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Source: *AMBIO: A Journal of the Human Environment*, 35(7) : 347-358

Published By: Royal Swedish Academy of Sciences

URL: [https://doi.org/10.1579/0044-7447\(2006\)35\[347:CCEOHO\]2.0.CO;2](https://doi.org/10.1579/0044-7447(2006)35[347:CCEOHO]2.0.CO;2)

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Climate Change Effects on Hydroecology of Arctic Freshwater Ecosystems

In general, the arctic freshwater-terrestrial system will warm more rapidly than the global average, particularly during the autumn and winter season. The decline or loss of many cryospheric components and a shift from a nival to an increasingly pluvial system will produce numerous physical effects on freshwater ecosystems. Of particular note will be reductions in the dominance of the spring freshet and changes in the intensity of river-ice breakup. Increased evaporation/evapotranspiration due to longer ice-free seasons, higher air/water temperatures and greater transpiring vegetation along with increase infiltration because of permafrost thaw will decrease surface water levels and coverage. Loss of ice and permafrost, increased water temperatures and vegetation shifts will alter water chemistry, the general result being an increase in lotic and lentic productivity. Changes in ice and water flow/levels will lead to regime-specific increases and decreases in habitat availability/quality across the circumpolar Arctic.

INTRODUCTION

Arctic freshwater systems are particularly sensitive to climate change because numerous hydro-ecological processes respond to even small changes in climate. These processes may adjust gradually to changes in climate, or abruptly as environmental or ecosystem thresholds are exceeded (Box 1). This is especially the case for cryospheric components that significantly affect the water cycle of lakes, rivers, and ponds; the habitat characteristics of these freshwater systems; and the flora and fauna that occupy them. In the case of large arctic rivers (e.g., the Lena, Mackenzie, Ob, and Yenisey), the effects of climate change must be evaluated for areas outside of as well as within the Arctic. The dynamics of such large systems depend on hydrologic processes prevailing within their water-rich headwaters in more temperate southern latitudes. In addition, many of these headwater areas are regulated in some way, a factor that may interact in some way with downstream arctic climate change impacts.

Prior to considering the specific effects of climate change on arctic freshwater systems, it is useful to place the climate projections generated by the five ACIA-designated atmosphere-ocean general circulation models (AOGCMs) for the Arctic as a whole into a more suitable freshwater context. For the most part, this requires focusing on model projections for the major arctic terrestrial landscapes, including some extra-arctic head-

water areas, since these are the domains of freshwater systems. The following paragraphs review the ACIA-designated model projections (primarily for the final time slice, 2071–2090, to illustrate the most pronounced changes) and, through additional processing of the model projections, provide a perspective on how such changes may be important to broad-scale features of arctic freshwater ecosystems, and a background template for the subsequent discussions of specific effects.

For the area north of 60° N, the five ACIA-designated models project that the mean annual temperature will increase by 3.7 °C (five-model average) between the 1981–2000 baseline and the 2071–2090 time slice, or approximately twice the projected increase in global mean annual temperature (2). At a global scale, AOGCMs used in the Third Assessment Report of the Intergovernmental Panel on Climate Change (3) project that it is very likely that nearly all land areas, which include freshwater systems, will warm more rapidly than the global average, particularly during the cold season at northern high latitudes. Within the Arctic, the spatial distribution of the projected temperature increases in terrestrial areas is associated with even greater projected temperature increases over the central Arctic Ocean. For example, the five-model average projects that autumn (October–December) temperatures over large areas of the Arctic Ocean will increase by up to 9 °C by 2071–2090 compared to the 1981–2000 baseline (2). Adjacent to the Arctic Ocean, the models project substantial temperature increases for extensive terrestrial areas, with the largest projected temperature increases closest to the coastal margins and decreasing to the south.

This pattern of temperature increases is likely to have serious implications for high-latitude coastal areas such as the Russian polar desert and northern tundra, where temperature and associated species distribution gradients are steep (e.g., vascular species abundance increases fivefold from north to south on the Taymir Peninsula; see 4). Figure 1a shows the spatial pattern of October warming projected for the 2071–2090 time slice. (Note the spatial congruence of warming between the ocean and the adjacent arctic coastal zone and the extension to more southerly latitudes.) Areas where projected temperature increases are particularly pronounced include northern Siberia and the western portions of the Canadian Archipelago. Notably, however, the maximum projected air temperature increases in these areas are about 5 °C (greatest near the coasts), compared to the almost two-fold greater projected increases in temperature over the Arctic Ocean. Such pronounced potential temperature increases in freshwater systems in October are particularly important because this is typically the time when freshwater lake and river systems along the coastal margins

Box 1

Thresholds of response: step changes in freshwater systems induced by climate change.

Some climate change effects projected for arctic freshwaters are likely to result in small, slow responses in the environment; other changes are likely to exceed environmental or ecosystem thresholds and cause a dramatic switch in organisms or a change of state of the system. Thresholds may be physical (e.g., permafrost is likely to begin to slowly thaw when the mean annual air temperature approaches 0 °C); chemical (e.g., the bottom waters of a lake are likely to lose all oxygen when lake productivity increases or allochthonous carbon increases); or biological (e.g., insect larvae frozen in the bottom of tundra ponds will die when their temperature falls below -18 °C (1)). While thresholds are only a part of the whole picture of response, they are critical to the understanding and assessment of the full scope of climate change impacts.

One obvious physical threshold is the amount of heat necessary to melt the ice cover of a lake. At the northern limit of the terrestrial Arctic, such as on Ellesmere Island, there are lakes that have only recently begun to have open water during the summer; other lakes now have open water for more summers every decade than in the past. Sediment records of algae, in particular diatom species and chrysophyte abundance, show that in Finland and northern Canada, lakes were ice-bound for thousands of years but conditions began to change about 150 years ago. With open water, the algal community shifts from a predominance of benthic diatoms to planktonic forms, and chrysophytes begin to occur. This is the result of an increase in summer air temperatures caused by climate change and the earlier onset of melt. Some scientists believe that the likely increase in growing-season length may also be important in controlling algal species. Shifts in species composition at the level of primary producers are also likely to have consequences for higher trophic levels through the alteration of food pathways. This could possibly lead to local extirpation of benthic and planktonic animals, as well as overall shifts in productivity.

Another physical threshold is the onset of stratification in lakes. Once lakes begin to have open water, wind-driven water circulation becomes one of the controls of biological processes. Almost all lakes have a period of complete mixing of the water column immediately after the ice cover disappears. Very cold waters may continue to circulate for the entire summer so that each day algae spend a significant amount of time in deep waters where there is not enough light for growth. When a lake stratifies (i.e., when only the uppermost waters mix), algae have better light conditions and primary production increases. The higher temperatures in the upper waters increase the rates of all biotic processes. There is a threshold, probably tied to increased primary production, when entirely new trophic levels appear. For example, the sediment record from a lake in Finland shows that Cladocera, a type of zooplankton, began to appear around 150 years ago. Most lakes in the Arctic already exhibit summer stratification, so this threshold will apply mostly to lakes in the far north.

When air temperatures increase above a mean annual air temperature of -2 °C, permafrost begins to thaw. When the upper layers of ice-rich permafrost thaw, the soil is disturbed; lakes may drain, and ponds form in depressions. In eastern Siberia, newly thawed soils that are rich in organic matter slump into lakes. Microbial action depletes the oxygen in the lake allowing the bacteria to produce so much methane that the lakes and ponds become a significant source of this greenhouse gas, and enhance an important feedback to the climate system. This threshold is likely to affect lakes in the more southerly regions of the Arctic.

It is well known that lakes surrounded by shrubs and trees contain much more colored dissolved organic matter (CDOM) than lakes in the tundra zone. The CDOM comes from the organic matter produced by plants and modified by soil microbes. It strongly absorbs light, such that the algae of the upper waters become light limited and primary production is reduced. This may also be accompanied by a shift towards increasing primary production by attached algae in the shallow inshore zone relative to offshore planktonic production. The threshold described here is related to the treeline, often demarcated by patches rather than a continuous zone of vegetation. As air temperatures increase over the 21st century these patches are likely to expand, fuse, and move further north, resulting in a slowly moving band of affected lakes. Extreme polar-desert catchments in the high Arctic are very likely to experience their first arrival of higher plants, and a sudden increase in the transfer of organic materials from land to water.

As lakes warm, some species or populations of species will probably reach a temperature threshold for survival. This threshold is linked to increases in the rate of metabolism and growth. For example, a bioenergetic model based on laboratory studies projects that the young-of-the-year lake trout in northern Alaska will not obtain enough food for growth if their metabolic rate rises in response to a temperature increase of a degree or so. Evidence from field studies of a stream fish, the Arctic grayling (*Thymallus arcticus*), also suggests that a population at the northern limit of its distribution is unlikely to survive an increase of only a few degrees in summer water temperatures. Both these examples are of fish species at the northern limit of their distribution. Other types of widely distributed fish, such as whitefish (*Coregonus* spp.) and Arctic char (*Salvelinus alpinus*), are less likely to be affected unless new competing species arrive from southerly regions.

A different type of threshold involves a shift in the ecological behavior of migratory fish such as the Arctic char. In many arctic rivers, char migrate to the sea for some months every year; the productive marine food web allows them to grow to a large size. Local fishers harvest many of these sea-run fish in the rivers each time the fish congregate and migrate. When freshwaters become more productive, migrations to the sea are projected to decrease and may eventually cease, thus the char are likely to remain in freshwater rivers and lakes for the entire year. These freshwaters are much less productive than the marine ecosystems; therefore, adult freshwater char are likely to be much smaller than are migrating char. As a result of climate change, a valuable food resource for arctic peoples is likely to change with respect to sizes available, and could possibly be lost.

currently experience freezeup. Employing a typical rate of change for freeze-up of 1 day per 0.2 °C increase in temperature (5), the projected temperature increases could cause delays of up to 25 days in freeze-up by 2071–2090. This is likely to have the greatest effect on higher-latitude, near-coastal freshwater systems (see section on general hydro-ecology and 6).

Even more dramatic temperature increases are projected for coastal land areas in November (Fig. 1b). Significant temperature increases are projected for most coastal areas in Region 3 and more southerly latitudes in Region 2, including the headwater regions of the major Siberian Arctic rivers below 60°N (see 7 for Regions). Latitudinal gradients of temperature increases are especially important for arctic freshwater systems because of the influence of extra-arctic basins on the timing and magnitude of flow in the major northward-flowing arctic rivers. In the case of Region 2, projected temperature increases in November south of 60° N are significant because this is typically the month that marks the beginning of major snow accumulation. Similar to the delay in freeze-up, such higher temperatures

would effectively decrease the length of time available to accumulate a winter snowpack. This would subsequently be reflected in the magnitude of the spring snowmelt that forms the major hydrologic event of the year at northern latitudes and is known to significantly affect downstream arctic river and delta systems. The effect of a reduced period of winter snow accumulation on the freshet magnitude, however, is likely to be offset by the projected increase in winter precipitation. The terrestrial regions of North America and Eurasia are among the areas with the greatest projected precipitation increases; similar to temperature, the largest increases are projected for autumn and winter (2). Although caution must be used in interpreting regional trends from the simulated precipitation patterns because of large variations in model projections, the average of the five ACIA-designated model projections also shows winter increases in precipitation for the extra-arctic headwater regions of the large northern rivers (Fig. 2). The degree to which this would compensate for the reduced duration of winter snow accumulation, however, requires detailed regional analysis.

