

EFFECTS OF CLIMATE CHANGE ON THE FRESHWATERS OF ARCTIC AND SUBARCTIC NORTH AMERICA

WAYNE R. ROUSE,¹ MARIANNE S. V. DOUGLAS,² ROBERT E. HECKY,³ ANNE E. HERSHEY,⁴
GEORGE W. KLING,⁵ LANCE LESACK,⁶ PHILIP MARSH,⁷ MICHAEL MCDONALD,⁸
BARBARA J. NICHOLSON,⁹ NIGEL T. ROULET¹⁰ AND JOHN P. SMOL¹¹

¹*Department of Geography, McMaster University, Hamilton, ON L8S 1V2, Canada*

²*Department of Geology, University of Toronto, Toronto, ON M5S 3B1, Canada*

³*Freshwater Institute, Fisheries and Oceans Canada, 501 University Cres., Winnipeg, MN R3T 2N6, Canada*

⁴*Department of Biology, University of Minnesota, Duluth, MN 55812, USA*

⁵*Department of Biology, University of Michigan, Ann Arbor, MI 48109, USA*

⁶*Departments of Geography and Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada*

⁷*National Hydrology Research Institute, 11 Innovation Blvd., Saskatoon, SK S7N 3H5, Canada*

⁸*Department of Chemical Engineering, 231 Engineering Bldg., University of Minnesota, Duluth, MN 55812, USA*

⁹*Department of Biological Sciences, Central Connecticut State University, New Britain, CT 06050-4010, USA*

¹⁰*Department of Geography and the Centre for Climate and Global Change Research, McGill University, Montreal, QC H3A 2K6, Canada*

¹¹*Departmental of Biology, Queen's University, Kingston, ON K7L 3N6, Canada*

ABSTRACT

Region 2 comprises arctic and subarctic North America and is underlain by continuous or discontinuous permafrost. Its freshwater systems are dominated by a low energy environment and cold region processes. Central northern areas are almost totally influenced by arctic air masses while Pacific air becomes more prominent in the west, Atlantic air in the east and southern air masses at the lower latitudes. Air mass changes will play an important role in precipitation changes associated with climate warming. The snow season in the region is prolonged resulting in long-term storage of water so that the spring flood is often the major hydrological event of the year, even though, annual rainfall usually exceeds annual snowfall. The unique character of ponds and lakes is a result of the long frozen period, which affects nutrient status and gas exchange during the cold season and during thaw. GCM models are in close agreement for this region and predict temperature increases as large as 4°C in summer and 9°C in winter for a 2 × CO₂ scenario. Palaeoclimate indicators support the probability that substantial temperature increases have occurred previously during the Holocene. The historical record indicates a temperature increase of > 1°C in parts of the region during the last century. GCM predictions of precipitation change indicate an increase, but there is little agreement amongst the various models on regional disposition or magnitude. Precipitation change is as important as temperature change in determining the water balance. The water balance is critical to every aspect of hydrology and limnology in the far north. Permafrost close to the surface plays a major role in freshwater systems because it often maintains lakes and wetlands above an impermeable frost table, which limits the water storage capabilities of the subsurface. Thawing associated with climate change would, particularly in areas of massive ice, stimulate landscape changes, which can affect every aspect of the environment. The normal spring flooding of ice-jammed north-flowing rivers, such as the Mackenzie, is a major event, which renews the water supply of lakes in delta regions and which determines the availability of habitat for aquatic organisms. Climate warming or river damming and diversion would probably lead to the complete drying of many delta lakes. Climate warming would also change the characteristics of ponds that presently freeze to the bottom and result in fundamental changes in their limnological characteristics. At present, the food chain is rather simple usually culminating in lake trout or arctic char. A lengthening of the growing season and warmer water temperature would affect the chemical, mineral and nutrient status of lakes and most likely have deleterious effects on the food chain. Peatlands are extensive in region 2. They would move northwards at their southern boundaries, and, with sustained drying, many would change form or become inactive. Extensive wetlands and peatlands are an important component of the global carbon budget, and warmer and drier conditions would most likely change them from a sink to a source for atmospheric carbon. There is some evidence that this may be occurring already. Region 2 is very vulnerable to global warming. Its freshwater systems are probably the least studied and most poorly understood in North America. There are clear needs to improve our current knowledge of temperature and precipitation patterns; to model the thermal behaviour of wetlands, lakes and rivers; to understand better the interrelationships of cold region rivers with their basins; to begin studies on the very large lakes in the region; to obtain a firm grasp of the role of northern peatlands in the global carbon cycle; and to link

the terrestrial water balance to the thermal and hydrological regime of the polar sea. Overall, there is a strong need for basic research and long-term monitoring. © 1997 by John Wiley & Sons, Ltd.

Hydrol. Process., Vol. 11, 873–902 (1997).

(No. of Figures: 8 No. of Tables: 4 No. of Refs: 148)

KEY WORDS freshwater; climate change; global warming; arctic and subarctic North America

INTRODUCTION

Region 2 (Figure 1; Figure 1 in Leavesley *et al.*, 1997) extends across 30° of latitude (52°N to 82°N) and approximately 80° of longitude (62°W to 142°W). This large area, of approximately six million km², includes the Mackenzie River Basin, the Yukon River Basin and north slope of Alaska, Keewatin, the Hudson Bay Lowland, northern Quebec and Labrador and the Canadian Arctic Islands. Lakes and deltas are abundant and are an important resource for indigenous people. The surface area of freshwater is about 350 000 km². Some of the largest freshwater lakes on the earth lie within the Mackenzie Basin. These are Great Bear and Great Slave Lakes and Lake Athabasca. There are innumerable smaller lakes and ponds. Major river deltas include the Mackenzie Delta (25 000 lakes within its approximately 12 000 km² area alone), Peace–Athabasca Delta and the Yukon Delta. Other smaller deltas are formed by most north-flowing rivers. The freshwater ecosystems include approximately 450 000 km² of peatlands. Of these, 280 000 km² are in the Hudson Bay Lowland, which is the second largest peatland in the world. The entire region is underlain by continuous or discontinuous permafrost (Figure 1a). The covering vegetation is boreal forest, subarctic open forest (taiga) and tundra.

This paper outlines the general climatic and hydrological characteristics of region 2. It then examines model predictions of the magnitude of climate warming and precipitation change for the region and places this in context using historical and palaeoclimatic evidence. Following a discussion of the likely broad-scale effects of climate change on freshwaters, the paper focuses in more detail, on potential effects on small ponds and lakes, rivers and northern peatlands.

CLIMATIC CHARACTERISTICS

As would be expected in a region with such geographic diversity, climate is highly variable. There are very few meteorological stations in region 2 so the generalizations stated below should be accepted with reservations. Exclusive of the ice cap areas in the eastern Queen Elizabeth Islands, annual mean temperature spans 21°C (–18 to +3°C), annual precipitation ranges from 60 to 460 mm, the frost-free period from 10 to < 125 days, the median snow-free period from 80 to 245 days and the average global solar radiation from 90 to 160 W/m² (Hare and Thomas, 1979). Average net radiation at the surface varies from 3 to 53 W/m² (Rouse, 1993). In the most southerly parts about 33% of solar radiation is realized as effective surface net radiant energy. This decreases to about 3% in the most northerly parts. There is a marked seasonality in the climate. Typically, air temperature in the summer months (JJA) is between 34 and 41°C warmer than in the winter months (DJF).

Circulation Patterns, Air Masses and Winds

In both summer and winter, the regional winds are westerly in the southern portions of region 2, but in the north, the flow is north-westerly. In the Arctic Islands the flow is part of a circumpolar vortex that is particularly well developed in winter and centred over northern Baffin and Cornwallis Islands (Hare and Thomas, 1979; Maxwell, 1980). Surface winds are heavily influenced by local and regional factors. For example, in the Arctic Islands at Resolute (latitude 74° 40′) the measured annual mean wind speed is 6.3 m/s,

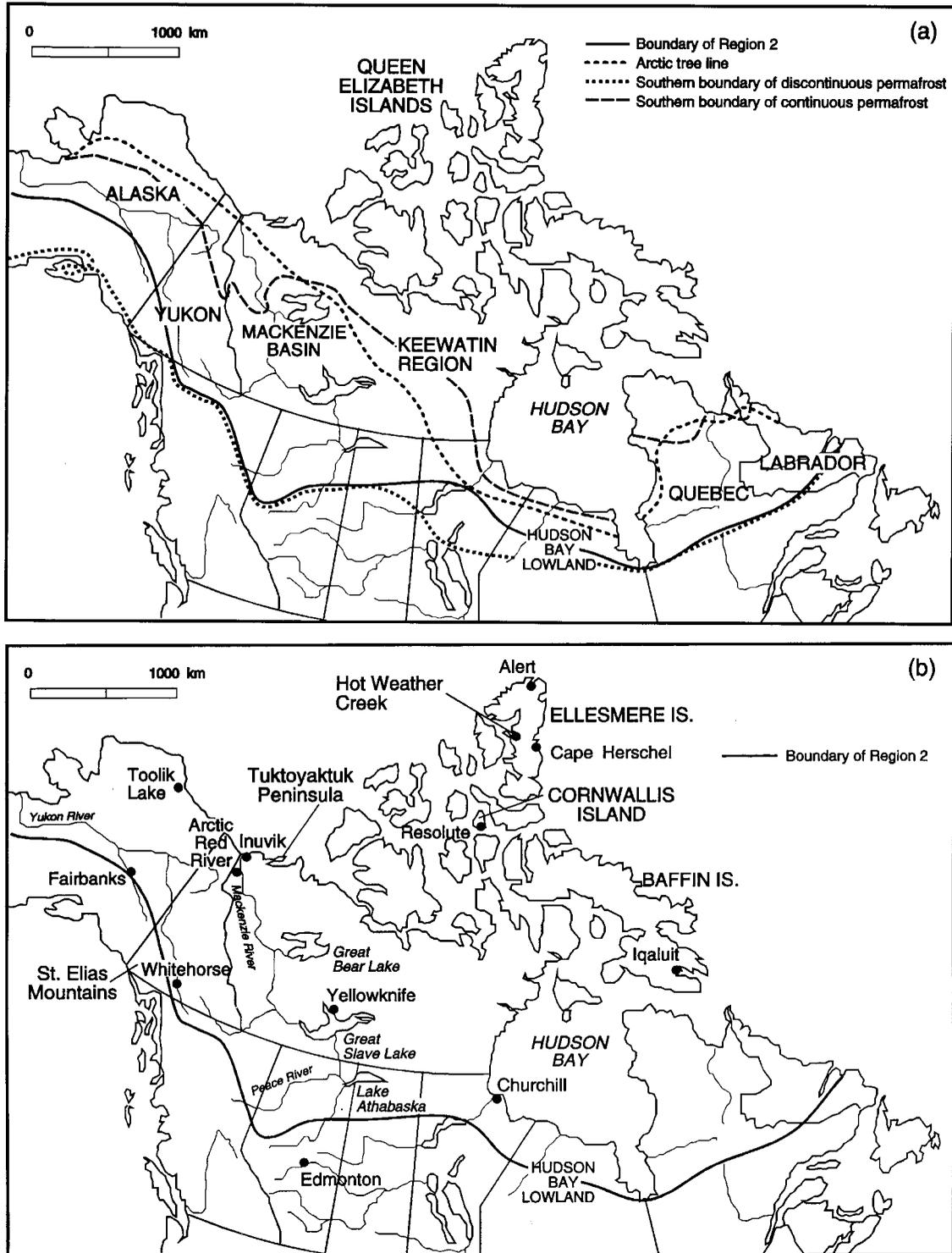


Figure 1. Map of region 2 showing (a) the location of continuous and discontinuous permafrost, Arctic tree-line and specific study areas, and (b) place names referred to in this paper

Table I. Air mass frequency (%) by season. W — winter (DJF); SP — spring (MAM); S — summer (JJA); F — autumn (SON). Estimates are derived from Bryson (1966) and Maxwell (1980)

Station	Air mass source*																			
	Arctic				Pacific				Atlantic				Southern				Hudson Bay			
	W	SP	S	F	W	SP	S	F	W	SP	S	F	W	SP	S	F	W	SP	S	F
Alert	100	100	100	100																
Resolution	100	100	100	100																
Aqaluit	100	100	66	100							34									
Baker Lake	100	100	70	100										30						
Fairbanks†	100	66	30	45		34	70	55												
Whitehorse	100	65	25	45		35	75	55												
Inuvik	100	85	55	88		15	45	12												
Churchill	100	90	48	85									10	30	3				22	12
Schefferville	100	85	45	88						15	30	10			20				5	2

* All frequencies $\geq 30\%$ are in bold.

