. In general, present-day forest types were established in Alaska by 6000 years BP and northwestern Canada by approximately 5000 years BP.

Prolonged development and expansion of peatlands in North America commencing between 8000 and 6000 years BP have been attributed to progressive solar-insolation driven moisture increases towards the late Holocene (7).

#### **Region 4: Northeastern Canada, Labrador Sea, Davis Strait, and West Greenland**

The climate change and ecosystem response in northeastern Canada is distinguished from northwestern regions by generally colder conditions during the early Holocene because of delayed melting of ice sheet remnants until close to 6000 years BP. Consequently, tundra and taiga with abundant alder (*Alnus* spp.) covered more of Labrador and northern Québec than at present (28). Shrub tundra and open boreal forest were also denser than at present (28). Warming in the eastern Arctic reached a maximum shortly after 6000 years BP, with higher sea surface temperatures and decreased sea-ice extent. Peatland expansion was apparently similar to that of northwestern Canada, and is likewise attributed to insolation-driven increases in moisture and cooler conditions in the late Holocene. In contrast with other parts of the circumpolar north, this region has had a relatively stable climate over the last few thousand years but may experience significant temperature increases in the future (see Box 1).

#### **CLIMATE CHANGE AND FRESHWATER ECOSYSTEM RESPONSE DURING THE INDUSTRIAL PERIOD**

An abrupt shift in the rate of climate and related ecosystem changes occurred around 1840 that distinguish these impacts from those due to climate change observed during the preceding part of the Holocene. A compilation of paleoclimate records from lake sediments, trees, glaciers, and marine sediments (24) suggests that in the period following the Little Ice Age (~1840 until the mid-20th century), the circumpolar Arctic experienced unprecedented warming to the highest temperatures of the preceding 400 years. The last few decades of the 20th century have seen some of the warmest periods recorded, thus continuing this early industrial trend. The effects of this increase in temperature include glacial retreat, thawing permafrost, melting sea ice, and alteration of terrestrial and aquatic ecosystems. These climate changes are attributed to increased atmospheric concentrations of greenhouse gases, and to a lesser extent shifts in solar irradiance, decreased volcanic activity, and internal climate feedbacks. Examples of profound responses to the recent temperature increases relevant to freshwater systems are numerous. Selected examples are given below.

Sorvari and Korhola (79) studied the recent (~150 years) environmental history of Lake Saanajärvi, located in the barren tundra at an elevation of 679 m in the northwestern part of Finnish Lapland. They found distinctive changes in diatom community composition with increasing occurrences of small planktonic diatoms starting about 100 years ago. Since no changes in lake water pH were observed, and because both airborne pollution and catchment disturbances are known to be almost nonexistent in the region, they postulated that recent arctic temperature increases are the main reason for the observed ecological change.

To further test the hypothesis that temperature increases drove the system, (80) analyzed additional sedimentary proxy indicators from Lake Saanajärvi. The biological and sedimentological records were contrasted with a 200-year climate record

specifically reconstructed for the region using a compilation of measured meteorological data and various proxy sources. They found synchronous changes in lake biota and sedimentological parameters that seemed to occur in parallel with the increasing mean annual and summer temperatures starting around the 1850s, and hypothesized that the rising temperature had increased the metalimnion steepness and thermal stability in the lake, which in turn supported increasing productivity by creating more suitable conditions for the growth of plankton.

Sorvari et al. (56), using high-resolution (3–10 yr) paleolimnological data from five remote and unpolluted lakes in Finnish Lapland, found a distinct change in diatom assemblages that parallels the post-19th century arctic temperature increase detected by examination of regional long-term instrumental data, historical records of ice cover, and tree-ring measurements. The change was predominantly from benthos to plankton and affected the overall diatom richness. A particularly strong relationship was found between spring temperatures and the compositional structure of diatoms as summarized by principal components analysis. The mechanism behind the change is most probably associated with decreased ice-cover duration, increased thermal stability, and resultant changes in internal nutrient dynamics.

Douglas et al. (81), using diatom indicators in shallow ponds of the high Arctic (Ellesmere Island), found relatively stable diatom populations over the past 8000 years, but striking successional changes over the past 200 years. These changes probably indicate a temperature increase leading to decreased ice- and snow-cover duration and a longer growing season (81). Although temperature changes are difficult to assess, they were sufficient to change the pond communities. In these ponds, there are no diatoms in the plankton; however, a shift occurred from a low-diversity, perolithic (attached to rock substrates) diatom community to a more diverse periphytic (attached to plants) community living on mosses.

Diatom indicators in lakes also show shifts in assemblages, most likely caused by temperature increases over the past 150 years. Rühland et al. (82) documented changes in 50 lakes in western Canada between 62° and 67° N, spanning the treeline. Shifts in diatoms from *Fragilaria* forms to a high abundance of the planktonic *Cyclotella* forms are consistent “with a shorter duration of ice cover, a longer growing season, and/or stronger thermal stratification patterns,” such as a shift from unstratified to stratified conditions. Char Lake on Cornwallis Island, Canada (74° N) is the most-studied high-arctic lake. Recent studies (83) show no change in water quality over time but do show a subtle shift in diatom assemblages as evidenced in the paleolimnological record. These changes are consistent with recent climate changes (1988–1997) and are probably a result of “reduced summer ice cover and a longer growing season.” Walsh et al. (84) reviews recently documented observations of the general, although not ubiquitous, decline in the duration of lake and river ice cover in the Arctic and subarctic.

Chrysophyte microfossils show changes that parallel diatom changes (85) and are also probably related to reduced ice-cover duration. For example, chrysophyte microfossils were absent or rare in Sawtooth Lake (Ellesmere Island, 79° N) over the past 2500 years but suddenly became abundant 80 years ago. Similarly, in Kekerturnak Lake Baffin Island, 68° N), planktonic chrysophytes increased greatly in the upper sediments dated to the latter part of the 20th century. In contrast, lakes in regions without temperature increases show no change in sediment-based indicators. For example, Paterson et al. (86) found no change in chrysophyte and diatom indicators over the past 150 years in the sediment of Saglek Lake (northern Labrador, Canada).

## CONCLUSIONS

The stability, sensitivity, rate and mode of the response of freshwater ecosystems to past climate changes provides a valuable tool for determining the scope of potential responses to future climate changes. This article reviews the various forms of ecosystem-based climate proxies that have been used in assessing past arctic change but points to a basic in paleoclimatic analyses of lentic over lotic environments, primarily because of greater disturbance in the latter as a result of the reworking of riverine deposits. Lentic records extend back to the end of the Pleistocene and deglaciation of the circumpolar Arctic. During the early Holocene a much larger arctic freshwater zone existed compared to today primarily because of the extensive near-shore environment associated with lower sea level. In general, the Holocene was characterized by variations in insolation/heat balances and airflow patterns, partly due to changes in the shrinking effect of glacier coverage, all of which would have significantly affected the hydrology and by extension, freshwater ecosystems. The spatial and temporal nature of such effects are highly variable throughout the circumpolar Arctic as reviewed in this manuscript. Of particular note were major drying (wetting) periods that led to the contraction (expansion) of shallow water bodies, most notably including peatlands.

In the period following the Little Ice age, paleolimnological records derived from various lake biota and sedimentological data reflect the general warming trend that has occurred over this period and suggest links to associated changes in freshwater characteristics, such as ice-cover duration and thermal stratification patterns. These records provide a baseline against which future effects of climate change can be both projected and measured.

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