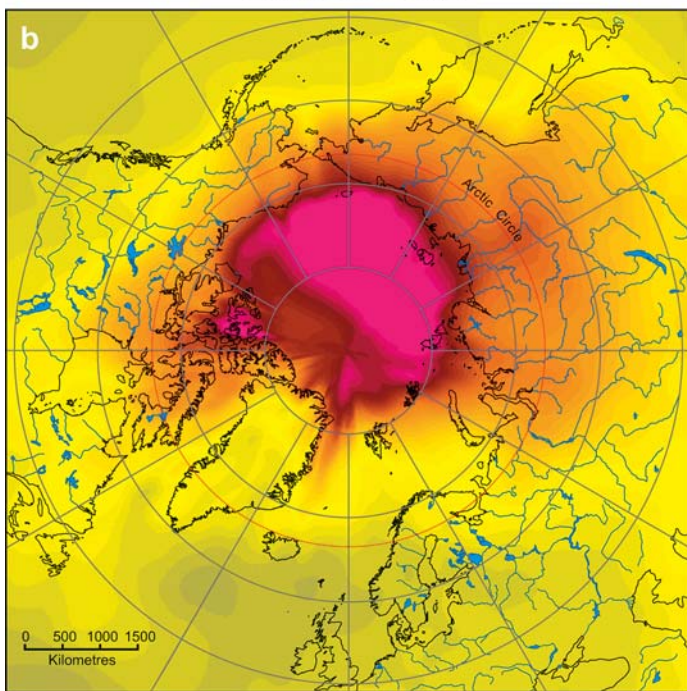
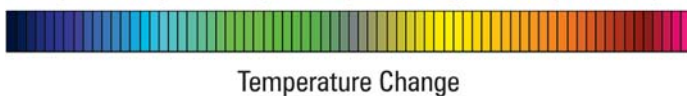
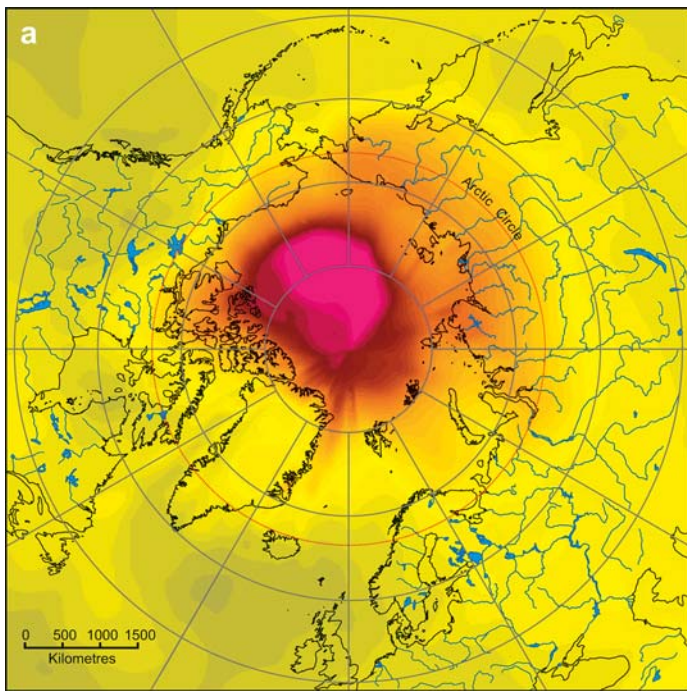


Figure 1. Changes in mean monthly air temperature (°C) between 1981–2000 and 2071–2090 projected by the ACIA-designated models (five-model average) for (a) October and (b) November.

Over the terrestrial regions of the northern latitudes, it is the cold season (defined here as October to May, the current period of dominant snow and ice cover for freshwater systems) that is characterized by the steepest latitudinal gradients in projected temperature increases. Figure 3 displays the projected changes in average temperature (from the ACIA 1981–2000 baseline) over terrestrial areas for the four ACIA regions broken into three latitudinal bands of 70°–85°, 60°–70°, and 50°–60° N. The latter represents the zones of higher precipitation that feed the major arctic rivers in Region 2 (Lena, Ob, and Yenisey) and

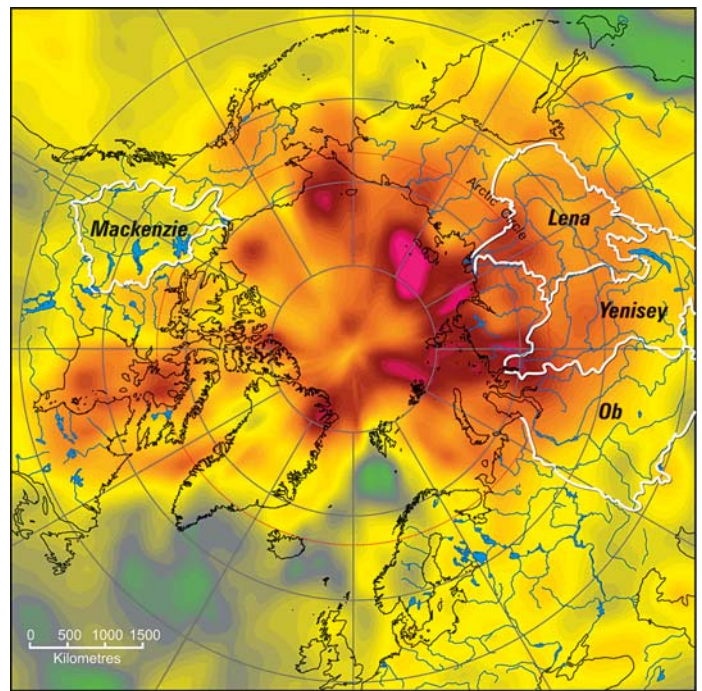


Figure 2. Percentage changes in November to April precipitation between 1981–2000 and 2071–2090 projected by the ACIA-designated models (five-model average). The basins of four major arctic rivers are also shown.

eastern Region 3 plus western Region 4 (Mackenzie River). The steepest latitudinal gradients in projected cold-season temperature increases are evident in Regions 1 and 3, becoming particularly magnified in the latter by 2071–2090, whereas Region 4 shows a slight decrease in the level of warming with latitude. Hence, except for Region 4, it appears that with continued temperature increases the higher-latitude zones will continue to experience the relatively highest degree of warming. This would lead to a reduction in the thermal gradient along the course of some of the major arctic rivers. If such reductions prevail during particular parts of the cold season, they are likely to have major implications for the dynamics of particular hydrologic events such as the spring freshet and ice breakup.

In general, the most severe spring floods on cold-region rivers are associated with a strong climatic gradient between the headwaters and the downstream reaches – typically from south to north on most large arctic rivers (e.g., 8). In such cases, the spring flood wave produced by snowmelt must “push” downstream into colder conditions, and hence towards a relatively competent ice cover that has experienced little thermal decay. Changes in the strength of this climatic gradient would alter the severity of breakup and the associated flooding. Figure 4a illustrates the change in average air temperature projected for April 2071–2090. This is currently the month of freshet initiation, with May the primary month of freshet advance, in the southern headwaters of the major arctic rivers. With projected advances in the timing of ice and flow conditions (see also 6), April should become the primary month of freshet advance by 2071–2090. Of particular note in Figure 4a are the substantial projected temperature increases in the downstream areas of the major Russian rivers. Such high-latitude temperature increases are likely to lead to less severe ice breakups and flooding as the spring flood wave pushes northward. A

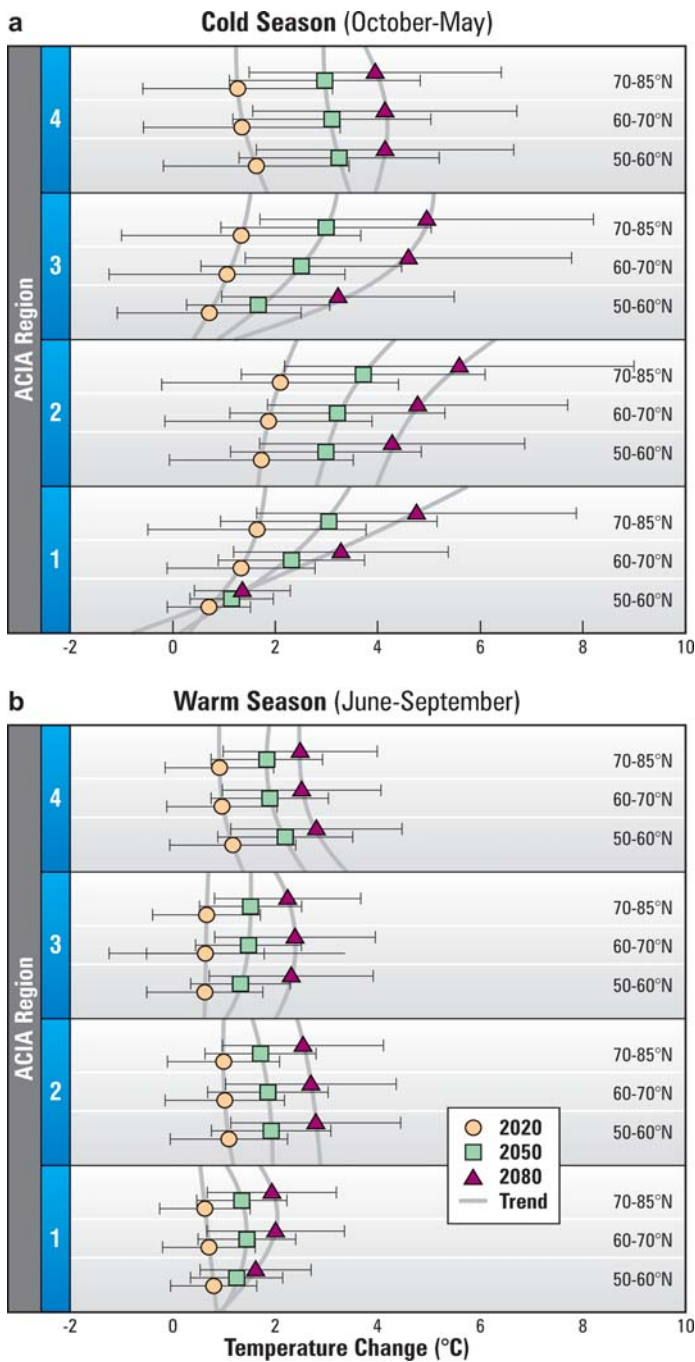


Figure 3. Changes in mean air temperature projected by the ACIA-designated models (five-model average) for the land areas of the four ACIA regions at three time slices in three latitudinal bands. Error bars represent standard deviation from the mean. The (a) cold season (October–May) and (b) warm season (June–September) were divided based on approximate ice-covered and open-water conditions prevailing in the current climate for major freshwater systems located in the 60°–70° N band. Longer (shorter) duration ice-covered periods prevail in the more northerly (southerly) latitudinal band.

comparable degree of high-latitude temperature increase is absent for the Mackenzie River. Of additional note in Figure 4 is the degree of warming projected to occur in the headwater regions of the three large Russian rivers during April and March. This is very likely to result in an early onset of snowmelt along these rivers. Again, however, a comparable degree of headwater warming and hence snowmelt runoff is not projected for the Mackenzie Basin. This regional dichotomy is likely to produce future differences in the spring timing of lake and river-ice breakup and associated freshet, including the ultimate export of freshwater to the Arctic Ocean.