† Fairbanks data are estimated by extrapolation.

whereas at Alert (latitude $82^{\circ} 30'$) it is 3.0 m/s (Maxwell, 1980). These differences are the result of local topographical and instrument-siting factors. In general terms, wind speeds increase from south to north and are about 50% higher in winter than in summer (Rouse, 1993). The biggest increase in surface wind accompanies emergence from the boreal forest into open tundra and is a result of the reduced surface drag.

Annual air mass dominance varies widely within the region (Table I). For the high Arctic Islands, arctic air masses dominate for most of the year. As one moves south-eastwards, Atlantic air achieves more importance, whereas south-westwards, Pacific air becomes increasingly common. In south-central parts of region 2, such as the Hudson Bay Lowland, while arctic air is dominant annually, southern air and air from Hudson Bay achieve some importance in summer and autumn. Since arctic air is much drier than Atlantic, Pacific and especially southerly air masses, in scenarios of climate warming, the changing air mass dominance patterns become important, particularly to precipitation. Substantial changes to less domination by arctic air masses can be anticipated for northern Alaska and Yukon, the Mackenzie Basin, Keewatin, the Hudson Bay Lowland, northern Quebec and Labrador and the more southern islands of the Arctic Archipelago.

HYDROLOGICAL CHARACTERISTICS

Extent of Snow, Ice and Permafrost

For most of region 2, snow accounts for 40–80% of the annual precipitation, the majority of which is stored on the ground for 6–9 months of the year. Actual snowfall can be up to two to three times greater than that measured by standard snow collectors at weather stations. This is because of under catch and large numbers of trace precipitation events in the wind-swept tundra (Goodison, 1981; Woo *et al.*, 1983). The hydraulic conductivity of permafrost soils is significantly lower than for unfrozen soils, thus limiting groundwater flows. Consequently, the occurrence of permafrost is important in controlling the areal and spatial distribution of wetlands in many areas of the region.

Snow Redistribution Processes

Intercepted snow in forest canopies and blowing snow on tundra enhance sublimation of the snow and reduce the total snow on the ground at spring melt. In regions of low precipitation, such as most of the tundra and the drier northern regions of the boreal forest, sublimation limits the water available for runoff. In dense coniferous canopies, interception can result in up to 40% of the snow sublimating, while in open or

deciduous forests it may be less than 10% (Pomeroy and Gray, 1994). Snow becomes entrained into the atmosphere during high wind events, which both redistribute snow on the ground and result in considerable sublimation. At the northern edge of the prairies, sublimation can comprise up to 40% of the snowfall (Pomeroy and Gray, 1994) and in tundra, over 10% (Marsh *et al.*, 1996).

Cold, high latitude snow covers behave differently to their temperate counterparts (Marsh, 1991a). Beneath temperate snow covers the ground heat flux is seldom important and a small flux into the basal snow helps to increase melt. In northern permafrost soils, heat flows from the snow to the ground. This increases the energy required to melt the snowpack, and delays melt runoff. Significant amounts of meltwater refreeze within the snow, soil and as basal ice. This also delays the start of melt runoff and extends the snowmelt period. Snowmelt infiltration into frozen soils plays an important part in controlling runoff. Depending on the magnitude of autumn rains and soil moisture content at freeze-up, snowmelt infiltration varies from zero to greater than the entire snowpack water equivalent. In addition, soil temperature controls the portion of the frozen soil infiltration that refreezes and will not be available for immediate runoff.

Effects of River and Lake Ice

Seasonal ice cover affects the characteristics of aquatic ecosystems. It controls the amount of light reaching the unfrozen water beneath the ice cover (Prowse and Stephenson, 1986). The high surface albedo of snow atop the ice means that any significant accumulation of snow reflects most of the incident radiation. Beneath the snowpack, black ice transmits most of the solar radiation through to the unfrozen waters, whereas white ice is strongly reflective. The duration of lake ice varies considerably over the study area. For example, Lake Athabasca (58°N) has a mean duration of ice cover from early November to mid-May, and an average maximum thickness of about 1 m. In contrast, lake ice cover near Alert, at 82°N, extends on average from late August to mid-July, with an average maximum thickness of about 2 m. Meanwhile, some high arctic lakes maintain their ice cover throughout the summer (Smol, 1988).

Ice prevents gas exchange between underlying waters and the atmosphere and may commonly lead to depletion of dissolved O₂ and the build up of reduced gases such as CO₂, CH₄ and H₂S. In shallow lakes, a substantial portion of the water column and total lake volume is incorporated into the ice cover, while a smaller portion remains unfrozen. Because solutes are excluded from the ice during freezing, the chemistry of the underlying water changes dramatically over the winter (Schindler *et al.*, 1974; Hobbie, 1980; Welch and Bergmann, 1985; Welch and Legault, 1986; Lesack *et al.*, 1991). Finally, the processes accompanying ice formation during freeze-up and break-up have a wide range of effects on the bed and banks of lakes and rivers. These include frazil ice impact on fish, anchor ice growth, elevated water levels, channel blockage and increased scouring of river banks and beds (Prowse, 1994). These processes have a large effect on the riparian geomorphology and vegetation (Scrimgeour *et al.*, 1994).

River Hydrology

The complexity of runoff magnitude can be illustrated for the Mackenzie Basin (Figure 2). Runoff varies from 100 mm/yr in the northern portions of the basin, to over 1000 mm/yr in the southern, mountainous parts. Mean annual discharge of 173 mm/yr averaged over the whole basin is approximately 42% of total precipitation input to the basin, with the remaining 58% being evapotranspired (Marsh and Prowse, 1993).

On an annual basis, it is often assumed that changes in storage are zero. However, that is not always the case and long-term fluctuations in groundwater, lake and glacial storage can occur. The hydrological effect of glaciers in a watershed is to store water during cold or wet periods, and to release water during warm periods. Lakes and wetlands also store water, although on shorter time scales.

Seasonal variations in flow are important to the freshwater ecosystems in river basins. Four regimes common to northern regions can be identified (Church, 1974; Woo, 1986). Arctic nival regimes occur in areas of continuous permafrost. Spring snowmelt dominates the hydrograph, and runoff from summer rain is generally small since precipitation is low. Winter stream flow is usually very low owing to limited groundwater contribution. Subarctic nival regimes are dominated by spring snowmelt, but summer rain

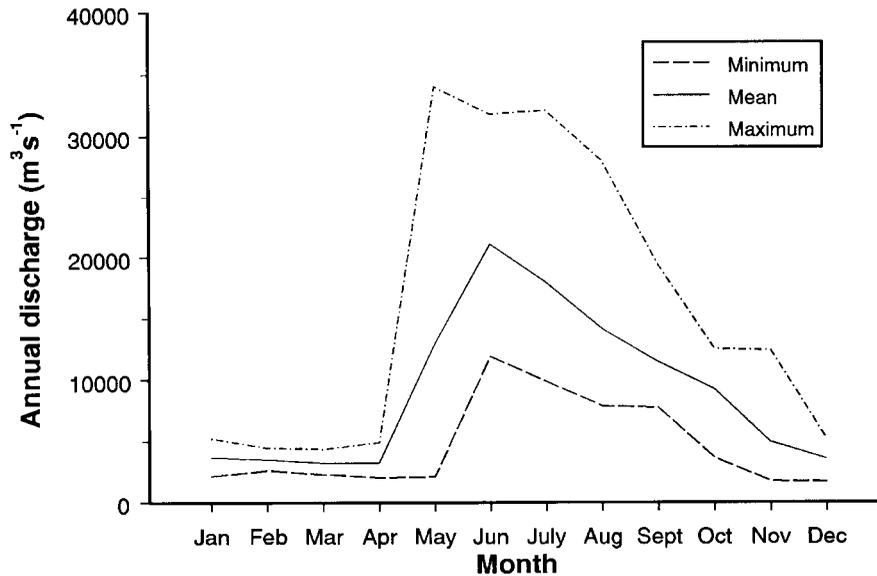


Figure 2. The average monthly discharge for the Mackenzie River at Arctic Red River. The basin at this point is 1.66×10^6 km²

storms may produce peak flow of similar size to the spring snowmelt (Watt, 1989). Discontinuous permafrost increases groundwater contributions and winter flow may be significant. Wetland regimes occur where drainage is poor owing to low relief or an impermeable substrate. Wetland basins, with low energy gradients, have significant temporary storage capacity, and therefore they tend to attenuate peak flows but still retain high yields. Finally, in proglacial streams, snowmelt runoff is important, but instead of a brief spring peak, flow increases throughout the spring snowmelt period and then continues to increase as meltwater is contributed from higher regions of the glaciated basin.

The Mackenzie River integrates the runoff from major sub-basins that display the characteristics of all four regimes. The main stream flow can be described as subarctic nival, with a dominant spring flood, significant summer peaks owing to rainfall runoff and discharge that continues throughout the winter (Figure 2).

The dramatic effects of ice on river flows are evident in the Mackenzie Basin. In northern portions, channels begin to freeze over in October, with a complete ice cover forming by January. Freeze-up is an important event because the flow conveyance of the channel is reduced as downstream ice cover is formed (Gray and Prowse, 1992). This is mainly a response to the higher roughness of ice-covered channels. As a result, upstream water levels rise as water is placed into storage behind the accumulating ice cover and a period of low discharge prevails downstream. The lowest discharge of the year may occur during freeze-up, not later in the winter when water delivery to the channel is at a minimum. In some cases, river icings can lead to a complete blockage of the channel system (Van Everdingen, 1974).

The Mackenzie, like most rivers in region 2, flows northwards from areas that are warmer to those that are colder. Thus, melt progresses from upstream to downstream. The resulting flood wave often progresses downstream more rapidly than the melt proceeds, and the flood wave encounters thick, resistant ice covers, resulting in very large ice jams (e.g. Andres and Doyle, 1984; Gray and Prowse, 1992). Ice jams make it impossible to measure discharge during what is often the major flood event of the year.

Lake Hydrology

In cold regions, lake ice plays an important hydrological role during the spring break-up. If a significant portion of the snowmelt runoff occurs before the lake ice has melted, floating ice may prevent wind-induced

Table II. Scenarios of temperature change ($^{\circ}\text{C}$) for a $2 \times \text{CO}_2$ scenario. GCM models: A, Atmospheric Environment Service, Canada; B, Geofluids Dynamics Laboratory, USA; C, United Kingdom Meteorological Service, UK (adapted from Mitchell *et al.*, 1990)

	Alaska–Yukon	Mackenzie	Keewatin, N. Manitoba, N. Ontario	N. Quebec Labrador	High Arctic
Winter					
A	2–8	4–8	4–12	8–12	8–12
B	2–8	0–4	2–8	6–12	8–12
C	2–8	2–6	4–8	6–8	4–8
Summer					
A	2–6	2–4	4–6	4–6	4–6
B	2–6	2–6	2–6	2–6	0–4
C	2–6	2–6	2–4	2–6	2–4

intermixing of the runoff and lake water. As previously mentioned, solute exclusion during the growth of the lake ice can increase solute concentrations substantially in the unfrozen water beneath the ice. The resulting differences in salinity between the unfrozen lake water and inflowing runoff can prevent intermixing while the lake remains frozen (Lesack *et al.*, 1991). In other small lakes with large catchments, a substantial portion of snowmelt can pass through the lake without mixing and this can reduce the utilization of the snowmelt nutrient load by the lake ecosystem (Welch and Bergman, 1985).

CLIMATE CHANGE

GCM Scenarios

A general idea of the potential magnitude of climate change in region 2 can be obtained from GCM (general circulation model) scenarios for $2 \times \text{CO}_2$ warming (Table II). In both summer and winter, composite GCM results indicate that Alaska, Yukon and the Mackenzie Basin could undergo increases of about 4°C ; in central parts of region 2, this changes to 4 and 7°C for summer and winter, respectively, and, in the east and the Canadian Arctic Archipelago, increases of the order of 4 and 9°C are suggested. Models generally concur that precipitation will increase in summer and winter, but little agreement exists on the magnitude and regionality (Mitchell *et al.*, 1990). Given that present day precipitation in region 2 is poorly known, there can be little confidence in $2 \times \text{CO}_2$ projections for this variable. Cohen (1993) reports on a composite scenario for the Mackenzie Basin that is derived from a GCM model, contemporary station data and historical and palaeoclimatic information to predict an increase of 3°C in annual temperature and a 10% increase in precipitation. From a selected suite of different GCMs, Maxwell (1992) also provides averages for the lower Mackenzie that indicate substantial temperature and precipitation increases. Models, thus, generally agree in indicating moderately large temperature increases throughout region 2 in summer, and, in winter, large to very large temperature increases in the central and northern portions of the region.

Historical Variability and Palaeoclimatic Reconstructions

The instrumental record indicates a temperature increase of 1.7°C in the forested Mackenzie Basin between 1895 and 1991, and about 0.6°C in areas of tundra region between 1922 and 1991 (Skinner and Gullet, 1993). No cause or effect can be ascribed to these short-term changes and patterns since they are well within the natural variability of the temperature record. Also, regional consistency in temperature change in region 2 has not been demonstrated.

For a 30-year period, Isaac and Stuart (1992) demonstrated a close correspondence between higher than normal precipitation and above-average daily temperatures. This suggests that the amelioration of very cold temperatures in these regions has the potential to increase precipitation, particularly in winter, and especially

in the central, eastern and northern areas. This is encouraging because without increased precipitation many systems would dry up under warmer temperatures.

Palaeoclimatic reconstructions during the Holocene cast some light on the magnitude of climate change or variability. From dendroclimatology analysis, Szeicz and MacDonald (1995) reconstructed June–July temperatures for the central Yukon and northern and middle Mackenzie Basin for the period 1638 to 1988. Szeicz's record generally agrees with that of Bradley and Jones (1993), which uses composite tree ring and Greenland ice core proxy data. Both records show a fairly steady increase in temperatures in the last 150 years, of the magnitude of 2°C, and also indicate that late 20th century summer temperatures are as warm or warmer than any in the period 1638–1980. There is also general agreement with the dendroclimatic reconstruction of Jacoby *et al.* (1985) for Alaska and the central Yukon, except that this latter study indicates a post-1950 temperature decrease. All summertime dendroclimatic records indicate that medium-term temperature variations of a similar but lesser magnitude to those suggested by GCM results have been experienced in the recent Holocene. Evidence from eastern parts of region 2 is less easily interpreted because of the dominance of fire in the northern forest dynamics during the last 3000 years (Payette and Morneau, 1993). Palynological evidence suggests that on the Tuktoyaktuk Peninsula near the Mackenzie River Delta, forest limits were at least 70 km polewards of the current tree-line between 9500 and 5000 BP (Ritchie, 1984; Spear, 1993). This evidence is important because it illustrates that the boreal forest has migrated to the Arctic coast during the Holocene (Roots, 1989) and that high latitudes respond strongly to global climate warming of the magnitude indicated by GCM scenarios.

Based on stratigraphic evidence in the central and southern Yukon, Burn (1993) argues that the Holocene has been the only non-glacial period with widespread permafrost. The temperature of the permafrost in these regions is close to 0°C and with small warming could undergo substantial thaw. Burn (1993) notes particularly that cold surface temperatures and thin snow cover caused by the blocking effect of the St Elias Mountains may be responsible for maintaining the permafrost, and that these blocking effects are not simulated by output of GCMs for $1 \times \text{CO}_2$. The implication is that $2 \times \text{CO}_2$ scenarios probably do not model that influence either.

Koerner's (1991) analysis of stable isotope ratios in glacier ice cores features the following variability. Whereas at higher elevations in Antarctica and Greenland no melting occurs at all, in the Canadian Arctic, melting over the entire ice cap surface occurs nine years out of ten. From 1200 AD to the 1970s there have been several periods in which strong melting persisted over five or more decades, but the period with the strongest magnitudes of melt has occurred during the last 100 years. Koerner cautions, however, that this warming is not unusual in the longer record, and much larger changes are apparent in the last one hundred thousand years. He also notes that the occurrence of the coldest period of the Holocene just 200 years ago (Little Ice Age) tends to highlight the present warm period.

Douglas *et al.* (1994), using diatom indicators and palaeolimnological techniques in the High Arctic, found relatively stable diatom populations over the last 8000 years, but then noted striking successional changes over the last 200 years. They attribute climate warming as the most likely cause of these successional changes.

Overall, there appears to be a congruence in the various indicators that suggests a substantial 20th century warming trend in much of region 2. There is convincing evidence that high latitudes do give a unique high magnitude response to global climate change.

BROAD-SCALE EFFECTS OF CLIMATE WARMING

The permafrost that underlies region 2 varies in thickness along an air temperature and general latitudinal gradient (Table III). It is in those regions where the annual mean temperature is higher than -6°C , or the annual mean ground temperature is hovering around 0°C , that permafrost could disappear completely. By analogy, with current climate–permafrost distribution, the long-term effects of warming scenarios produced by GCM scenarios would be to move the permafrost boundaries polewards by about 500 km or so

Table III. Permafrost thicknesses (m), sample ground temperatures (°C) and mean air temperatures (°C) for select Canadian stations (after Brown, 1970). Stations are ordered according to decreasing daily mean air temperatures

Location	Latitude Longitude	Thickness (m)	Ground temp (°C), Depth (m)	Air temp. (°C)
Thompson, Manitoba	55°45' N 97°54' W	15	0, 8	-4.0
Uranium City, Saskatchewan	59°32' N 108°43' W	9	0, 9	-4.0
Schefferville, Quebec	54°50' N 67°00' W	>75	-0.2, 60	-4.5
Yellowknife, NWT	62°28' N 114°27' W	60-90	0, 12	-5.5
Normal Wells, NWT	65°19' N 126°46' W	45-60	-2.8, 50	-6.2
Churchill, Manitoba	58°45' N 94°04' W	30-60	-2.2, 10	-7.2
Inuvik, NWT	68°18' N 133°29' W	>90	-3.9, 30	-9.1
Rankin Inlet, NWT	62°45' N 92°05' W	300	-9.0, 30	-11.6
Winter Harbour, NWT	74°50' N 110°46' W	460	ND	-16.0
Resolute, NWT	74°43' N 54°59' W	400	-13.0, 30	-1.6

(Woo *et al.*, 1992). This would reduce the area of permafrost to less than 80% of its present coverage. Probably the most profound effect from warming would be the melting of widespread massive ground ice (Figure 3a) which is concentrated in the top few metres of permafrost terrain, and which is particularly susceptible to climate warming. This would induce massive terrain slumping (thermokarst) with effects on all surface features, including drainage patterns and sediment loads in rivers and lakes, thus affecting aquatic ecosystems.

Groundwater in permafrost areas may be found above (suprapermafrost), within (inrapermafrost) or below (subpermafrost) the frozen layer (Woo *et al.*, 1992). The suprapermafrost zone provides little water storage in winter and in early spring when the active layer is frozen. In summer its storage capacity changes with thawing and refreezing. Occurrence of inrapermafrost groundwater is governed by the vertical distribution of permafrost. The subpermafrost groundwater often has higher chemical concentrations because it has a longer residence time to be in contact with earth materials. Warming of the permafrost will extend the thaw season, allowing a longer period of water infiltration and deeper active layer development (Hinzman and Kane, 1992; Kane *et al.*, 1992), and a concomitant increase in hydrological activities in the suprapermafrost zone (Woo *et al.*, 1992).

A deeper active layer and a longer unfrozen period will reduce overland flow as both infiltration and active layer water storage capacity increase. Patchy arctic wetlands, currently supported by surface flow from late lying snowbanks, would disappear. Increasing the depth of the active layer will threaten the survival of many arctic wetlands which exist because impermeable permafrost prohibits deep percolation and impedes drainage of the active layer. Similarly, some small lakes exist because the permafrost isolates them from the regional groundwater system or from surface flow. Permafrost degradation will open subsurface flow connections, thereby draining these lakes (Mackay, 1992; Woo *et al.*, 1992).