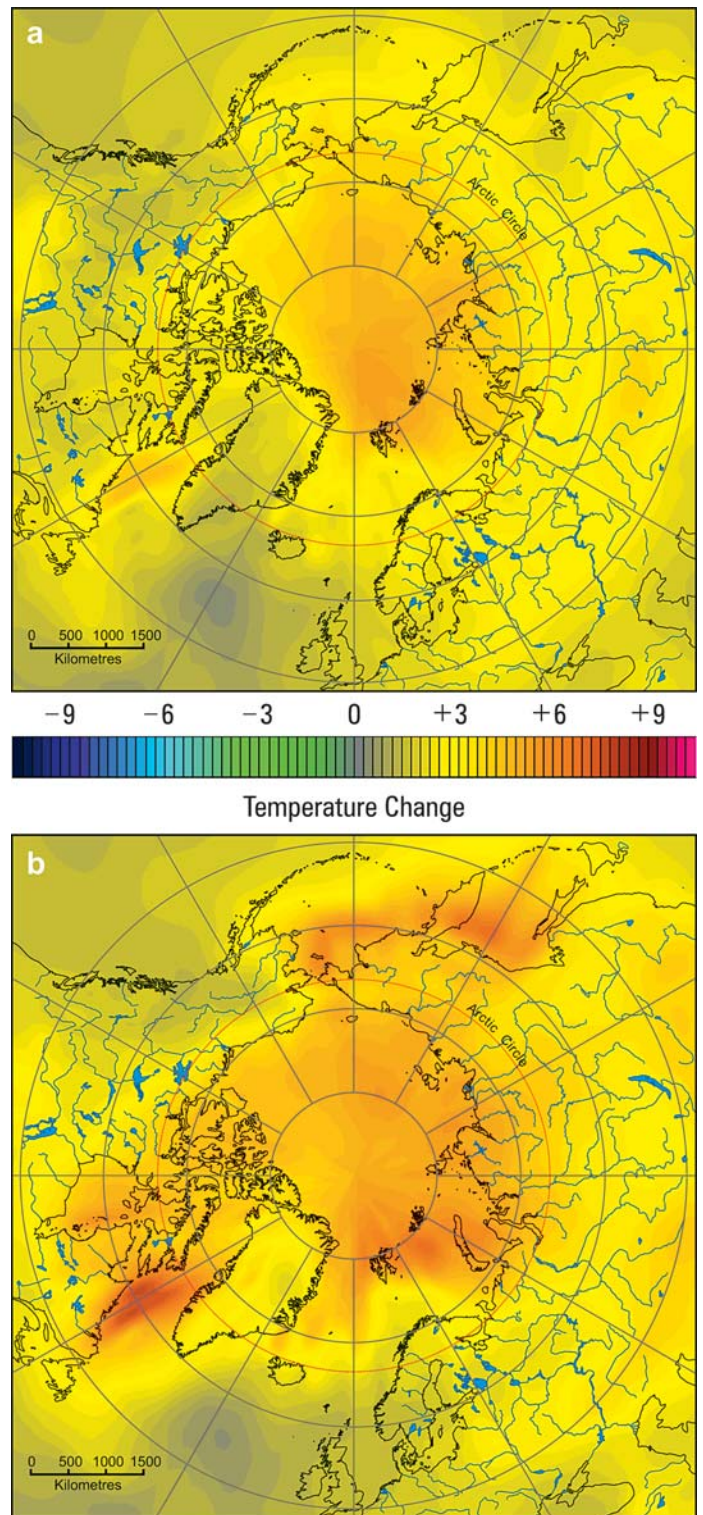


Figure 4. Changes in mean air temperature (°C) between 1981–2000 and 2071–2090 in (a) April and (b) March projected by the ACIA-designated models (five-model average).

Although the smallest temperature increases are projected for the open-water warm season in all regions and at all latitudes (Fig. 3b), even the projected ~1 to 3 °C temperature increase is likely to significantly increase evaporative losses from freshwater systems, especially with a shortened ice season, and via evapotranspiration from the terrestrial landscape that feeds them. Similar to changes in winter snowpack, increases in precipitation could offset such temperature-induced evaporative losses, but the five-model average projects that precipitation increases will be smallest during the summer. More detailed

consideration of the changes and effects on cold-regions hydrology that could result from the changes in climate projected by the ACIA-designated models are provided below and in (6).

EFFECTS ON HYDRO-ECOLOGY OF CONTRIBUTING BASINS

The regional patterns of projected changes in temperature and precipitation reviewed in the previous section are useful to understand some of the broad-scale effects that may occur. Specific effects, however, will be much more diverse and complex, even within regions of similar temperature and precipitation changes, because of intra-regional heterogeneity in freshwater systems and the surrounding landscapes that affect them. For example, elevational difference is one physical factor that will produce a complex altered pattern of snow storage and runoff. Although warmer conditions are very likely to reduce the length of winter, snow accumulation could either decrease or increase, with the latter most likely to occur in higher-elevation zones where enhanced storm activity combined with orographic effects will probably increase winter snowfall. Increased accumulation is likely to be most pronounced at very high elevations above the elevated freezing level, where the summer season is likely to remain devoid of major melt events, thereby creating the conditions for the preservation of more semi-permanent snowpacks at high altitudes (9). In contrast, temperature increases at lower elevations, especially in the more temperate maritime zones, are likely to increase rainfall and rain-on-snow runoff events. Snow patterns will be affected by a number of other factors, including vegetation, which is also projected to be altered by climate change (10). For example, shifts from tundra vegetation to trees have led to greater snow interception and subsequent losses through sublimation (e.g., 11), whereas shifts from tundra to shrubs have been shown to reduce snow losses (12), thereby affecting the magnitude of the snowpack available for spring melt.

An advance of the spring warming period means that snowmelt will occur during a period of lower insolation, which, other things being equal, will lead to a more protracted melt and less intense runoff. Traditional ecological knowledge indicates that through much of northern Canada, including the western Canadian Arctic and Nunavut, spring melt is already occurring earlier than in the past, and spring air temperatures are higher (13), although observations near eastern Hudson Bay indicate a delay in the initiation of spring melt (14). See Huntington et al. (15) for local accounts of such changes in the Arctic. The effects of early and less intense spring melt will be most dramatic for catchments wholly contained within the northern latitudes, where snowmelt forms the major and sometimes only flow event of the year. Reductions in the spring peak will be accentuated where the loss of permafrost through associated warming increases the capacity to store runoff, although there will also be a compensating increase in summer base flow. Overall, the magnitude and frequency of high flows will decline while low flows will increase, thereby flattening the annual hydrograph. This impact is similar to that observed as a result of river regulation, and hence will tend to compound such effects.

Loss of permafrost or deepening of the active layer (seasonal melt depth; see Walsh et al. (6) for changes in permafrost) will also reduce the peak response to rainfall events in summer, increase infiltration, and promote groundwater flow. This is consistent with the analogue of northern basins where those with less permafrost but receiving comparable amounts of precipitation have a lowered and smaller range of discharge (16). Changes in the rate of evapotranspiration and its seasonal duration will also directly affect stream runoff from permafrost

basins. As suggested by the modeling results of Hinzman and Kane (17) for areas of Alaska, the greatest reduction in summer runoff is likely to occur in years experiencing light, uniformly spaced rainfall events whereas in years characterized by major rainfalls comprising most of the summer precipitation, total runoff volume is likely to be affected least.

Changes in the water balance will vary by regional climate and surface conditions, but particular areas and features are believed to be especially sensitive to such alterations. Such is the case for the unglaciated lowlands of many arctic islands where special ecological niches, such as found at Polar Bear Pass on Bathurst Island or Truelove Lowland on Devon Island, are produced by unique hydro-climatic regimes and are largely dependent on ponded water produced by spring snowmelt. On a broad scale, arctic islands and coastal areas are likely to experience significant changes in local microclimates that will probably affect water balance components, especially evaporation rates. Here, longer open-water seasons in the adjacent marine environments are likely to enhance the formation of fog and low clouds and reduce associated solar radiation. Increased water vapor and lower energy flux would thereby offset any potential increase in evaporation resulting from higher air temperatures (16).

Large regional differences in water balance will also occur because of differences in plant communities (see also 18). For example, surface drying of open tundra is restricted when non-transpiring mosses and lichens overlie the tundra. Over the longer term, a longer growing season combined with a northward expansion of more shrubs and trees will very probably increase evapotranspiration. Quite a different situation is very likely to exist over the multitude of wetlands that occupy so much of the northern terrain. Although evaporation is inhibited after initial surface drying on those wetlands covered by sphagnum moss or lichen, evapotranspiration continues throughout the summer in wetlands occupied by vascular plants over porous peat soils, and only slows as the water table declines. Higher summer temperatures have the ability to dry such wetlands to greater depths, but their overall storage conditions will depend on changes in other water balance components, particularly snowmelt and rainfall inputs.

As the active layer deepens and more unfrozen flow pathways develop in the permafrost, an enhancement of geochemical weathering and nutrient release is very likely (e.g., phosphorus; 19 see also 6). Ultimately, this is very likely to affect productivity in arctic freshwater systems such as Toolik Lake, Alaska (Box 2). In the short term, the chemical composition of surface runoff and groundwater flows is very likely to change. In addition, suspended sediment loads will very probably increase as a result of thermokarst erosion, particularly in ice-rich locations. Suspended sediment and nutrient loading of northern freshwater systems will probably also increase as land subsidence, slumping, and landslides increase with permafrost degradation, as traditional ecological knowledge has documented in the western Canadian Arctic where the depth of the active layer has increased (13). Thermokarst erosion is very likely to continue until at least the large near-surface ice deposits are depleted and new surface flow patterns stabilize. Such fluvial-morphological adjustment is likely to be very lengthy, of the order of hundreds of years, considering the time that has been estimated for some northern rivers to reach a new equilibrium after experiencing a major shift in their suspended-sediment regimes (e.g., 20). A major reason for such a protracted period is the time it takes for new vegetation to colonize and stabilize the channel landforms. The stabilization that will occur in the Arctic under climate change is further complicated by the projected change in vegetation regimes, particularly the northward advance of shrubs and trees (see 10).

Box 2

Ecological transitions in Toolik Lake, Alaska, in the face of changing climate and catchment characteristics.

Toolik Lake (maximum depth 25 m, area 1.5 km²) lies in the foothills north of the Brooks Range, Alaska, at 68° N, 149° W. The river study site is the headwaters of the Kuparuk River. Details of the research project and related publications are available on the Arctic Long-Term Ecological Research site (<http://ecosystems.mbl.edu/ARC/>). The mean annual temperature of the area is -9 °C, and annual precipitation is approximately 300 to 400 mm. Permafrost is 200 m thick with an active layer up to 46 cm deep. Acidic tussock tundra covers the hillslopes. Sedges dominate a small area of wetlands in the study site, while the dry uplands have a cover of lichens and heaths. Lakes and streams are ultra-oligotrophic, and are ice-free from July to September with strong summer stratification and oxygen saturation. Stream flow is nival, and carries DOC-enriched spring runoff from peaty catchments to Toolik Lake. Primary producers in Toolik Lake consist of 136 species of phytoplankton, dominated by chrysophytes with dinoflagellates and cryptophytes, as well as diatoms. Annual primary productivity averages 12 g C/m² and is co-limited by nitrogen and phosphorus. Zooplankton are sparse. Fish species are lake trout (*Salvelinus namaycush*), Arctic grayling (*Thymallus arcticus*), round whitefish (*Prosopium cylindraceum*), burbot (*Lota lota*), and slimy sculpin (*Cottus cognatus*), which feed on benthic chironomid larvae and snails, the latter controlling epilithic algae in the lake. Dissolved organic carbon drives microbial productivity (5–8 g C/m²/yr).

The average air temperature of northern Alaska has increased by nearly 2 °C over the past 30 years. Warming of Alaskan waters will possibly have a detrimental effect on adult grayling, which grow best during cool and wet summers and which may actually lose weight during warm and dry summers (31). Approximately 20 km from Toolik (32), permafrost temperatures at 20 m depth increased from -5.5 to -4.5 °C between 1991 and 2000. This warming of frozen soils probably accounts for recent increases in stream- and lake-water alkalinity.

Climate has been shown to have a significant control on the vegetation of the site, which in turn has affected aquatic resources for productivity. Runoff from thawing soils within the catchment of Toolik Lake has affected lake productivity in a number of ways. Dissolved organic carbon from excretion, leaching, and decomposition of plants in the catchment, along with associated humic materials, has been found to reduce photosynthesis in the lake and absorb 99% of the UV-B radiation in the upper 20 cm (33). In spring, meltwater carries terrestrially derived DOC and abundant nutrients. Upon reaching the lake, meltwater flows cause a two-week high in bacterial productivity (~50% of the annual total) beneath the lake-ice cover (see Figure 5). This peak in production, which takes place at 2 °C, illustrates that bacteria are carbon- and energy-limited, not temperature-limited, and as such will be indirectly affected by climate change. Phytoplankton biomass and primary production peak soon after the ice leaves the lake, and as solar radiation peaks. The lake stratifies so rapidly that no spring turnover occurs, causing oxygen-depleted bottom waters to persist over the summer. This effect is very likely to be amplified with higher temperatures, and will probably reduce the habitat available to fish species such as lake trout.

Future increases in average air temperature and precipitation are very likely to further affect freshwater systems at Toolik. Lakes will very probably

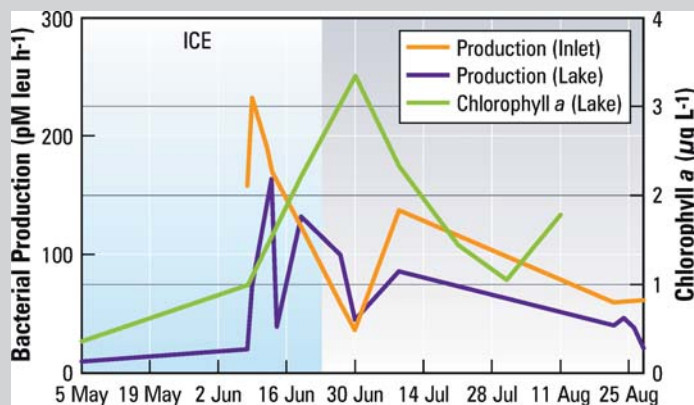


Figure 5. Bacterial productivity and chlorophyll over the spring and summer of 2002 in Toolik Lake (averaged over depths of 3 to 12 m; adapted from 34).

experience early breakup and higher water temperatures. Stream waters are very likely to warm as well, and runoff is very likely to increase, although evapotranspiration could possibly offset increased precipitation. As waters warm, primary production in lakes and rivers at the site is very likely to increase, although most species of aquatic plants and animals are unlikely to change over the 21st century. Lake and river productivity are also very likely to increase in response to changes in the catchment, in particular, temperature increases in permafrost soils and increased weathering and release of nutrients. Increased precipitation will also affect nutrient supply to freshwater systems, and is likely to result in increased decomposition of organic matter in soils (35), formation of inorganic nitrogen compounds, and increased loss of nitrogen from land to water. The shift in terrestrial vegetation to predominantly shrubs is very likely to cause greater loading of DOC and humic materials in streams and lakes, and a reduction in UV-B radiation penetration. However, increases in organic matter are likely to have detrimental effects on the stream population of Arctic grayling at this site, resulting in their disappearance in response to high oxygen depletion. Lake trout, on the other hand, are likely to survive but their habitat will probably be slightly reduced by the combination of reduced deep-water oxygen and warmer surface waters.

Such vegetation shifts will cause further changes in stream water chemistry by altering DOC concentrations. Current data indicate that DOC is negatively correlated with latitude (21, 22) and decreases with distance from treeline (23, 24) and along gradients from boreal forest to tundra (25). Hence, as vegetation shifts from mosses and lichens to grasses and woody species, runoff is very likely to contain increasing concentrations of DOC and particulate detrital material. Verification of enhanced DOC supply associated with northward treeline advance is provided by various paleolimnological and paleoclimatic studies (e.g., 26–28). Although such increases will be long-term, given the slow rates of major vegetation shifts (see 9), earlier increases in DOC and DIC are very likely to result from the earlier thermal and mechanical erosion of the permafrost landscape (see 6). Zepp et al. (29) and Häder et al. (30) provided comprehensive reviews of the projected interactive effects of changes in UV radiation levels and climate on DOC and DIC and related aquatic biogeochemical cycles.

Changes in freshwater catchments with climate change will affect not only loadings of nutrients, sediments, DOC, and DIC

to freshwater systems but also the transport and transformation of contaminants. Contaminant transport from surrounding catchments to freshwaters is likely to increase as permafrost degrades and perennial snow melts (36, 37, 38). The contaminants released from these frozen stores, and those originating from long-range transport and deposition in contributing basins, can then be stored in sediments or metabolized and biomagnified through the food web. Wrona et al. (39) discusses this topic in more detail.

EFFECTS ON GENERAL HYDRO-ECOLOGY

Streams and Rivers, Deltas, and Estuaries

A number of hydrologic shifts related to climate change will affect lakes and rivers, including seasonal flow patterns, ice-cover thickness and duration, and the frequency and severity of extreme flood events. In the present climate, most streams and rivers originating within the Arctic have a nival regime in which snowmelt produces high flows and negligible flow occurs in winter. In areas of significant glaciers, such as on some

Canadian and Russian islands, Greenland, and Svalbard, ice melt from glaciers can sustain flow during the summer, whereas many other streams produce summer flow only from periodic rainstorm events unless they are fed by upstream storage in lakes and ponds.

The subarctic contains a much broader range of hydrologic regimes, which vary from cold interior continental (comparable to those of the Arctic) to maritime regimes fed moisture directly from open seas even during winter. Overall, a warmer climate is very likely to lead to a shift toward a more pluvial runoff regime as a greater proportion of the annual precipitation falls as rain rather than snow; the magnitude of the peak of spring snowmelt declines; thawing permafrost increases near-surface storage and reduces runoff peaks; and a more active groundwater system augments base flows.

Enhancement of winter flow will very probably lead to the development of a floating ice cover in some streams that currently freeze to the bed. This is very likely to be beneficial to the biological productivity of arctic streams and fish survival where winter freshwater habitat is limited to unfrozen pools (40–42). For other arctic streams and rivers, warming is very likely to result in a shortened ice season and thinner ice cover (6). Since river ice is such a major controller of the ecology of northern streams and rivers, there are likely to be numerous significant impacts. Under conditions of overall annual temperature increases, a delay in the timing of freeze-up and an earlier breakup will very probably reduce the duration of river-ice cover. Data compiled over the last century or more indicate that changes in timing of these events are likely to be at a rate of approximately one day per 0.2 °C increase in air temperature (5, 6). For freeze-up, higher water and air temperatures in the autumn combine to delay the time of first ice formation and eventual freezeup. If there was also a reduction in the rate of autumn cooling, the interval between these two events would increase. Although all major ice types would continue to form, unless there were also significant changes in the flow regime, the frequency and magnitude of, for example, periods of major frazil ice growth will probably be reduced. This has implications for the types of ice that constitute the freeze-up cover and for the creation of unique under-ice habitats such as air cavities and those influenced by frazil concentrations (42–44).

Changes in the timing and duration of river ice formation will also alter the dissolved oxygen (DO) regimes of arctic lotic ecosystems. Following freeze-up and the elimination of direct water–atmosphere exchanges, DO concentrations steadily decline, sometimes to near-critical levels for river biota (e.g., 41, 42, 43, 44). Reductions in ice-cover duration and a related increase in the number of open-water re-aeration zones are very likely to reduce the potential for this biologically damaging oxygen depletion. Such benefits will possibly be offset by the projected enhanced input of DOC and its subsequent oxidation (e.g., 47, 48), the rate and magnitude of which would also be increased as a result of the above-noted higher nutrient loading. Worst-case scenarios would develop on rivers where the flow is already comprised of poorly oxygenated groundwater, such as that supplied from extensive bogs and peatlands. Some rivers in the West Siberian Plain offer the best examples of this situation. Here, the River Irtysh drains large quantities of de-oxygenated water from vast peatlands into the River Ob, resulting in DO levels of only about 5% of saturation (49, 50).

The greatest ice-related ecological impacts of climate change on arctic lotic systems are likely to result from changes in breakup timing and intensity. As well as favoring earlier breakup, higher spring air temperatures can affect breakup severity (51). While thinner ice produced during a warmer winter would tend to promote a less severe breakup, earlier

timing of the event could counteract this to some degree. Breakup severity also depends on the size of the spring flood wave. While greater and more rapid snowmelt runoff would favor an increase in breakup severity, the reverse is true for smaller snowpacks and more protracted melt. Hence, changes in breakup severity will vary regionally according to the variations in winter precipitation and spring melt patterns.

For regions that experience a more “thermal” or less dynamic ice breakup (8), the magnitude of the annual spring flood will very probably be reduced. For the many northern communities that historically located near river floodplains for ease of transportation access, reductions in spring ice-jam flooding would be a benefit. In contrast, however, reductions in the frequency and severity of ice-jam flooding would have a serious impact on river ecology since the physical disturbances associated with breakup scouring and flooding are very important to nutrient and organic matter dynamics, spring water chemistry, and the abundance and diversity of river biota (44, 52, 53). Specifically, ice-induced flooding supplies the flux of sediment, nutrients, and water that is essential to the health of the riparian system; river deltas being particularly dependent on this process (e.g., 54–56). More generally, given that the magnitude and recurrence interval of water levels produced by ice jams often exceed those of open-water conditions, breakup is probably the main supplier of allochthonous organic material in cold-regions rivers (52, 53). In the same manner, breakup serves as an indirect driver of primary and secondary productivity through the supply of nutrients – a common limiting factor for productivity in cold-regions rivers. Even the mesoscale climate of delta ecosystems and spring plant growth depends on the timing and severity of breakup flooding (41, 57, 58).

River ice is also a key agent of geomorphological change and is responsible for the creation of numerous erosional and depositional features within river channels and on channel floodplains (e.g., 41, 59). Since most geomorphological activity occurs during freeze-up and breakup, changes in the timing of these events are very unlikely to have any significant effect. If, however, climatic conditions alter the severity of such events, this is likely to affect particular geomorphological processes. Furthermore, breakup events affect the general processes of channel enlargement, scour of substrate habitat, and the removal and/or succession of riparian vegetation. All such major river-modifying processes would be altered by any climate-induced shift in breakup intensity.

In summary, if climate change alters the long-term nature of breakup dynamics, the structure and function of rivers and related delta ecosystems are very likely to be significantly altered with direct effects on in-channel and riparian biological productivity. If, for example, significant reductions in dynamic breakups and the related level of disturbance occur, this will reduce overall biological diversity and productivity, with the most pronounced effects on floodplain and delta aquatic systems.