The spring melt period should be earlier and possibly stretch over a longer time period because of lower radiation receipts occurring earlier in the year (Kane *et al.*, 1992; Figure 3b). Because of increased active layer storage capacity, peak flows associated with both snowmelt and rainfall events would be similar or lower than at present. These expectations are consistent with the analogue of northern basins. Those with

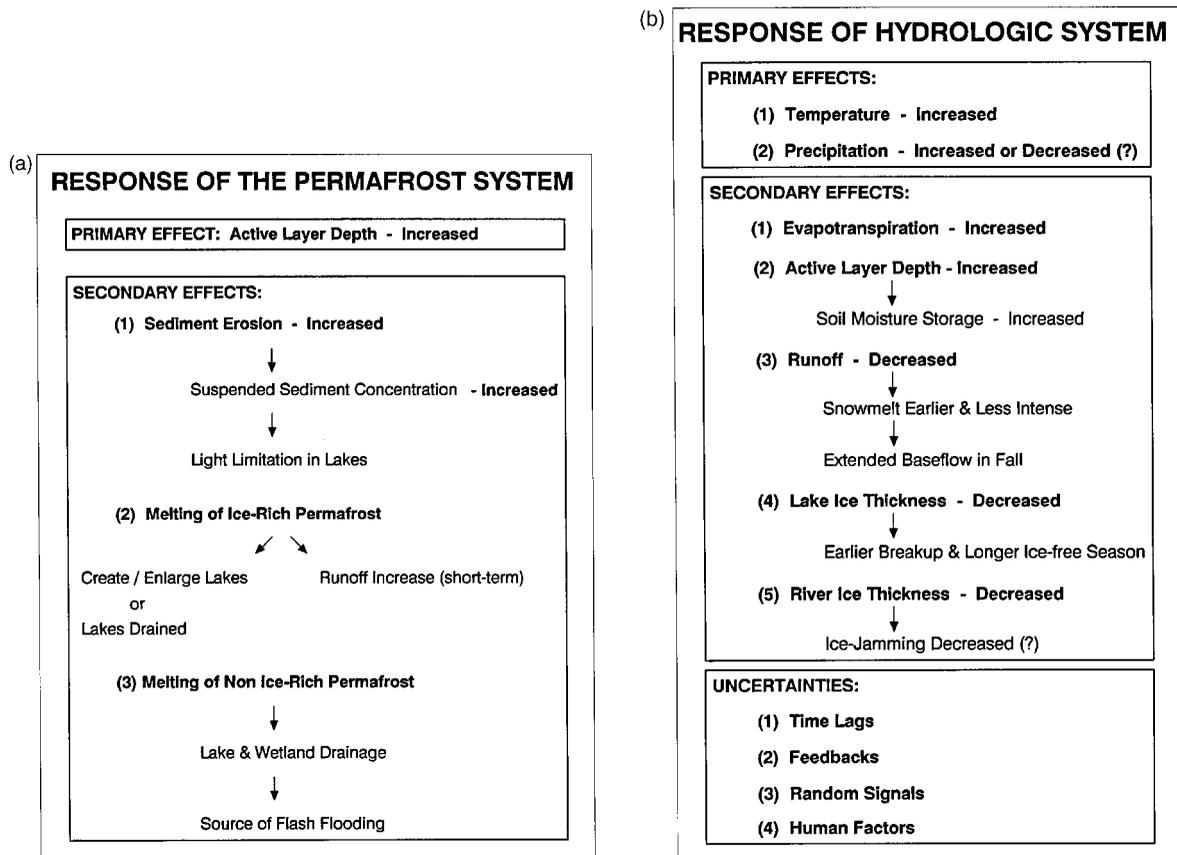


Figure 3. (a) A conceptual summary of the potential response of the permafrost system to climate change. Major primary and secondary effects are listed and potential higher order effects are indicated with arrows. (b) A conceptual summary of the potential response of the hydrological system to climate change. Major primary and secondary effects are listed and potential higher order effects are indicated with arrows

less permafrost, but receiving comparable amounts of precipitation, produce lesser amounts of runoff and smaller ranges in flow volumes.

Lake ice covers will be thinner, will break up earlier and freeze up later. Thus, there will be a longer ice-free season. For large north-flowing rivers, thinner ice covers, smaller temperature gradients between southern and northern portions of the basins and reduced spring flood peaks could lead to less frequent and less severe ice-jamming during the spring break-up.

In the snow-free season, evapotranspiration often exceeds precipitation giving a negative water balance (Woo *et al.*, 1992). An increase in the length of the snow-free period and in summer temperature will increase evaporation and transpiration. If precipitation does not change, or decreases, water balances will become more strongly negative. If there is an increase in precipitation that matches that of evaporation the water balance will not change. Only an increase in rainfall, which exceeds that of evaporation, will give a positive summer water balance to increase lake levels, recharge ground moisture and increase runoff and river flow. The critical equation with respect to the effect of greenhouse warming on the water balance thus involves both the magnitude of the warming effect and the responses of the precipitation regime. Changes in the water balance are particularly important to the surface moisture regime of the Arctic Islands, where, at present, in unglaciated basins, surface runoff and stream flow occur only during spring snowmelt. After melt the terrain becomes hydrologically inactive until the following early summer period. Wildlife is sustained through stored

water in localized ecological niches such as Truelove Lowland on Devon Island (Bliss, 1977) and Hot Weather Creek on Ellesmere Island (Figure 1b). Such niches will be strongly influenced by changes in the water balance.

Contemporary evidence suggests that hot and dry summer conditions will increase overall evapotranspiration from wetlands even when they develop a substantial moisture deficiency. This arises because of the large stomatal conductance of transpiring plants, and from the ability of porous peat soils to supply water from wet subsurface layers when atmospheric demand is large (Rouse *et al.*, 1992). Thus, where vascular plants are dominant, they will continue to transpire until the water table drops well below the surface. Where non-transpiring vegetation, such as *Sphagnum* moss or lichen, is dominant, however, evaporation is inhibited after surface drying. A hot, dry year promotes deeper thaw of the active layer than does a comparable wet year (Rouse *et al.*, 1992). At tree-line, with the same ambient conditions, wet tundra is more sensitive to changes in climate than is forest at tree-line and the differences in sensitivities are a function of both physical and physiological responses within the ecosystems (Lafleur and Rouse, 1995). Individual ecosystems in continuous permafrost near tree-line all have differing sensitivities to seasonal changes in temperature and precipitation. For example, the response in evaporative water loss to increases or decreases in air temperature is greatest for dwarf willow–birch forest, and decreases through sedge fens, open forest, upland lichen heath and shallow tundra lakes (W. R. Rouse, unpublished data).

Flora are more or less in equilibrium with the climate, including soil climate. Summer temperature, the length of the summer growing season and intensity of summer warmth show the greatest correlation with vegetation distribution and species diversity (Edlund and Alt, 1989). Seasonal snow cover and soil moisture availability also influence the distribution of species and communities. Permafrost can present a barrier to the downward development of roots. It also ties up water in the frozen state that is unavailable for transpiration. In addition, frost heaving dislocates and damages plant roots, and the maintenance of cold rooting zones and cold soil water add stress factors for all vascular plants. By maintaining a high water table, permafrost can promote anaerobic conditions within rooting zones. Such conditions favour the development of non-vascular plants and contribute to the poor growth of vascular plants, especially boreal forest species near tree-line (Woo *et al.*, 1992). Under a warmer and wetter climate change scenario, there is some consensus that contemporary vegetation belts would move polewards, although there would be a lag between temperature increase and migration. The palaeobotanical record supports this response. Under a warmer and drier scenario, there would also be a northwards migration, but this would favour xerophytic vegetation with less biomass.

GENERAL RESPONSES OF AQUATIC ECOSYSTEMS TO CLIMATE CHANGE

Aquatic Habitat and Primary Production

The general potential responses of aquatic ecosystems to increased temperature and decreased runoff are summarized in Figure 4. The response to increased temperature will be a longer ice-free season for lakes, which will increase the length of the stratified season and could increase the depth of mixing. The longer stratified season should lead to lower oxygen concentrations in the hypolimnion of lakes and an increased stress on cold water organisms.

A longer ice-free season should also enhance the underwater light climate for primary producers and increase the length of the growing season. However, this may be offset, potentially, by a deterioration in light availability because of two different mechanisms. First, in regions where extensive melting of permafrost may occur, land subsidence and formation of new drainage systems could lead to extensive erosion and increased turbidity in streams and lakes. In Southern Indian Lake (northern Manitoba), analogous factors decreased light penetration sufficiently to cause a switch from nutrient limitation to light limitation of primary production, which more commonly controls the primary production of northern lakes (Hecky and Guildford, 1984). Secondly, increases in average DOC concentrations and associated water darkening may also occur among lakes and streams.

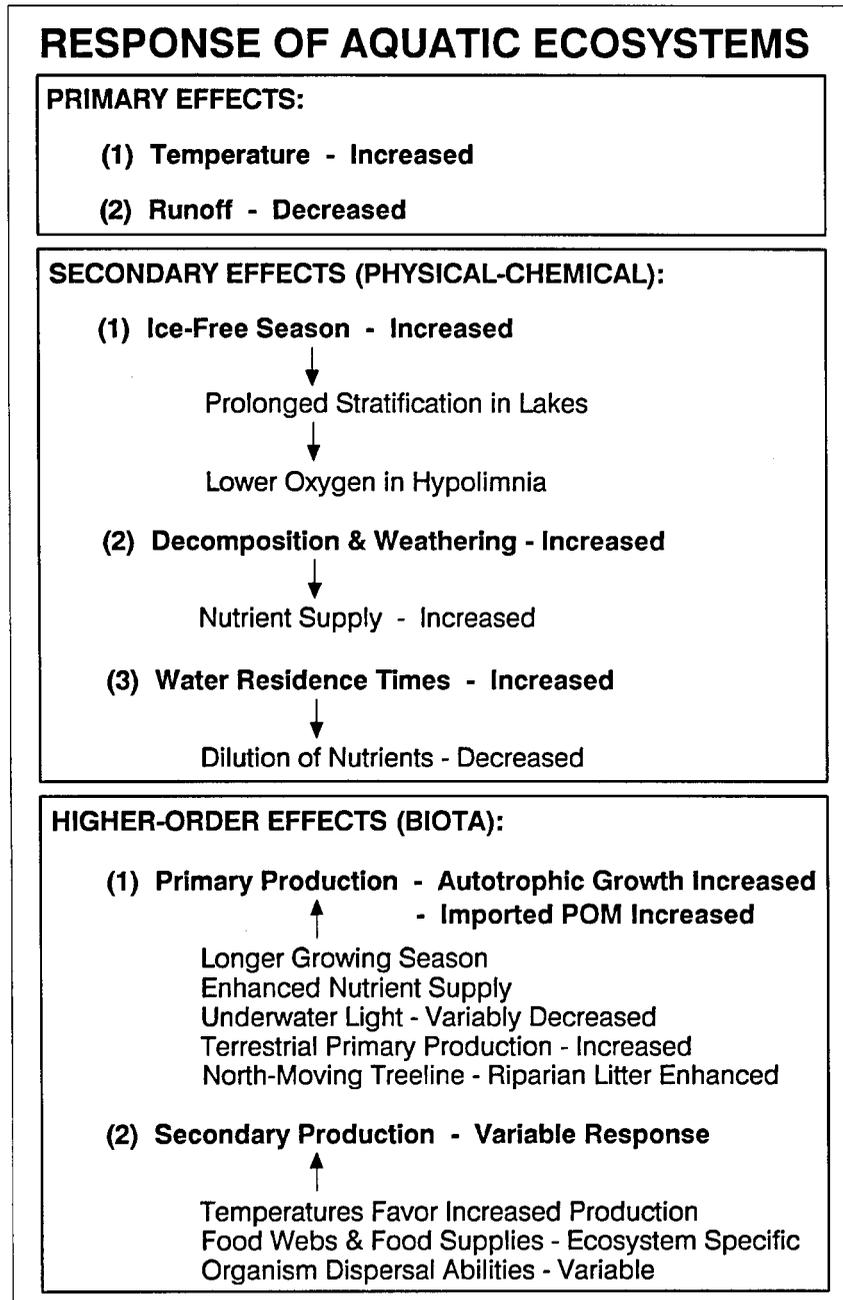


Figure 4. Potential response of aquatic ecosystems to a temperature increase and a runoff decrease

In northern aquatic ecosystems, both *in situ* primary production and imported organic matter from terrestrial ecosystems can be important sources of energy to fuel aquatic food chains. A general warming through the region should increase terrestrial primary production. It is expected that primary production would also increase because aquatic autotrophs tend to be limited by nutrients. The microbial degradation of organic matter is strongly temperature dependent. Consequently, both the amount of organic matter

imported from terrestrial ecosystems and the rate at which the matter is processed should increase. Increased rates of nutrient remineralization derived from microbial decomposition should lead to an enhanced nutrient supply in northern aquatic ecosystems. A general decrease in the amount of runoff would lead to lower flushing rates and the decreased dilution of nutrients and longer contact times with rock minerals within their catchments. In addition, increased temperatures would, at least modestly, increase rates of rock weathering. The net effect of increased weathering plus decreased dilution would be to further enhance the nutrient supply. If an enhanced nutrient supply stimulates the growth rates of aquatic autotrophs, and this is coupled with a longer growing season, there should be an overall increase in annual primary production.