Owing to the reduced ice-cover season and increased air temperatures during the open-water period, summer water temperatures will very probably rise. Combined with greater DOC and nutrient loadings, higher water temperatures are likely to lead to a general increase in total stream productivity, although it is unclear whether temperature will have a significant direct effect on the processing rate of additional particulate detrital material. Irons et al. (60), for example, found a comparable rate of litter processing by invertebrates in Michigan and Alaska and concluded that temperature was not a main factor. The effect of increased temperature on processing efficiency by “cold-climate” species of invertebrates, however, has not been evaluated. The effect of enhanced nutrient loading to arctic streams is more predictable. The current nutrient

Table 1. A synthesis of the potential effects of climate change on arctic estuarine systems from both the bottom-up and top-down ecological perspectives (63).

Bottom-up: nutrients/production/biota etc.

- More open water, more wind mixing, upwelling and greater nutrient availability for primary producers (+)
- More open water, more light penetration especially seasonally hence more primary production (+); potential for increased UV radiation levels (-/?)
- Decreased ice cover, decreased ice-associated algal production, and subsequent impacts on pelagic and benthic food webs (-)
- Increased basin rainfall, increased export of carbon to nearshore (+)
- Increased storms and open water, increased coastal erosion (-), increased sediment loads, nutrients and mixing (+), possibly increased productivity especially in late season (?) but offset by decreased light penetration (-)
- Potential positive feedback to climate change processes (e.g., permafrost thawing, release of methane, and increased radiative forcing) (-)
- Contaminant inputs, mobilization, or increased fluxes driven by temperature changes will increase availability and biomagnification of contaminants in food chains (-)

Top-down: humans/predators/biota etc.

- Shifting water masses and currents will affect biotic cues for habitat use and migrations of biota such as fish and marine mammals (?)
- Redistribution of grazers will affect underlying trophic structure (-/?)
- Climate-induced changes in freshwater, estuarine, and marine habitats seasonally used by anadromous fishes will affect distribution and suitability for use, with consequences for the prey communities and possibly fish availability for humans (-/?)
- Physical absence or alteration of seasonality or characteristics of ice platforms will affect ice-associated biota (e.g., polar bears, seals, algae) (-), with cascading consequences for fish (+/-)
- Increased open water will facilitate whale migrations (+) but increase predator risk to calves (-); shifts in whale populations may cascade through the trophic structure (e.g., shifted predation on fish by belugas; increased predation on plankton by bowhead whales) with unknown trophic consequences for anadromous and marine fish (?)

Cascading consequences from a human perspective as generally: positive (+); negative (-); neutral (0); or unknown (?).

limitation of many arctic streams is such that even slight increases in available phosphorus, for example, will produce a significant increase in primary productivity (61). Where productivity responses of stream biota are co-limited by phosphorus and nitrogen (e.g., as suggested by the experimental results of Peterson et al. [62]), increased loadings of both nutrients would be required to sustain high levels of enhanced productivity.

Table 1 summarizes the potential impacts of climate change on the dynamics of arctic estuaries (63). The major factor affecting arctic estuarine systems given the degree of climate change projected by the ACIA-designated models will be the increase in freshwater discharge (6). In some arctic basins, such as the Chukchi Sea, there is presently very little freshwater runoff and consequently no estuarine zones. Increased river discharge could possibly create estuarine areas, providing new habitat opportunities for euryhaline species. In established estuarine systems, such as the Mackenzie River system and the Ob and Yenisey Rivers, increased freshwater input in summer (e.g., 64) is likely to increase stratification, making these habitats more suitable for freshwater species and less suitable for marine species. There are likely to be shifts in species composition to more euryhaline and anadromous species. In addition, increased freshwater input is likely to deposit more organic material, changing estuarine biogeochemistry and perhaps increasing primary productivity, the positive effects of which will possibly be offset in part by increased resuspension of contaminated sediments in these systems.

A secondary impact of increased freshwater discharge that is of serious concern, particularly for Siberian rivers that traverse large industrialized watersheds, is the potential for increased contaminant input. The Ob and Yenisey Rivers, for example, have high levels of organochlorine contamination compared to the Lena River (65), which is considered relatively pristine (66). Larsson et al. (67) noted that arctic fishes have a life strategy that involves intensive feeding in spring and summer, allowing for the buildup of lipid stores and coping with food shortages in winter. The high body-lipid content of arctic fishes may make them more vulnerable to lipid-soluble pollutants such as polycyclic aromatic hydrocarbons (PAHs) or polychlorinated biphenyls (PCBs). In addition, reduced sea-ice coverage that leads to increased marine traffic is likely to have cascading negative consequences (e.g., pollution, risk of oil spills) for estuarine systems.

Arctic deltas provide overwintering habitat for many species that tolerate brackish waters. These areas are maintained as suitable habitat by a combination of continuous under-ice freshwater flow and the formation of the nearshore ice barrier in the stamukhi zone (area of grounded, nearshore ice pressure ridges). As temperatures rise, the seasonal ice zone of estuaries is likely to expand and the ice-free season lengthen (63). Disruption of either the flow regime or the ice barrier could possibly have profound effects on the availability of suitable overwintering habitat for desired fish species. Given that such habitat is probably limited and hence limits population abundance, the consequences for local fisheries will probably be significant. In addition, in early winter, subsistence and commercial fisheries target fish that overwinter in deltas. Thinning ice is likely to limit access to these fisheries.

Similar to freshwater systems, ecological control of marine systems can be viewed from bottom-up (i.e., nutrients–production–biota linkages) and/or top-down (i.e., human activities–predators–keystone biota) perspectives (68). The special role of ice as both a habitat and a major physical force shaping the estuarine and nearshore arctic environment suggests that climate change will work in both modes to affect these systems (63). One example is the loss of the largest epishelf lake (fresh and brackish water body contained behind the ice shelf) in the Northern Hemisphere with the deterioration and break up of the Ward Hunt ice shelf (69). The loss of this nearshore water body has affected a unique community of marine and freshwater planktonic species, as well as communities of cold-tolerant microscopic algae and animals that inhabited the upper ice shelf.

Lakes, Ponds, and Wetlands

Lentic systems north of the Arctic Circle contain numerous small to medium lakes and a multitude of small ponds and wetland systems. Relatively deep lakes are primarily contained within alpine or foothill regions such as those of the Putorana Plateau in the lower basin of the Yenisey River. One very large and deep lake, Great Bear Lake (Northwest Territories, Canada), is found partly within the Arctic Circle. Variations in its water budget primarily depend on flows from its contributing catchment, comprised largely of interior plains lowlands and exposed bedrock north of 60° N. Its southern counterpart, Great Slave Lake, provides a strong hydrologic contrast to this system. Although also part of the main stem

Box 3

Lake-ice duration and water column stratification: Lake Saanajärvi, Finnish Lapland.

Lake Saanajärvi (maximum depth 24 m, area 0.7 km²; 69° N, 20° E) is the key Finnish site in the European research projects Mountain Lake Research and European Mountain Lake Ecosystems: Regionalisation, Diagnostics and Socio-economic Evaluation. Lake Saanajärvi has been intensively monitored since 1996. The data presented here have been published in several papers, including those by (79, 80, 81, 82, 83). The mean annual temperature of the area is -2.6 °C, and annual precipitation is approximately 400 mm. The catchment area is mostly covered by bare rocks and alpine vegetation. Lake Saanajärvi is a dimictic, ultra-oligotrophic, clear-water lake. The lake is ice-free for nearly four months of the year, with highly oxygenated waters, and is strongly stratified for two months after spring overturn. Phytoplankton biomass and densities are low (80, 84, 85), consisting predominantly of chrysophytes and diatoms. Bacterial biomass is low as well, and zooplankton are not very abundant. Freshwater shrimp (*Gammarus lacustris*) are common and form an important food source for fish, which include Arctic char and brown trout (*Salmo trutta lacustris*).

Changes in water temperature and stratification of Lake Saanajärvi have been associated with climate changes in Finnish Lapland over the past 200 years (83, 86, 87). Mean annual air temperatures in Finnish Lapland, as in much of the Arctic, rose 1 to 2 °C following the Little Ice Age. During this period of warming, diatom communities changed from benthic-periphytic to pelagic, Cladocera increased in abundance, and chrysophytes became less numerous. These changes have been shown to be associated with increased rates of organic matter accumulation and increased concentrations of algal pigments during the climatic warming (79, 81, 83, see Figure 6). After a period of cooling from the 1950s to the 1970s, air temperatures in the Arctic continued to rise. More recently, interannual variability in temperatures has been shown to account for changes in the thermal gradient and mixing of Lake Saanajärvi surface waters. For example, Lake Saanajärvi normally stratifies in early July, two weeks after ice breakup, and retains a distinct, steep thermocline at a depth of 10 to 12 m throughout the summer. In 2001, this summer stratification was broken after a period of slight cooling in early August, after which the lake was only weakly stratified. In 2002, on the other hand, spring and summer temperatures were extremely warm. Spring ice breakup was early and waters warmed quickly, resulting in a very sharp thermocline that was stable during the entire summer stratification period.

Future temperature increases are therefore very likely to affect the thermal structure of lakes in Finnish Lapland and throughout the Arctic, which is likely to have dramatic consequences for lake biota. Rising mean annual temperatures are very likely to influence the duration of summer stratification and the stability and depth of the thermocline in Finnish lakes. As such, many of the presently isothermal lakes are likely to become dimictic as temperatures increase. In addition, the prolonged thermal stratification that is likely to accompany rising temperatures could possibly lead to lower oxygen concentrations and increased phosphorus concentrations in the hypolimnion, benefiting nutrient-limited primary production. As spring temperatures rise and the ice-free period extends, not only is thermal stratification likely to stabilize, but production in many high latitude lakes could possibly peak twice rather than once during the open-water season (e.g., 80, 89, 90, 91, 92, 93). On a broader scale, changes in lake stratification and water mixing will probably affect species composition (e.g., diatoms; 94).

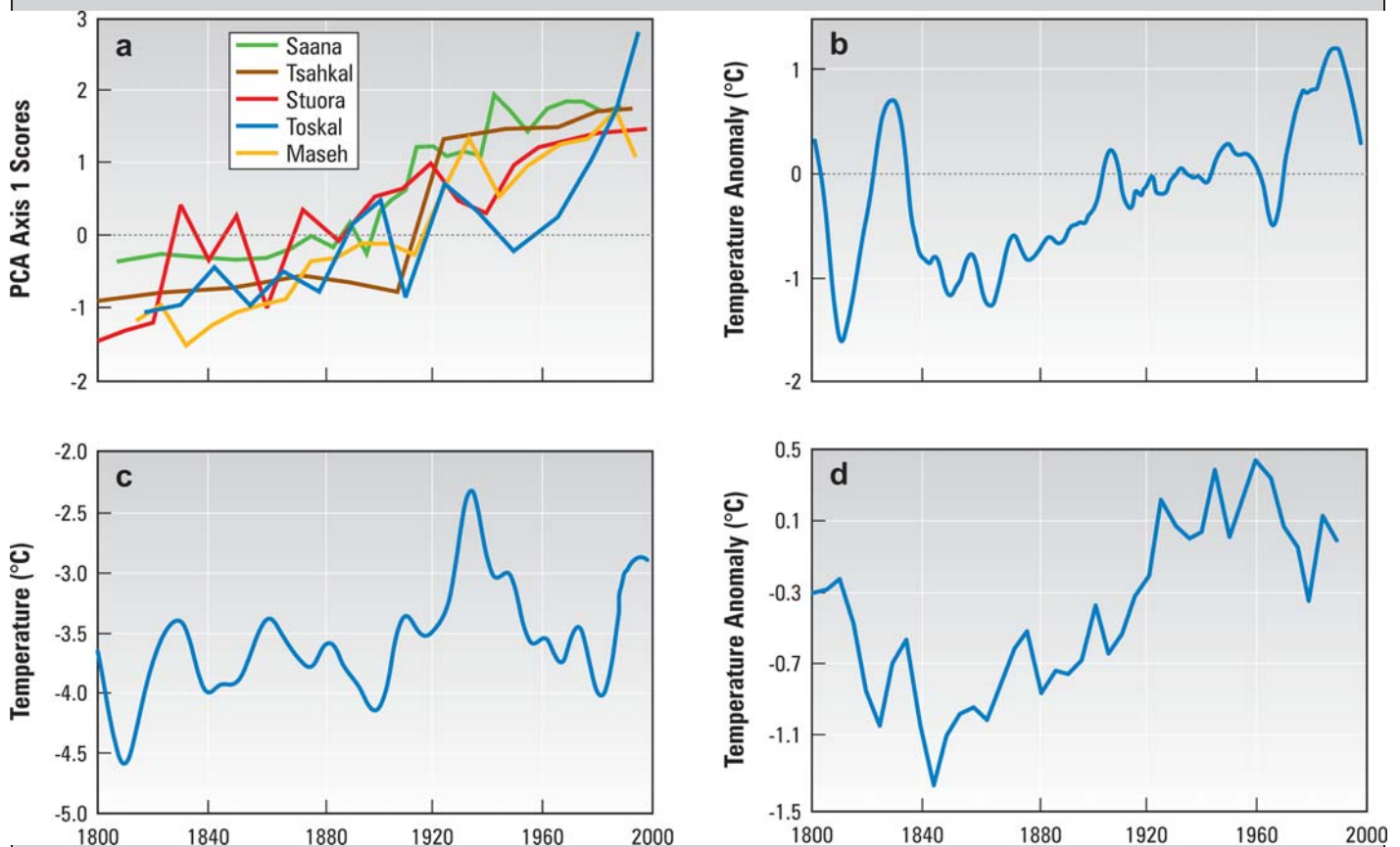


Figure 6. Comparison of diatom assemblage changes with regional and arctic-wide temperature anomalies, showing (a) principal components analysis (PCA) primary axis scores derived from the correlation matrices of the diatom percentage counts from the five study sites; (b) spring (March–May) temperature anomalies for northwestern Finnish Lapland, smoothed using a 10-year low-pass filter; (c) trend in mean annual air temperature in northwestern Finnish Lapland, smoothed using a 10-year low-pass filter; and (d) standardized proxy arctic-wide summer-weighted annual temperature, plotted as departure from the mean (panels a–c from 82, panel d from 88).

Mackenzie River basin and wholly located north of 60° N, its water budget is primarily determined by inflow that originates from Mackenzie River headwater rivers located much further to the south. Moreover, its seasonality in water levels reflects the effects of flow regulation and climatic variability in one of its major tributaries, the Peace River, located about 2000 km upstream in the Rocky Mountain headwaters of western Canada (70, 71). As such, the Mackenzie River system offers the best example of a northern lentic system that is unlikely to be significantly affected by changes in hydrologic processes operating within the north (e.g., direct lake evaporation and precipitation) but will be dependent principally on changes in water-balance processes operating well outside the Arctic.

The other major arctic landscape type that contains large, although primarily shallower, lakes is the coastal plains region found around the circumpolar north. As mentioned previously, these shallow systems depend on snowmelt as their primary source of water, with rainfall gains often negated by evapotranspiration during the summer. Evaporation from these shallow water bodies is very likely to increase as the ice-free season lengthens. Hence, the water budget of most lake, pond, and wetland systems is likely to depend more heavily on the supply of spring meltwater to produce a positive annual water balance, and these systems are more likely to dry out during the summer. Another possible outcome of climate change is a shift in vegetation from non-transpiring lichens and mosses to vascular plants as temperatures rise and the growing season extends (16), potentially exacerbating water losses. However, factors such as increasing cloud cover and summer precipitation will possibly mitigate these effects.

Loss of permafrost increases the potential for many northern shallow lotic systems to dry out from a warmer temperature regime. Ponds are likely to become coupled with the ground-water system and drain if losses due to downward percolation and evaporation are greater than resupply by spring snowmelt and summer precipitation. Patchy arctic wetlands are particularly sensitive to permafrost degradation that can link surficial waters to the supra-permafrost groundwater system. Those along the southern limit of permafrost, where increases in temperature are most likely to eliminate the relatively warm permafrost, are at the highest risk of drainage (72). Traditional ecological knowledge from Nunavut and eastern arctic Canada indicates that recently there has been enhanced drying of lakes and rivers, as well as swamps and bogs, enough to impair access to traditional hunting grounds and, in some instances, fish migration (13, 15).

Warming of surface permafrost, however, will very probably enhance the formation of thermokarst wetlands, ponds, and drainage networks, particularly in areas characterized by concentrations of massive ground ice. Thawing of such ice concentrations, however, is very likely to lead to dramatic increases in terrain slumping and subsequent sediment transport and deposition in rivers, lakes, deltas, and nearshore marine environments. This is likely to produce distinct changes in channel geomorphology in systems where sediment transport capacity is limited, and will probably have a significant impact on the aquatic ecology of the receiving water bodies. Catastrophic drainage of permafrost-based lakes that are now in a state of thermal instability, such as those found along the western arctic coast of Canada, is also very likely (73–75). Losses of thermokarst lakes within low-lying deltaic areas are also likely to result from rising sea levels. Marine inundation resulting from continually rising sea level commonly drains lakes in the outer portion of the Mackenzie Delta, northern Richards Island (76). Moreover, Mackay (73) estimated that one lake per year has drained in the Tuktoyaktuk coastlands of northern Canada over

the last few thousand years. Future, more pronounced rises in sea level are likely to accelerate this process.

Changes in the water balance of northern wetlands are especially important because most wetlands in permafrost regions are peatlands, which can be sources or sinks of carbon and CH₄ depending on the depth of the water table (see 77). An analysis by Rouse et al. (16) of subarctic sedge fens in a doubled-CO₂ climate suggested that increases in temperature (4 °C) would reduce water storage in northern peatlands even with a small and persistent increase in precipitation. While acknowledging that storage changes depend on variability in soil moisture and peat properties, projected declines in the water table were 10 to 20 cm over the summer.

As the ice cover of northern lakes and ponds becomes thinner, forms later, and breaks up earlier (6), concomitant limnological changes are very likely. Thinner ice covers with less snow cover will increase the under-ice receipt of solar radiation, thereby increasing under-ice algal production and oxygen (e.g., 78) and reducing the potential for winter anoxia and fish kills. Lower water levels, which reduce under-ice water volumes and increase the likelihood of winterkill, could possibly counteract this effect. Similarly, greater winter precipitation on a thinner ice cover is very likely to promote the formation of more highly reflective snow and white-ice layers. Such layers would reduce radiation penetration well into the spring because they also tend to delay breakup compared to covers comprised of only black ice. Notably, the ACIA-designated models project that incident radiation will decline. Reductions are likely to be relatively small (i.e., 10–12 W/m² in May–June between 1981–2000 and 2071–2090; 2), however, compared to the major reductions that are likely to result from greater reflective loss from enhanced white-ice formation.

A longer ice-free season will also increase the length of the stratified season and generally increase the depth of mixing (Box 3), although the magnitude and duration of the effects will depend on factors such as basin depth and area. This is likely to lower oxygen concentrations in the hypolimnion and increase stress on cold-water organisms (16). Furthermore, such an enhancement of mixing processes and reduction in ice cover will probably increase the potential for many northern lakes and ponds to become contaminant sinks (39).

With a longer and warmer ice-free season, total primary production is likely to increase in all arctic lakes and ponds, and especially in the oligotrophic high-arctic ponds that are currently frozen for a majority of the year (95). Similar to the situation for arctic lotic systems, an enhanced supply of nutrients and organic matter from the more biologically productive contributing basins is likely to boost primary productivity (19). Again, however, there are likely to be offsetting effects because of reductions in light availability resulting from enhanced turbidity due to higher inputs of DOC and suspended sediment. Hecky and Guildford (96) noted that analogous factors caused a switch from nutrient limitation, which is a common control of primary production in northern lakes, to light limitation.

CONCLUSIONS

Largely because many hydro-ecological processes in the Arctic are strongly influenced by cryospheric components, even small changes in climate can produce large effects in freshwater ecosystems. Although some responses may be gradual, others might be very abrupt including those associated with the loss of some snow and ice components. In general, the arctic freshwater-terrestrial system will warm more rapidly than the global average, particularly during the winter season. Moreover, in some of the circumpolar arctic, the high latitudes will

warm more than the south resulting in decreased latitudinal thermal gradients. This, combined with a shift from nival to more pluvial regimes, will affect major hydrologic processes, such as the magnitude and severity of the spring freshet and river-ice breakup that play a dominant role in controlling lotic freshwater ecology.

Within the Arctic, projected temperature increases will delay freeze-up and advance break-up of rivers and lakes thereby increasing the open-water period, surface freshwater heating and thereby evaporative losses. Related evapotranspiration losses from vegetated surfaces are also likely to increase with shifts in plant communities. Projected increases in precipitation are unlikely to outweigh such losses and the net result will be a decline in overall water levels. Declines in surface water will be further enhanced by increased infiltration capacity resulting from the loss of surface permafrost. The associated increase in sub-surface storage and increased base flows from groundwater supplies will reduce peak flows and result in an overall flattening of the annual hydrograph compared to its spring-spiked shape typical of current climatic conditions.

Enhanced geochemical weathering accompanied by increased supplies of DIC, DOC, sediment and nutrients are very likely to accompany permafrost degradation and related shifts in vegetation. All of these combined with decreasing ice cover and increasing water temperatures are likely to lead to a general increase in freshwater productivity in both lotic and lentic systems. Reduced ice cover will create new habitat, especially in high-latitude zones that are currently frozen for most of the year and/or to the bed during the main winter. In coastal delta, however, losses of ice barriers and changes in seasonal flows could have profound effects on the availability of winter and summer habitat for freshwater and marine fish species.