Secondary Production

Secondary production represents a combination of complex microbial and animal communities that process autotrophic production and imported organic matter for their own growth, maintenance and reproduction. Food supply and temperature represent primary regulators on the growth of consumer populations (Benke, 1984; Sweeney, 1984). While the effect of warmer temperatures should generally be favourable throughout the region, the food supply available for consumers would be ecosystem specific, thus giving a variable response of secondary production to climate warming.

The dispersal ability of the organisms may control overall changes in secondary production. Most of the fauna contributing to secondary production, except fishes, have high dispersal ability and should quickly take advantage of warmer temperature regimes. However, there are the glacial relict fauna, which represent animals distributed by and surviving in large proglacial lakes during the last deglaciation. Some of these, such as *Pontoporeia affinis* and *Mysis relicta*, are important fish food in many northern lakes. The potential loss of this fauna under warmer, less oxic conditions, could cause short-term (years to decades) disruptions in the food chain until a warmer water fauna became established.

Climate warming would probably initiate a complex series of immigrations and extinctions of fish species over broad areas. The present distribution originated from a few major refugia that existed during the Pleistocene. As the glaciers waned, the proglacial lakes at the southern boundary of the ice receded northwards and provided ready access for fishes into what became modern lakes. These fishes acclimatized (Legendre and Legendre, 1984) and many species have never before been exposed to temperatures as high as those forecast by GCM models. If these lakes become warmer and less oxygen rich, at least some of these species could be extirpated in southern lakes and in shallower northern lakes in the region. Warmer water species could invade and the short-term effects of the potential invasion of numerous species is largely unknown. However, the destabilizing effects of past introductions of species into a variety of aquatic ecosystems is well documented.

There is some evidence that the total biomass of fish communities may not change significantly in response to climate warming. For example, there is no relation between temperature and yield in Canadian lakes (Schlesinger and Regier, 1982). Schlesinger and Regier (1983) suggest that this is a result of lakes having fish species with different thermal optima. Hence, although the yield of individual species does vary with temperature, there are trade-offs so that the aggregate is independent of temperature. This inference is based on stable fish communities under present temperature conditions, and it is unknown whether this will be maintained after climate warming occurs and the fish communities become destabilized.

Stream Communities

The break-up of river ice represents a major annual disturbance even in high latitude rivers. It is characterized by large increases in current velocity, stage, water temperature, concentrations of suspended materials and substrate scouring (Prowse, 1994). Scrimgeour *et al.* (1994) have argued that if the intermediate disturbance hypothesis (Connell, 1978) is applicable to streams, a shift from intense, dynamic break-ups to less severe, thermal events could potentially alter community richness. Such a shift could well occur in north-flowing rivers as a consequence of climatic warming. Moreover, alteration to flow regimes as a result of climate warming could also alter the structure of aquatic and riparian communities in rivers by affecting ice

break-up intensity. Despite the potential importance of river ice break-up, there are few empirical investigations thus far that have addressed the effects on river communities.

Small streams represent shallow-water habitat that has close linkages to riparian vegetation. Because stream communities can be highly dependent on organic matter derived from riparian vegetation, temperature effects can be important. Microbial processing of organic matter and organismal growth and survival may be strongly linked to temperature. Oswood *et al.* (1992) have argued that a 4°C increase in water temperature over a four-month ice-free season can represent an increase of about 500 degree days, or roughly a 50–100% increase in yearly cumulative warmth among Alaskan rivers and streams. An increase in the length of the ice-free season and decreased freezing to the substrate in shallow areas would, potentially, be beneficial to invertebrates and fish (Oswood *et al.*, 1992). However, the potential effect of increased temperature on net processing of organic matter by invertebrate shredders and microbes in concert is less clear. Irons *et al.* (1994) examined litter processing rates along a latitudinal gradient involving streams in Costa Rica, Michigan and Alaska. Surprisingly, the processing rates were similar at the Michigan and Alaskan sites, which should not be the case if temperature were the principal factor controlling the breakdown rate. The authors suggest that the relative importance of invertebrate versus microbial processing may change on a latitudinal gradient, with invertebrates being more important in high latitude systems. A potential consequence is that processing rates may not increase in association with climate warming.

RESPONSES TO CLIMATE WARMING IN SELECTED ARCTIC ECOSYSTEMS

High Arctic Ponds

Arctic ponds are standing water bodies less than 2 m deep that freeze to the bottom, whereas lakes are sufficiently deep that water remains unfrozen under the ice cover (Sheath, 1986). As an example of high arctic ponds, this paper focuses on a suite of 36 ponds from Cape Herschel, Ellesmere Island (Figure 1b), which have been studied extensively over a number of years. Cape Herschel (78°37' N, 74°42' W) is a rugged peninsula (2 × 5 km²) of high relief (0–285 m asl) which lies close to the northern extent of the North Water, a polynya that remains ice free most of the year.

The physical and chemical characteristics of the study ponds have been summarized in Douglas and Smol (1994). The ponds are small (the largest being about 1 km long) and shallow (typically <1 m deep, and usually <0.5 m deep). These clear, oligotrophic ponds are completely frozen for at least 10 months of the year. During the short summers, water temperature warms substantially to a recorded maximum of 17°C. Temperatures, however, are typically less than 10°C. The majority of ponds are alkaline, reflecting the presence of calcareous tills overlying the granitic bedrock. Major ion concentrations are similar at most sites, and change over the summer owing to the combined effects of cryoconcentration, snowmelt dilution, evaporation and other factors (Douglas and Smol, 1994). Because the ponds are frozen most of the year, vertebrate predators are generally absent, with the possible exception of some migratory birds. As a result, the ponds are teeming with *Daphnia*, copepods, chironomids, rotifers and other invertebrates (Nogrady and Smol, 1989).

Small, shallow water bodies, such as the Cape Herschel ponds, may be especially sensitive to climate warming (Smol *et al.*, 1991; Douglas *et al.*, 1994), but will be dependent on the amount and timing of precipitation that the area might receive. However, assuming air temperature will increase, the following scenarios are proposed.

With increased temperatures and a longer growing season, many limnological changes would be expected. Presently, the ponds are only free of ice from late June or early July, and may refreeze by August (Douglas and Smol, 1994). The length of the ice-free period, and hence growing season, would significantly increase with small warming (Figure 3b). Total annual primary production may increase in the ponds, and more complex periphytic communities could also develop (Douglas and Smol, 1993). Decomposition processes would accelerate, with concomitant increases in nutrient cycling. Assuming that precipitation does not

also increase, evaporation and concentration in the ponds would be enhanced, resulting in elevated conductivities. Since many of the ponds are presently very shallow, some could desiccate completely.

Tree-line Lakes

Strong climatic and limnological gradients exist across north–south transects through the Yukon and North-west Territories (Pienitz, 1993; Pienitz and Smol, 1993; Pienitz *et al.*, 1995). For example, a typical transect that included 59 lakes from Whitehorse to north of Tuktoyaktuk showed most lakes to be dilute (mean conductivity = 160 $\mu\text{S}/\text{cm}$) and slightly acidic to alkaline ($\text{pH} = 5.9\text{--}9.3$). Although several limnological variables could change polewards, dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) concentrations clearly change. DOC and DIC also appear to be important chemical variables influencing diatom species assemblages in lakes and some streams (Miller *et al.*, 1992; Pienitz and Smol, 1993). Water depth, surface water temperatures, ice and snow cover are also variables that influence the diatom assemblages (Pienitz *et al.*, 1995). For lakes located near the arctic tree-line, changes in DOC may be especially important. Of particular significance to northern lakes, DOC is closely related to the composition and density of terrestrial vegetation (e.g. spruce trees) in the catchment. Consequently, any climate-induced changes in the position of tree-line will affect the limnology of lakes at this ecotonal boundary. Forsberg (1992) estimates that, in Fennoscandia, increased warming would promote higher DOC levels in lakes. In areas north of tree-line, DOC concentrations in groundwater vary with overlying vegetation type (Kling, 1995), and DOC concentrations may change if climate alters the vegetation composition.

DOC has an important influence on, for example, arctic diatom species assemblages (Pienitz and Smol, 1993), although the specific causative factors are not yet determined. In addition, DOC concentrations control the activity of decomposition by bacteria in some lakes on the Alaskan North Slope (Kling, 1995). Lakes with the smallest lake volume:catchment area ratios are likely to be most affected. As with all these regions, however, lake water DOC is only one of several variables that will be changing with a warming climate.

Changes in DOC and related chemical changes would be only one limnological effect of trees migrating to a lake's catchment. For example, evapotranspiration rates will change, with resulting hydrological effects. The amount of wind mixing that a lake would be subjected to would decrease, thus affecting the physical limnology of the system. Many related limnological variables would also be affected.

A few saline lakes are found in the central Yukon (Pienitz *et al.*, 1992). Preliminary data indicate that changes in these high latitude saline lakes are similar to those recorded in more southern regions (Pienitz *et al.*, 1992; Veres *et al.*, 1995). If, with greenhouse warming, evaporation rates are higher, and precipitation does not increase concurrently, these athalassic lakes would increase in salinity, with accompanying dramatic effects on the aquatic biota. Moreover, because these lakes are situated in low precipitation areas, possible further decreases in snow and rainfall, as well as increased evaporation rates, may greatly decrease their size or they may disappear completely.

Shallow Tundra Lakes and the Food-web

Shallow arctic tundra lakes can be surprisingly productive. Some in the western Arctic have annual productivities higher than temperate lakes much further south (Ramlal *et al.*, 1994). Myriad such lakes on the Tuktoyaktuk Peninsula support the feeding activities of abundant migratory and non-migratory populations of broad whitefish and northern pike (Hesslein *et al.*, 1991). A detailed lake carbon budget demonstrated that benthic photosynthesis provided 50% of the organic carbon available to the food-web of the lake, while phytoplankton (20%) and allochthonous carbon (30%) provided lesser amounts (Ramlal *et al.*, 1994). Benthic photosynthetics were most likely carbon limited as in many lakes (Hecky and Hesslein, 1995). Carbon dioxide limitation of benthic photosynthesis occurs within a diffusion-limited boundary layer overlying benthic algae. A $2 \times \text{CO}_2$ atmosphere would retard lake degassing and raise PCO_2 in bulk solution. Consequently, benthic photosynthesis could be enhanced if the lakes maintain a positive hydrological balance, and benthic carbon production would provide an even larger share of total organic

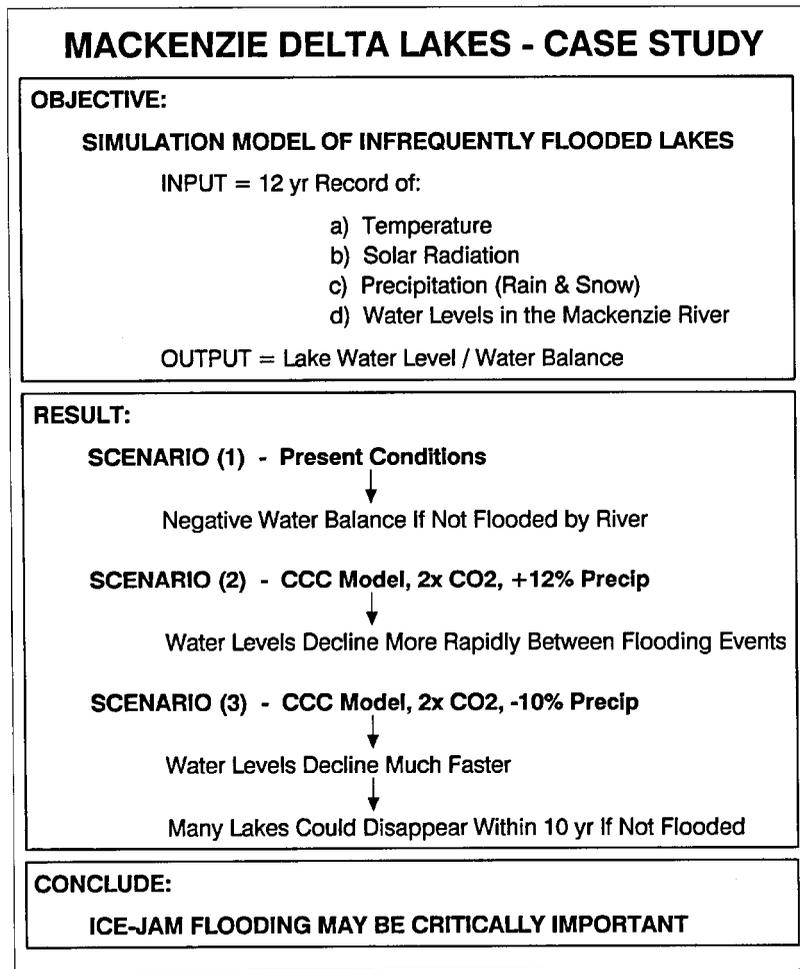


Figure 5. A conceptual summary of the results of a simulation model (Marsh and Lesack, 1996) to evaluate the potential effects of climate change on lakes in the Mackenzie River, Delta. The study focused on lakes that are not necessarily flooded by the river each year (i.e. infrequently flooded lakes) and utilized climate change scenarios forecast by the GCM of the Atmospheric Environment Service, Environment Canada

carbon flow in these shallow lakes. Warmer atmospheric temperatures and longer open water periods would also contribute to higher productivity.

Mackenzie Delta Lakes: an Example of River–Lake Synergism

Lakes in the Mackenzie River Delta may be particularly sensitive to climate change. Water levels are controlled primarily by Mackenzie and Peel River discharge to the delta, growth of river ice, ice break-up and jamming, and changes in sea level (Marsh and Schmidt, 1993). The resulting variations in channel water levels control the flooding of approximately 25 000 delta lakes (Marsh and Hey, 1989). Since these delta lakes tend to have a negative water balance between flooding events (Marsh, 1991b), and changes in the hydrological regime of the Mackenzie Basin could have significant environmental effects (Marsh and Ommanney, 1991).

Figure 5 shows a model that simulates the water balance and lake water levels for Mackenzie Delta lakes that are infrequently flooded (Marsh and Lesack, 1996). A 12-year record of daily air temperature, solar

radiation, rain and snowfall, and river levels is used as model input to simulate ice growth rate, maximum ice thickness, melting of the ice cover, duration of the ice-free period and evaporation and lake water levels during the ice-free period (Figure 5). It successfully predicts the major hydrological dynamics of a representative lake over the period of record.

Under present climatic conditions, the 'model lake' consistently shows a slight negative water balance if not flooded by the river. For the Mackenzie Delta region, the GCM of the Canadian Climate Centre (Boer *et al.*, 1990) indicates an increase in air temperature of 3°C for JJA, and 5°C for DJF, and precipitation increases of 15 and 10%, respectively, are forecast. Under this $2 \times \text{CO}_2$ scenario, water levels in the 'model lake' decline more rapidly between flooding events than under the present climate. Since it is generally recognized that forecasts of precipitation by GCMs are not as reliable as temperature, the effect of a 10% precipitation decrease was also modelled. Under this scenario, water levels in the 'model lake' decline much faster between flooding events than at present and many lakes within the delta would disappear within 10 years. In both climate warming scenarios the lake ice cover is generally thinner and the ice-covered period is consistently shorter.

The above evidence indicates that, despite potential increases in precipitation, evapotranspiration may increase sufficiently so that less water will be available to lakes than under the present climate. Also, the model demonstrates the potential importance of ice-jam flooding in maintaining the water balance of delta lakes in north-flowing river systems. Significant changes in the frequency or severity of ice-jam flooding by itself would have a major effect on these lakes.

Indirect evidence of the effects of flooding is provided by the hydrological regime of the Peace–Athabasca Delta, which has been changed significantly by the Bennet Dam on the Peace River. Simulations of natural and regulated water levels in the delta (Farley and Cheng, 1986) demonstrated that peak water levels in the delta have been significantly lower than under natural conditions. Less frequent flooding of perched lake basins within the delta has been evident with significant effects on the delta ecosystem (Peace–Athabasca Delta Implementation Committee, 1987). A number of perched lakes last received water in 1974, and even during 1990, when the highest flows on record occurred, the perched lakes did not receive any floodwater. Ice-jams represent a critical process that, historically, had raised floodwaters sufficiently to flood these lakes (Prowse and Lalonde, 1996).

Alaska Lakes and Rivers, Nutrient Cycling and the Food-web

Global climate change may affect arctic aquatic ecosystems directly through increased temperatures or through increases or decreases in nutrients to these systems. Nutrient input to Toolik Lake is primarily through the inlet streams and occurs during spring snowmelt, with up to 30% occurring in the first 10 days of stream flow (Whalen and Cornwell, 1985). The primary productivity in lakes and ponds (Miller *et al.*, 1986; Kling *et al.*, 1992) and rivers (Petersen *et al.*, 1985) on the North Slope of Alaska is very low owing to low levels of phosphorus or colimitation of phosphorus and nitrogen. The range of chlorophyll in lakes and ponds is 0.3 to 148 $\mu\text{g}/\text{l}$, and in rivers it is 0.1–9.4 $\mu\text{g}/\text{cm}^2$ (Kling *et al.*, 1992).

Understanding of these effects is often complicated by complex food-web interactions. Arctic lake ecosystems near Toolik Lake, Alaska, are trophically simple (Kling *et al.*, 1992; McDonald *et al.*, 1996; Figure 6). Lakes may have some or all of the trophic linkages shown; food-web complexity is determined by the fish species present, landscape position, geological history and lake depth. Typically, ponds in the area have no fish. Rivers in the area have grayling in them, and in some cases anadromous arctic char.

In a survey of lakes in the Alaskan arctic coastal plain, no significant correlations of zooplankton species and chlorophyll *a* concentration were found (Kling *et al.*, 1992). O'Brien *et al.* (1992) found that with a 12-fold experimental increase in primary production, grazing zooplankton increased less than twofold. Although microplankton densities appear to be correlated with increased primary production (Ruble, 1992), fish predation plays an important role in structuring the macrozooplankton community.

Previous work has shown that arctic lakes and rivers near Toolik have strong benthic–pelagic coupling through the food-web. In lakes, the distribution of the large snail *Lymnea elodes* is controlled by lake trout

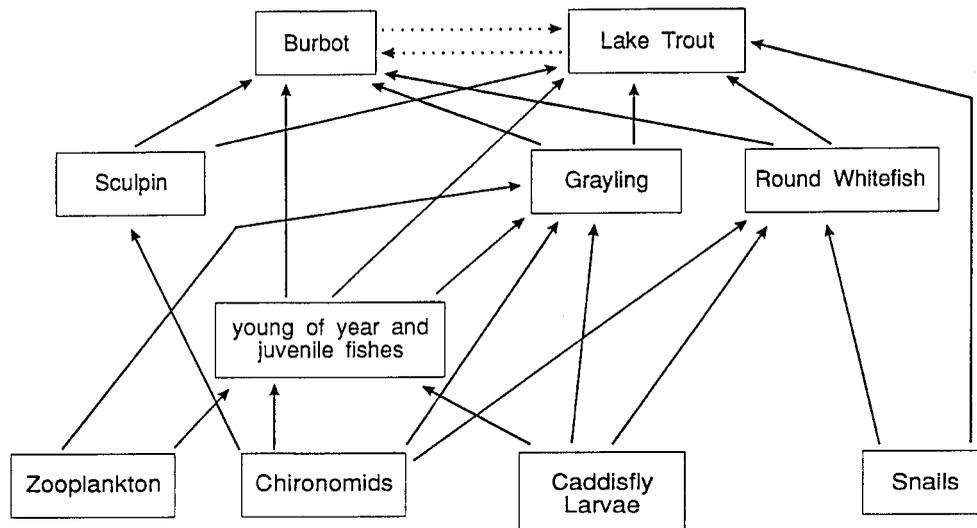


Figure 6. Lake trout are the dominant predator in the Toolik Lake food-web in arctic Alaska because of their numeric superiority and large adult size (based on McDonald *et al.*, 1996)

(*Salvelinus namaycush*) (Merrick *et al.*, 1992). In the absence of lake trout, algal biomass limits snail growth and abundance (Hershey, 1992a). Chironomids dominate the benthic insect fauna found in lakes; their abundance, biomass and community structure are controlled by slimy sculpin (*Cottus cognatus*), invertebrate predation and habitat complexity (Goyke and Hershey, 1992). In rivers, macroinvertebrate consumers are food limited (Hiltner and Hershey 1992; Peterson *et al.*, 1993).

Lake trout are the dominant fish in most large lakes in the Toolik Lake area (Figure 6), but arctic char (*Salvelinus alpinus*) hold a similar position in the food chain in some lakes. Lake trout control the distribution and abundance of large snails (Hershey, 1992b; Merrick *et al.*, 1991), slimy sculpin (McDonald and Hershey, 1992; Hanson *et al.*, 1992), and most likely limit recruitment and in-lake distribution of all salmonines (McDonald *et al.*, 1992). Arctic grayling (*Thymallus arcticus*), present in lakes, feed primarily on zooplankton when small (O'Brien *et al.*, 1979), and switch to emerging and ovipositing insects as they get larger (Merrick *et al.*, 1992). Grayling also occur in rivers, and feed primarily on drifting insects (Hobbie *et al.*, 1995). Round whitefish (*Prosopium cylindraceum*) feed on small-bodied snails (Merrick *et al.*, 1992). Burbot (*Lota lota*) feed primarily on sculpin.

Lake trout act as a keystone predator in these systems. However, because of the low food supply and low temperatures, lake trout are near their physiological limits for survival, and may be particularly sensitive to changes in temperature and food supply (McDonald *et al.*, 1996). When the temperature rises, the fish's metabolic rate increases, and if food availability decreases, stays the same or increases only slightly, then the growth rate of the fishes will decline (Brett and Groves, 1979). Because the fishes in the Toolik Lake area are already food limited, subsequent increases in temperature or decreases in food could have deleterious effects on the populations. Modelling of young lake trout in the epilimnion of Toolik Lake has suggested that these small fish will not survive with the current availability of food and a 3°C increase in water temperature (McDonald *et al.*, 1996). Other fishes, such as arctic char, sculpin and grayling, that use the epilimnetic areas extensively, may be similarly affected. However, sculpin and grayling, in the absence of large lake trout predators, may change their use of habitats and resources (McDonald and Hershey, 1992; McDonald *et al.*, 1992). Changes in the growth rates of fishes, especially predators, can greatly affect the survival of the population, and may result in cascading effects through the entire trophic structure (Carpenter *et al.*, 1985).