References and Notes

- Scholander, P.F., Flagg, W., Hock, R.J. and Irving, L. 1953. Studies on the physiology of frozen plants and animals in the Arctic. *J. Cell. Comp. Physiol.* 42, 1–56.
- Kattsov, V.M., Källén, E., Cattle, H., Christensen, J., Drange, H., Hanssen-Bauer, I., Jóhannessen, T., Karol, I., et al. 2005. Future climate change: modeling and scenarios for the Arctic. ACIA. In: *Arctic Climate Impact Assessment*. Cambridge University Press, Cambridge, UK, chap. 4, pp. 99–150.
- IPCC. 2001. Climate change 2001: the scientific basis. In: *Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K. and Johnson, C.A. (eds.) Cambridge University Press, Cambridge, UK, pp. 881.
- Callaghan, T.V., Bjorn, L.O., Chernov, Y., Chapin, T., Christensen, T.R., Huntley, B., Ims, R.A., Johansson, M., et al. 2004. Biodiversity, distributions and adaptations of arctic species in the context of environmental change. *Ambio* 33, 404–417.
- Magnuson, J.J., Robertson, D.M., Benson, B.J., Wynne, R.H., Livingstone, D.M., Arai, T., Assel, R.A., Barry, R.G., et al. 2000. Historical trends in lake and river ice cover in the Northern Hemisphere. *Science* 289, 1743–1746.
- Walsh, J., Anisimov, O., Hagen, J.O., Jakobsson, T., Oerlemans, T., Prowse, T.D., Romanovsky, V., Savelieva, N., Serreze, M., et al. 2005. Cryosphere and hydrology. In: *Arctic Climate Impact Assessment*. Cambridge University Press, Cambridge, UK, chap. 6, pp. 183–242.
- Wrona, F.J., Prowse, T.D., Reist, J.D., Hobbie, J.E., Lucie, M.J., Levesque, L.M.J. and Vincent, W.F. 2006. Climate Impacts on Arctic Freshwater Ecosystems and Fisheries: Background, Rationale and Approach of the Arctic Climate, *Ambio* 35, 326–329.
- Gray, D.M. and Prowse, T.D. 1993. Snow and floating ice. In: *Handbook of Hydrology*. Maidment, D.R. (ed.). McGraw-Hill, New York, NY, 1–7. 58.
- Woo, M.K. 1996. Hydrology of northern North America under global warming. In: *Regional Hydrological Responses to Climate Change*. Jones, J.A.A., Liu, C., Woo, M.-K. and Kong, H.-T. (eds.). Kluwer, Dordrecht, Belgium, pp. 73–86.
- Callaghan, T.V., Bjorn, L.O., Chernov, Y., Chapin, T., Christensen, T.R., Huntley, B., Ims, R.A., Johansson, M., et al. 2004. Effects of changes in climate on landscape and regional processes and feedbacks to the climate system. *Ambio* 33, 459–468.
- Pomeroy, J.W., Gray, D.M. and Landine, P.G. 1993. The prairie blowing snow model: characteristics, validation, operation. *J. Hydrol.* 144, 165–192.
- Liston, G.E., McFadden, J.P., Sturm, M. and Pielke, R.A. Sr. 2002. Modelled changes in arctic tundra snow, energy and moisture fluxes due to increased shrubs. *Glob. Change Biol.* 8, 17–32.
- Krupnik, I. and Jolly, D. 2002. *The Earth is Faster Now: Indigenous Observations of Arctic Environmental Change*. Research Consortium of the United States, Fairbanks, Alaska.
- McDonald, M.A., Arragutainaq, L. and Novalinga, Z. 1997. *Voices from the Bay: Traditional Ecological Knowledge of Inuit and Cree in the Hudson Bay Bioregion*. Ottawa, Canada.
- Huntington, H.H., Fox, S., Berkes, F., Krupnik, I., Whiting, A., Zacharof, M., McGlashan, G., Brubaker, M., et al. 2005. The changing Arctic: indigenous perspectives. ACIA. In: *Arctic Climate Impact Assessment*. Cambridge University Press, Cambridge, UK, chap. 3, pp. 61–98.
- Rouse, W.R., Douglas, M.S.V., Hecky, R.E., Hershey, A.E., Kling, G.W., Lesack, L., Marsh, P., McDonald, M., Nicholson, B.J., et al. 1997. Effects of climate change on the freshwaters of Arctic and subarctic North America. *Hydrol. Process.* 11, 873–902.
- Hinzman, L.D. and Kane, D.L. 1992. Potential response of an Arctic watershed during a period of global warming. *J. Geophys. Res.* 97, 2811–2820.
- Callaghan, T.V., Bjorn, L.O., Chapin, T., Christensen, T., Huntley, B., Ims, R.A., Johansson, M., Jolly, D., et al. 2004. Effects on the structure of arctic ecosystems in the short- and long-term perspectives. *Ambio* 33, 436–447.
- Hobbie, J.E., Peterson, B.J., Betzet, N., Deegan, L., O'Brien, W.J., Kling, G.W., Kipphut, G.W., Bowden, W.B., et al. 1999. Impact on global change on the biogeochemistry and ecosystems of an arctic freshwater system. *Polar Res.* 18, 207–214.
- Church, M. 1995. Geomorphic response to river flow regulation: case studies and time-scales. *Regulated Rivers Res. Manage.* 11, 3–22.
- Fallu, M.-A. and Pienitz, R. 1999. Diatomées lacustres de Jamésie-Hudsonie (Québec) et modèle de reconstitution des concentrations de carbone organique dissous. *Écoscience* 6, 603–620.
- Rühland, K.M. and Smol, J.P. 1998. Limnological characteristics of 70 lakes spanning arctic treeline from Coronation Gulf to Great Slave Lake in the central Northwest Territories, Canada. *Int. Rev. Hydrobiol.* 83, 183–203.
- Korhola, A., Weckström, J. and Blom, T. 2002. Relationships between lake and land-cover features along latitudinal vegetation ecotones in arctic Fennoscandia. *Arch. Hydrobiol. Suppl. (Monograph Studies)* 139, 203–235.
- Pienitz, R. and Smol, J.P. 1994. The ecology and physicochemical characteristics of lakes in the subarctic and arctic regions of the Yukon Territory, Fennoscandia (Finland, Norway), the Northwest Territories and Northern Quebec. In: *Proceedings of the Fourth Arctic-Antarctic Diatom Symposium*. Hamilton, P.B. (ed.). Canadian Technical Report of Fisheries and Aquatic Sciences No. 1957. Fisheries and Oceans, Canada, Ottawa.
- Vincent, W.F. and Hobbie, J.E. 2000. Ecology of Arctic lakes and rivers. *The Arctic: Environment, People, Policy*. Nuttal, M. and Callaghan, T.V. (eds.). Harwood Academic Publishers, Amsterdam, pp. 197–231.
- Korhola, A. and Weckström, J. 2005. Paleolimnological studies in arctic Fennoscandia and the Kola peninsula (Russia). In: Pienitz, R., Douglas, M.S.V. and Smol, J.P. (eds.). *Long-Term Environmental Change in Arctic and Antarctic Lakes*. Springer, Dordrecht, Belgium, pp. 381–418.
- Seppä, H. and Weckström, J. 1999. Holocene vegetational and limnological changes in the Fennoscandian tree-line area as documented by pollen and diatom records from Lake Tsuolbajavri, Finland. *Écoscience* 6, 621–635.
- Solovieva, N. and Jones, V.J. 2002. A multiproxy record of Holocene environmental changes in the central Kola Peninsula, northwest Russia. *J. Quaternary Sci.* 17, 303–318.
- Zepp, R.G., Callaghan, T.V. and Erickson, D.J. III 2003. Interactive effects of ozone depletion and climate change on biogeochemical cycles. In: *Environmental Effects of Ozone Depletion and its Interactions with Climate Change: 2002 Assessment*. Bormann, J.F., Solomon, K. and van der Leun, J.C. (eds.). *Photochem. Photobiol. Sci.* 2, 51–61.
- Häder, D.-P., Kumar, H.D., Smith, R.C. and Worrest, R.C. 2003. Aquatic ecosystems: effects of solar ultraviolet radiation and interactions with other climatic change factors. In: *Environmental Effects of Ozone Depletion and its Interactions with Climate Change: 2002 Assessment*. Bormann, J.F., Solomon, K. and van der Leun, J.C. (eds.). *Photochem. Photobiol. Sci.* 2, 39–50.
- Deegan, L.A., Golden, H.E., Harvey, C.J. and Peterson, B.J. 1999. Influence of environmental variability on the growth of age-0 and adult Arctic grayling. *Trans. Am. Fish. Soc.* 128, 1163–1175.
- Hobbie, J.E., Shaver, G., Laundre, J., Slavik, K., Deegan, L.A., O'Brien, J., Oberbauer, S. and MacIntyre, S. 2003. Climate forcing at the Arctic LTER site, Greenland, D. In: *Climate Variability and Ecosystem Response in Long-Term Ecological Research (LTER) Sites*. Goodin, D.G. and Smith, R.C. (eds.). Oxford University Press, Oxford, pp. 74–91.
- Morris, D.P., Zagarese, H.E., Williamson, C.E., Balseiro, E.G., Hargreaves, B.R., Modenutti, B., Moeller, R. and Queimados, C. 1995. The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. *Limnol. Oceanogr.* 40, 1381–1391.
- Crump, B.C., Kling, G.W., Bahr, M. and Hobbie, J.E. 2003. Bacterioplankton community shifts in an Arctic lake correlate with seasonal changes in organic matter source. *Applied and Environmental Microbiology* 69, 2253–2268.
- Clein, J.S., Kwiatkowski, B.L., McGuire, A.D., Hobbie, J.E., Rastetter, E.B., Melillo, J.M. and Kicklighter, D.W. 2000. Modelling carbon responses of tundra ecosystems to historical and projected climate: a comparison of a plot- and a global-scale ecosystem model to identify process-based uncertainties. *Glob. Change Biol.* 6(S1) 127–140.
- Blais, J.M., Schindler, D.W., Muir, D.C.G., Kimpe, L.E., Donald, D.B. and Rosenberg, B. 1998. Accumulation of persistent organochlorine compounds in mountains of western Canada. *Nature* 395, 585–588.
- Blais, J.M., Schindler, D.W., Muir, D.C.G., Sharp, M., Donald, D.B., Lafreniere, M., Braekvelt, E. and Strachan, W.M.J. 2001. Melting glaciers: a major source of persistent organochlorines to subalpine Bow Lake in Banff National Park, Canada. *Ambio* 30, 410–415.
- McNamara, J.P., Kane, D.L. and Hinzman, L.D. 1999. An analysis of an arctic channel network using a digital elevation model. *Geomorphology* 29, 339–353.
- Wrona, F.J., Prowse, T.D., Reist, J.D., Beamish, R., Gibson, J.J., Hobbie, J., Jeppesen, E., King, J., et al. 2006. Effects of ultraviolet radiation and contaminant-related stressors on arctic freshwater ecosystems. *Ambio* 35, 388–401.
- Craig, P.C. 1989. An introduction to anadromous fishes in the Alaskan Arctic. In: *Research Advances on Anadromous Fish in Arctic Alaska and Canada*. Norton, D.W. (ed.). Biological Papers of the University of Alaska, 24. Institute of Arctic Biology, Fairbanks, AK, pp. 27–54.
- Prowse, T.D. 2001. River-ice ecology. I: hydrology, geomorphic and water-quality aspects. *J. Cold Regions Engineering* 15, 1–16.
- Prowse, T.D. 2001. River-ice ecology. II: biological aspects. *J. Cold Regions Eng.* 15, 17–33.
- Brown, R.S., Stanislawski, S.S. and Mackay, W.C. 1994. Effects of frazil ice on fish. *Proceedings of the Workshop on Environmental Aspects of River Ice*. Prowse, T.D. (ed.). National Hydrology Research Institute, Saskatoon, Symposium No.12, pp. 261–278.
- Cunjak, R.A., Prowse, T.D. and Parrish, D.L. 1998. Atlantic salmon (*Salmo salar*) in winter: the season of parr discontent? *J. Fish. Aquat. Sci.* 55(S1), 161–180.
- Chambers, P.A., Scrimgeour, G.J. and Pietroniro, A. 1997. Winter oxygen conditions in ice-covered rivers: the impact of pulp mill and municipal effluents. *Can. J. Fish. Aquat. Sci.* 54, 2796–2806.
- Power, G., Cunjak, R., Flannagan, J. and Katopodis, C. 1993. *Environmental Aspects of River Ice*. National Hydrology Research Institute, Saskatoon.
- Shreier, H., Erlebach, W. and Albright, L. 1980. Variations in water quality during winter in two Yukon rivers with emphasis on dissolved oxygen concentration. *Water Res.* 14, 1345–1351.
- Whitfield, P.H. and McNaughton, B. 1986. Dissolved-oxygen depressions under ice cover in two Yukon rivers. *Water Resour. Res.* 22, 1675–1679.
- Harper, P.P. 1981. Ecology of streams at high latitudes. In: *Perspectives in Running Water Ecology*. Lock, M.A. and Williams, D.D. (eds.). Plenum Press, New York, NY, pp. 313–337.
- Hynes, H.B.N. 1970. *The Ecology of Running Waters*. University Press, Liverpool.
- Prowse, T.D. and Beltaos, S. 2002. Climatic control of river-ice hydrology: a review. *Hydrol. Process.* 16, 805–822.