In addition to changing temperature, changing precipitation will affect these aquatic ecosystems. Current precipitation levels in the Toolik area are very low, and if precipitation decreases, nutrient inputs into the Toolik region could be further reduced. Resulting decreases in primary production could cause cascading effects and reduce biomass at higher trophic levels (Sommer, 1979). Alternatively, precipitation could increase, or melting permafrost could increase the nutrient loading to the lakes. Primary productivity will respond to an increase in nutrients (Hobbie *et al.*, 1995), but under the extremely oligotrophic conditions found in arctic Alaskan lakes, primary consumers appear only weakly coupled to planktonic primary productivity. Even after three years of a 10-fold experimental nutrient addition to limnocorrals in Toolik Lake, increases in zooplankton abundance and biomass of only two- to three-fold occurred (O'Brien *et al.*, 1992). It is unlikely that a 10-fold increase in nutrients to Toolik Lake from rainfall or melting of permafrost in the watershed, needed to produce a doubling of the available zooplankton, will occur. In the Kuparuk River near Toolik Lake, primary productivity and algal biomass increased with experimental nutrient addition (Peterson *et al.*, 1993). The invertebrates response also showed them to be food limited (Hershey *et al.*, 1988). Growth of adult grayling has typically increased with fertilization (Deegan and Peterson, 1992), but growth is also highly correlated with stream flow (Hobbie *et al.*, 1995). At low flows, low growth of adult fish occurs in the Kuparuk River (Hobbie *et al.*, 1995), but young-of-year grayling grow better with lower flow (L. Deegan and B. Peterson, unpublished data). Temperature increases in the rivers naturally coincide with low flow conditions, but with the increased temperatures associated with climate change the adult grayling metabolic demands may further reduce their growth at low flows. As grayling in these systems are food limited, the increased metabolic costs may result in decreased survival of riverine populations. Temperature increases may also alter the biogeography of stream insects and fish through an increase in degree-days and the amelioration of colder thermal regimes, allowing organisms to migrate northwards (Oswood *et al.*, 1992).

It appears that global warming may have the most significant effect on the predators of these, arctic Alaskan aquatic ecosystems. The predators in these systems are long lived, and population changes owing to recruitment failure may not be reflected in the adult populations for many years. However, the eventual loss of top predators from these systems will most likely cascade through the food-web, affecting the structure and function of both the benthic and planktonic communities (Hershey, 1990; Goyke and Hershey, 1992; Hanson *et al.*, 1992; O'Brien *et al.*, 1992).

Northern Peatlands

Most of the wetlands of discontinuous and continuous permafrost regions are peatlands (National Wetlands Working Group, 1988). The location of a peatland is related to regional climate controls on precipitation and evapotranspiration and is thus controlled by the water balance. The most important variable is the position of the water table because it controls the size of the aerobic and anaerobic layers in a peatland, and thus biomass productivity and decomposition, and ultimately peat accumulation. The degree of anaerobicity also determines, in part, the distribution of plants, and the magnitude of the exchange of carbon gas with the atmosphere and the export of dissolved organic carbon. The water table is also a key variable in determining the rate and magnitude of runoff. A secondary climate variable that is critical to peatland function is temperature. Productivity and decomposition rates are related to temperature once the general level of saturation of the peatland has been accounted for.

The wetlands in the interior of region 2 are largely bryophyte-dominated peatlands. These are a result of cool temperatures and an excess of precipitation over evapotranspiration (Gignac and Vitt, 1994). Along the southern boundary of region 2, in the grassland and low boreal forest, seasonal drought limits wetlands to *Typha* marshes and *Salix* swamps. Progressing northwards, a cooler, moister climate limits the frequency and severity of seasonal droughts and the wetlands become sedge- and bryophyte-dominated fens and bogs.

Climate produces variations in the peatland form (Belland and Vitt, 1995). In the southern areas of region 2, peatlands are spatially restricted and the predominant peatland form is the basin bog, basin fen or channel fen. Extensively developed peatlands are a northern feature (Nicholson, 1994). In Canada and Finland, peatland forms have been demonstrated to occur in distinct geographical bands related to climate

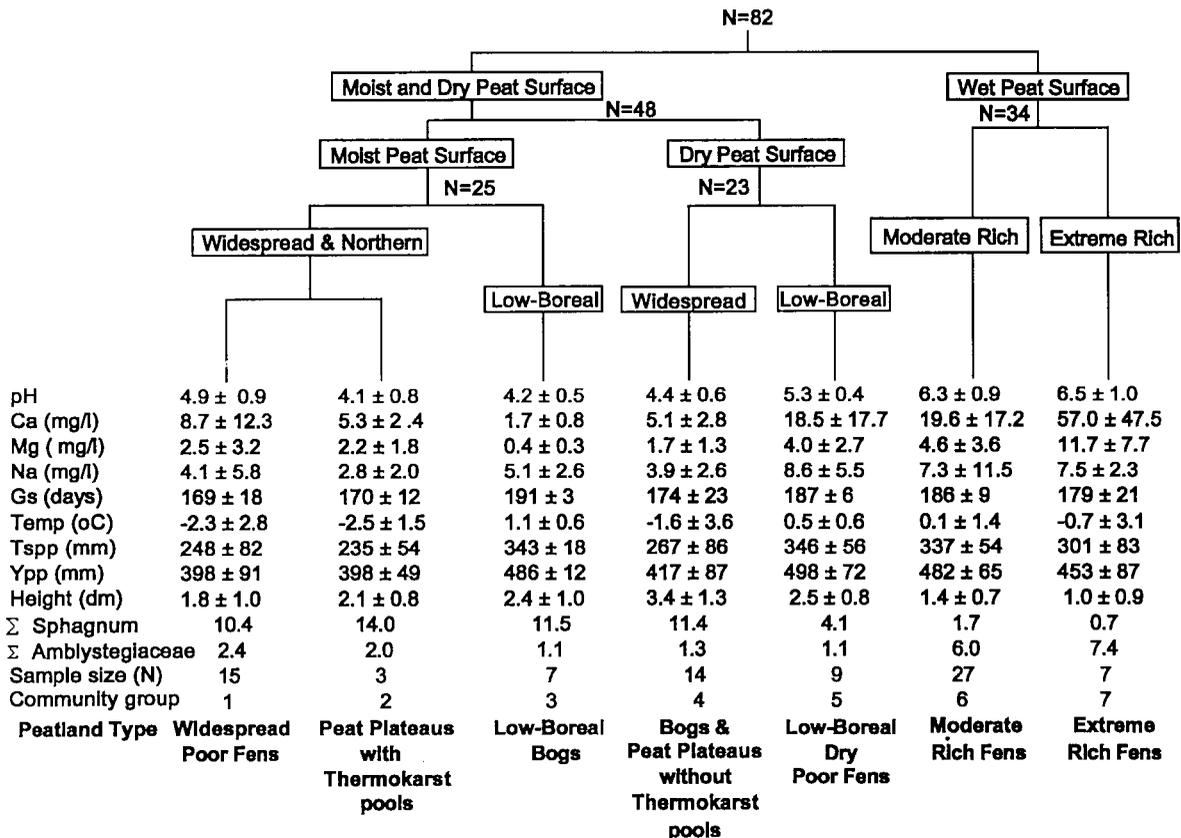


Figure 7. TWINSpan dendrogram outlining the division of 82 peatlands in the Mackenzie River basin into seven TWINSpan bryophyte stand groups and seven peatland types. Values are the means and standard deviations of climatic and environmental gradients significant on the first DCCA axis for each TWINSpan stand group

(Ruuhijärvi, 1983; Wells and Hirvonen, 1988). Permafrost supports the development of peat plateaux, thermokarst pools, ice wedge polygons, palsas and peat mounds.

Past climate has had a significant effect on the development of northern peatlands. Basal dates of peatlands in continental western Canada demonstrate that peatland formation was prevented during the early Holocene, south of latitude 54°30' until after 6000 years BP (Zoltai and Vitt, 1990). North of latitude 54°30' and in the mountains where it was cooler and moister, peatlands began to form as early as 8000 BP. On the North Slope of Alaska, organic soil accumulation began around 6000–8000 BP (Schell and Zieman, 1983; Eisner, 1991). In general, peatlands in North America have been expanding at a constant rate (Gorham and Janssens, 1992). A few peatlands are older than 10 000 years BP, but most range between 10 000 and 4000 years old.

Figure 7 shows a classification scheme relating peatland type, peatland form and climate. Seven peatland types are identified and it is apparent that there is a large range in floral, pedological, chemical, mineral and environmental characteristics, all of which will be affected by changes in temperature and the water balance.

From a climatological perspective the seven peatland types referred to above can be treated as only two distinct peatland types, based on the physical characteristics of the peat and on the dominant vegetation. The surface of ombrogenic peatlands receives water from precipitation only. In contrast, rheogenic peatlands, such as fens and swamps, may receive additional inputs from surface and subsurface flow systems. The sources of water to a peatland's surface determines how responsive the peatland water storage is to

atmospheric forcings. The ombrogenic systems are very responsive and storage changes are large and variable, while rheogenic systems are less responsive and change less. Ombrogenic peatlands are more susceptible to drought than peatlands that receive some groundwater (Siegel *et al.*, 1995). However, since the rheogenic system is dependent on external sources of water, any climate forcings that influence the basin in which the rheogenic peatland is located will result in a change in storage in the peatland.

It is commonly believed that peatlands evapotranspire at rates similar to those of open water surfaces (e.g. Verry, 1988), but recent studies have found peatlands usually evaporate less than lakes (Roulet *et al.*, 1997). If evaporative demand increases, the mechanisms that supply moisture to the surface will ultimately control the rate and magnitude of water loss. Bogs are dominated by mosses that have no active internal system that conducts water. Fens, dominated by vascular plants, are more effectively coupled to the atmosphere. This coupling is physiologically controlled by stomatal and root conductance (Lafleur, 1988). Desjardins *et al.* (1994) measured the regional sensible and latent heat fluxes from the continuous peatland of the Hudson Bay Lowland and observed that the latent heat flux dominated in the fens, but the latent and sensible heat flux were of equal magnitude in areas where bogs were more frequent.

The thermal regime is closely related to water storage. The drier surface layer of the peatland is an efficient insulator since air has a much lower thermal conductivity than water, while the saturated zone has a greater heat capacity (Roulet *et al.*, 1997). This results in a heat storage component similar to that of lakes, wherein substantial energy exchange is required to heat or cool a peatland. However, unlike a lake, the subsurface thermal exchange process is limited by a much smaller thermal conductivity and lack of convection.

When peatlands are frozen, they have a very limited storage capacity and many act as flow-through systems (Roulet and Woo, 1988), but when the frost table is at its lowest during the summer, the hydraulic properties of the peat itself control the storage and flow dynamics of the peatland (Roulet and Woo, 1986). Permafrost confines the water flow in peatlands to a thin 'active' layer, thus restricting the interaction of surface and groundwater in peatlands. As a result, northern peatlands will be more affected by climate change than their southern counterparts. An equally critical issue is the stability of permafrost in, and adjacent to, peatlands. Because of the unique thermal properties of peat, peatlands can contain permafrost in areas that are, in general, free of permafrost. However, permafrost degradation adjacent to peatlands could have a catastrophic effect on the exchange of water, and lead to large-scale mass wasting such as is observed in the collapse scars in peat plateaux and palsas.