52. Prowse, T.D. and Culp, J.M. 2003. Ice break-up: a neglected factor in river ecology. *Can. J. Civil Eng.* 30, 145–155.
53. Scrimgeour, G.J., Prowse, T.D., Culp, J.M. and Chambers, P.A. 1994. Ecological effects of river ice break-up: a review and perspective. *Freshw. Biol.* 32, 261–275.
54. Lesack, L., Hecky, R.E. and Marsh, P. 1991. The influence of frequency and duration of flooding on the nutrient chemistry of the Mackenzie Delta lakes. In: *Mackenzie Delta: Environmental Interactions and Implications for Development*. Marsh, P. and Ommanney, C.S.L. (eds.) National Hydrology Research Institute, Saskatoon, Symposium No. 4, pp. 19–36.
55. Martin, N.V. and Olver, C.H. 1980. The lake charr, *Salvelinus namaycush*. In: *Charrs: Salmonid Fishes of the Genus Salvelinus*. Dr. W. Junk BV Publishers, The Hague, pp. 205–277.
56. Prowse, T.D. and Conly, F.M. 2001. Multiple-hydrologic stressors of a northern delta ecosystem. *J. Aquat. Ecosystem Stress Recovery* 8, 17–26.
57. Gill, D. 1974. *The Coast and Shelf of the Beaufort Sea*. Arctic Institute of North America, Arlington, VA.
58. Hirst, S.M. 1984. Effects of spring breakup on microscale air temperatures in the Mackenzie River Delta. *Arctic* 37, 263–269.
59. Rae, R. and Vincent, W.F. 1998. Effects of temperature and ultraviolet radiation on microbial food web structure: potential responses to global change. *Freshw. Biol.* 40, 747–758.
60. Irons, J.G., Oswood, M.W., Stout, R.J. and Pringle, C.M. 1994. Latitudinal patterns in leaf litter breakdown: is temperature really important? *Freshw. Biol.* 32, 401–411.
61. Flanagan, K., McCauley, E., Wrona, F. and Prowse, T.D. 2003. Climate change: the potential for latitudinal effects on algal biomass in aquatic ecosystems. *Can. J. Fish. Aquat. Sci.* 60, 635–639.
62. Peterson, B.J., Deegan, L., Helfrich, J., Hobbie, J.E., Hullar, M., Moller, B., Ford, T.E., Hershey, A., et al. 1993. Biological responses of a tundra river to fertilization. *Ecology* 74, 653–672.
63. Carmack, E.C. and Macdonald, R.W. 2002. Oceanography of the Canadian Shelf of the Beaufort Sea: a setting for marine life. *Arctic* 55(S1) 29–45.
64. Peterson, B.J., Holmes, R.M., McClelland, J.W., Vorosmarty, C.J., Lammers, R.B., Shiklomanov, A.I., Shiklomanov, I.A. and Rahmstorf, S. 2002. Increasing river discharge to the Arctic Ocean. *Science* 298, 2171–2173.
65. Zhulidova, A.V., Headley, J.V., Robarts, R.D., Korotova, L.G., Fadeev, V.V., Zhulidova, O.V., Volovik, Y. and Khllobystov, V. 1998. Distribution of organochlorine insecticides in rivers of the Russian Federation. *J. Environ. Qual.* 27, 1356–1366.
66. Guieu, C., Huang, W.W., Martin, J.-M. and Yong, Y.Y. 1996. Outflow of trace metals into the Laptev Sea by the Lena River. *Marine Chem.* 53, 255–267.
67. Larsson, P., Okla, L. and Cronberg, G. 1998. Turnover of polychlorinated biphenyls in an oligotrophic and an eutrophic lake in relation to internal lake processes and atmospheric fallout. *Can. J. Fish. Aquat. Sci.* 55, 1926–1937.
68. Parsons, T.R. 1992. The removal of marine predators by fisheries and the impact of trophic structure. *Mar. Pollut. Bull.* 25, 51–53.
69. Mueller, D.R., Vincent, W.F. and Jeffries, M.O. 2003. Break-up of the largest Arctic ice shelf and associated loss of an epishelf lake. *Geophys. Res. Lett.* 30, doi:10.1029/2003GL017931
70. Gibson, J.J., Prowse, T.D. and Peters, D.L. in prep. Hydroclimatic controls on water balance and water level variability in Great Slave Lake. *Hydrol. Process.*
71. Peters, D.L. and Prowse, T.D. 2001. Regulation effects on the lower Peace River, Canada. *Hydrol. Process.* 15, 3181–3194.
72. Woo, M.-K., Lewkowicz, A.G. and Rouse, W.R. 1992. Response of the Canadian permafrost environment to climatic change. *Phys. Geogr.* 134, 287–317.
73. Mackay, J.R. 1992. Lake stability in an ice-rich permafrost environment. Examples from the Western Arctic Coast. In: *Aquatic Ecosystems in Semi-Arid Regions. Implications for Resource Management*. Roberts, R.D. and Bothwell, M.L. (eds.). National Hydrology Research Institute, Saskatoon, Symposium Series 7, pp. 1–26.
74. Marsh, P. and Neumann, N. 2001. Processes controlling the rapid drainage of two ice-rich permafrost-dammed lakes in NW Canada. *Hydrol. Process.* 15, 3433–3446.
75. Marsh, P. and Neumann, N. 2003. Climate and hydrology of a permafrost dammed lake in NW Canada. In: *Permafrost: Proceedings of the 8th International Conference on Permafrost*. Phillips, M., Springman, S.M. and Arenson, L.U. (eds.). A. A. Balkema, Switzerland, p.2.
76. Dallimore, A., Schröder-Adams, C.J. and Dallimore, S.R. 2000. Holocene environmental history of thermokarst lakes on Richards Island, Northwest Territories, Canada: Theocamobians as paleolimnological indicators. *J. Paleolimnol.* 23, 261–283.
77. Wrona, F.J., Prowse, T.D., Reist, J.D., Beamish, R., Gibson, J.J., Hobbie, J., Jeppesen, E., King, J., et al. 2006. Climate change effects on aquatic biota, ecosystem structure and function. *Ambio* 35, 359–369.
78. Prowse, T.D. and Stephenson, R.L. 1986. The relationship between winter lake cover, radiation receipts and the oxygen deficit in temperate lakes. *Atmosphere-Ocean* 24, 386–403.
79. Korhola, A., Sorvari, S., Rautio, M., Appleby, P.G., Dearing, J.A., Hu, Y., Rose, N., Lami, A., et al. 2002. A multi-proxy analysis of climate impacts on the recent development of subarctic Lake Sannajärvi in Finnish Lapland. *J. Paleolimnol.* 28, 59–77.
80. Rautio, M., Sorvari, S. and Korhola, A. 2000. Diatom and crustacean zooplankton communities, their seasonal variability and representation in the sediments of subarctic Lake Saanajärvi. *J. Limnology* 59, (Suppl.1), 81–96.
81. Sorvari, S. and Korhola, A. 1998. Recent diatom assemblage changes in subarctic Lake Saanajärvi, NW Finnish Lapland and their paleoenvironmental implications. *J. Paleolimnol.* 20, 205–215.
82. Sorvari, S., Rautio, M. and Korhola, A. 2000. Seasonal dynamics of subarctic Lake Saanajärvi in Finnish Lapland. In: *Internationale Vereinigung für Theoretische und Angewandte Limnologie: Verhandlungen*, 27th Congress. 27:507–512
83. Sorvari, S., Korhola, A. and Thompson, R. 2002. Lake diatom response to recent Arctic warming in Finnish Lapland. *Glob. Change Biol.* 8, 153–163.
84. Forström, L. 2000. *Seasonal Variability of Phytoplankton in Lake Saanajärvi*. University of Helsinki, Helsinki.
85. Forström, L., Sorvari, S., Korhola, A. and Rautio, M. 2005. Seasonality of phytoplankton in subarctic Lake Saanajärvi in NW Finnish Lapland. *Polar Biol.* 28, 846–861.
86. Alexandersson, H. and Eriksson, B. 1989. *Climate Fluctuations in Sweden 1860–1987*. Reports of Meteorology and Climatology. Swedish Meteorological and Hydrological Institute, Stockholm.
87. Tuomenvirta, H. and Heino, R. 1996. Climatic changes in Finland recent findings. *Geophysica* 32, 61–75.
88. Overpeck, J., Hughen, K., Hardy, D., Bradley, R., Case, R., Douglas, M., Finney, B.P., Gajewski, K., et al. 1997. Arctic environmental change of the last four centuries. *Science* 278, 1251–1266.
89. Catalan, J., Ventura, M., Brancelj, A., Granados, I., Thies, H., Nickus, U., Korhola, A., Lotter, A.F., et al. 2002. Seasonal ecosystem variability in remote mountain lakes: implications for detecting climatic signals in sediment records. *J. Paleolimnol.* 28, 1 25–46.
90. Hinder, B., Gabathuler, M., Steiner, B., Hanselmann, K. and Preisig, H.R. 1999. Seasonal dynamics and phytoplankton diversity in high mountain lakes (Jöri lakes, Swiss Alps). *J. Limnol.* 58, 152–161.
91. Lepistö, L. 1999. Phytoplankton assemblages reflecting the ecological status of lakes in Finland. *Monogr. Boreal Environ. Res.* 16, 97.
92. Lotter, A.F. and Bigler, C. 2000. Do diatoms in the Swiss Alps reflect the length of ice-cover? *Aquat. Sci.* 62, 125–141.
93. Medina-Sánchez, J.M., Villar-Argaiz, M., Sánchez-Castillo, P., Cruz-Pizarro, L. and Carrillo, P. 1999. Structure changes in a planktonic food web: biotic and abiotic controls. *J. Limnol.* 58, 213–222.
94. Agbeti, M.D., Kingston, J.C., Smol, J.P. and Watters, C. 1977. Comparison of phytoplankton succession in two lakes of different mixing regimes. *Arch. Hydrobiol.* 140, 37–69.
95. Douglas, M.S.V. and Smol, J.P. 1999. Freshwater diatoms as indicators of environmental change in the High Arctic. In: *The Diatoms: Applications for the Environmental and Earth Sciences*. Stoermer, E.F. and Smol, J.P. (eds.). Cambridge University Press, Cambridge, UK, pp. 227–244.
96. Hecky, R.E. and Guildford, S.J. 1984. Primary productivity of Southern Indian Lake before, during and after impoundment and Churchill River Diversion. *Can. J. Fish. Aquat. Sci.* 41, 591–604.

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