The results from two simple, physically based hydrology and climate models to assess changes in water storage in northern fens owing to changes in precipitation and temperature for $2 \times \text{CO}_2$ climate scenarios are presented in Figure 8. Roulet *et al.* (1992) assumed a 3.5°C increase in temperature and 1 mm d^{-1} increase in precipitation, while Lafleur (1993) did several model runs for temperature increases of 2, 4 and 8°C for June, July and August. The results from both studies indicate a substantial negative change in water storage in fens. Based on these results, it is reasonable to assume that an increase in temperature could reduce water storage in northern peatlands, even with a persistent, but small, increase in precipitation. Depending on the soil moisture characteristics and the physical properties of the peat, the estimated changes in storage could be an increase in depth to the water table of 10–20 cm during the summer months. Few studies have examined the change in thermal regime in northern peatlands, but Roulet *et al.* (1992) modelled a 0.8°C increase in the near-surface summer temperatures in peat for a 3.5°C increase in air temperature.

Table IV outlines the anticipated major effects of climate warming on the distribution, water relations and carbon cycle in peatlands. As permafrost melts, new drainage channels could form, rapidly removing the excess water, resulting in improved drainage and a drawdown in local water tables. Alternatively, local topography and fine-textured soils could result in the ponding and retention of much of the water currently frozen, creating many new ponds and lakes. Integrated drainage patterns appear on air photographs in permafrost-dominated peat plateaux, soon after forest fires. Forest fires have the effect of removing tree and lichen cover. This increases the amount of snow cover sitting on the peatland surface, slightly insulating the peat over the winter months. During the following summer, more heat is absorbed by the dark-hued ash and dead, standing trees. A greater amount of heat is transmitted into the peat, resulting in large-scale melting of

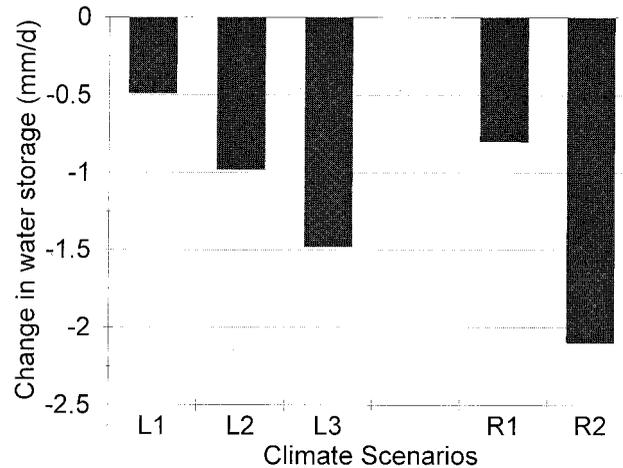


Figure 8. Change in the daily summer (JJA) moisture storage in northern peatlands based on two different climate change modelling scenarios. Cases L1, L2 and L3 (Lafleur, 1993) assume reference climate temperature, wind speed, net radiation and precipitation, and then perturbate the reference temperature by $+2^{\circ}\text{C}$ (L1), $+4^{\circ}\text{C}$ (L2) and $+8^{\circ}\text{C}$ (L3). Cases R1 and R2 (Roulet *et al.*, 1992) assume reference climate temperature, wind speed, net radiation and precipitation, and then perturbate temperature by $+0.8^{\circ}\text{C}$ at -10 cm depth of peat and increase precipitation $+1$ mm/d. R1 is the loss of water from a non-floating surface peatland and R2 is the loss from a floating surface peatland

the permafrost, collapse of the plateau surface and development of integrated drainage patterns. Under present climatic conditions, a forest fire in a permafrost peatland results in a temporarily wetter landscape. Over time the melting ceases, drainage subsides and the peat plateau is regenerated with the re-establishment of *Sphagnum* hummocks (Zoltai, 1993). This cycle has been documented to take anywhere from 600 to 2000 years to complete. Because of the uncertainties associated with precipitation predictions and the net effect

Table IV. Potential effects of a warmer climate on northern peatlands. \uparrow and \downarrow indicate an increase or a decrease in the various categories/effect

Regional effects		
Area of peatlands	\downarrow	\downarrow
Change in peatland form	\uparrow	\uparrow
Change in plant communities	\uparrow	\uparrow
Fire frequency	\uparrow	\uparrow
Site-specific effects		
Water relations in peatlands		
Evaporation	\uparrow	\downarrow
Runoff to streams	\uparrow	\downarrow
Growth of vegetation		
Trees	\downarrow	\uparrow
Mosses	\uparrow	\downarrow
Primary production	\uparrow	\uparrow
Decomposition	\downarrow	\uparrow
Carbon cycling		
Peat accumulation	\uparrow	\downarrow
Nutrients available for growth	\downarrow	\uparrow
CO ₂ fixation	\uparrow	\uparrow
CO ₂ release	\downarrow	\uparrow
CH ₄ release	\uparrow	\downarrow
DOC release	\uparrow	\uparrow

that permafrost melting will have on local peatland water tables, we will discuss the effects of climate change on peatlands under two scenarios; a net rise versus a net fall in the water table.

An increase in mean annual temperature will shift the zone where peatlands commonly occur. Peatland losses are anticipated to occur along the southern boundary, where a drop in the water table will increase decomposition of the accumulated peat, and may convert marginal peatlands into *Salix*- or *Picea mariana*-dominated swamps. In some cases, wetlands will cease to exist because of drought, and an increase in forest fires will serve to enhance the rate of peatland loss by removal caused by burning (Wein, 1983). Predictions from a climate change model (2°C increase) put forth by Gignac and Vitt (1994) indicate that the southern boundary of peatlands in northern Alberta will migrate to approximately 200–300 km north of its present position, and that only bryophytes normally found in upland boreal forest communities will exist. Predictions on the impact of a $2 \times \text{CO}_2$ climate change on peatland communities in the Mackenzie River Basin indicate that peatlands are likely to disappear from all of Alberta, and the southern limit will lie just beyond the border between Alberta and the North-west Territories (Nicholson and Gignac, 1996). Widespread poor fens, bogs with peat plateaux, moderate-rich fens and extreme-rich fens (Figure 6) will stretch north of the border to Inuvik. Peat plateaux with thermokarst pools will be pushed northwards to Inuvik, while low boreal bogs, the most southern group, will lie at the southern end of Great Slave Lake.

Gorham (1995) estimates that peatlands are growing in height at a rate of 0.5 mm/yr. Peat accumulation is dependant on the balance of primary production and decomposition. Primary productivity is controlled by nutrients and temperature, whereas decomposition is dependent upon temperature, nutrient levels, depth to the water table and nature of the material. Climate warming is expected to increase decomposition in peatlands owing to increased fungal and bacterial metabolic rates, and an increase in the aerobic zone. Recently, however, it has been demonstrated that in subsurface peats (30–40 cm), an increase in temperature and aeration does not lead to an increase in decomposition (Hogg *et al.*, 1992). Decay resistance of the subsurface peat was attributed to the recalcitrant nature of the material. Furthermore, studies of peat decomposition near Toolik Lake showed that increases in temperatures of less than 9°C had no effect on organic carbon respiration and nitrogen mineralization (Nadelhoffer *et al.*, 1991). Higher water tables have the effect of increasing the rate of peat accumulation by reducing the depth of the aerobic zone, and reducing the exposure of the surface material to aerobic decomposition by fungi and bacteria. Thus, temperature increases on wet peatlands are anticipated to have a negligible effect on the decomposition of the peat, if the water table stays constant or rises.

Exports of carbon from peatlands include particulate, dissolved inorganic and dissolved organic carbon from stream flow, carbon loss through deep seepage, methane efflux and CO₂ efflux. The magnitude of the fluxes of carbon in and out of a peatland is very small and this makes it extremely difficult to assess the contemporary carbon dynamics of northern peatlands, and estimating the future changes in carbon exchange is impossible at present.

A variety of different studies provide estimates of the sensitivity of the carbon balance to climate variability and change. Evidence suggests that the soil CO₂ efflux increases linearly with reduced water table, while the flux of CH₄ decreases exponentially (Moore and Knowles, 1989). The drainage of peatlands can convert them from a net CO₂ sink to a source (Armentano and Menges, 1986). A peatland can be a large sink for CO₂ one year and a large source the next year (Shurapli *et al.*, 1995). A change in water table position of only –10 cm is sufficient to convert a northern forested peatland from a source to a sink for atmospheric CH₄ (Moore and Roulet, 1993). In Finland, the annual soil efflux of CO₂ increased when bogs and fens were drained by about 40 and 90% respectively (Martikainen *et al.*, 1994). Laine *et al.* (1997) found that drained peatlands underwent a net carbon loss. Model results indicate that increased temperature can stimulate plant and soil respiration, but, providing conditions are moist, the losses of biomass are more than compensated for by increased photosynthesis, which results from the redistribution of nitrogen from soil to plants. However, when warming is accompanied by decreases in soil moisture, increased photosynthesis only partially compensates for increased respiration. Under this latter condition there is substantial loss of nitrogen from the ecosystem (McKane *et al.*, in press). Such loss may affect the receiving water bodies

(Kling, 1995). Conflicting field observations suggest that present day wet tundra ecosystems may be either a source of CO₂ (Oechel *et al.*, 1993) or a sink of CO₂ (Shaver *et al.*, 1992).

The plant community structure would likely change with changes in groundwater storage (Bubier and Moore, 1994). In addition, it is not clear how ecosystem productivity might change in a CO₂-enhanced environment. For example, Alaskan ecosystems respond little to CO₂ enhancement without an addition of nutrients or a lowering of the water table (Oechel and Vourlitis, 1994; McKane *et al.*, in press). It is also important to consider the role of changing plant and soil conditions and processes on surface waters. Some northern peatland and wetland areas contain as much as 40–80% water surface (Kling *et al.*, 1991; Roulet *et al.*, 1994), which yield very large fluxes of CO₂ and CH₄ (Kling *et al.*, 1991; Hamilton *et al.*, 1994). Changes in moisture supply and thermal regime could lead to topographical and vegetation changes that could alter the water surfaces of northern peatlands and thus alter the delivery of CO₂ and CH₄ from surface waters to the atmosphere. Oswood *et al.* (1992) provide a thorough summary of how changes in thaw depth could increase DOC loading from land to streams, and how changes in riparian vegetation may affect the quality of water.

SUMMARY AND RECOMMENDATIONS

Region 2 is clearly rich in lakes, ponds, rivers and wetland habitats and represents a major water resource in North America. It is also, arguably, the most susceptible to climate warming because of the high magnitude temperature response to global warming and because of the prevalence of permafrost. This response will have direct effects on habitat and equally important indirect effects through the water balance. Region 2 also has the sparsest research base because of its size and small human population. Thus, many fundamental processes are little understood. These involve both the need for basic research and for long-term monitoring.

Climate

The present day climate in much of region 2 is not well known. Temperatures are measured primarily at settlements, most of which are on coasts, rivers or lakes. They are not representative of the hinterland of the Arctic Islands or much of the terrestrial mainland. Because so much precipitation involves snow, which in tundra areas is blowing snow, precipitation measurements and estimates are unreliable. Thus scenarios involving $2 \times \text{CO}_2$ – $1 \times \text{CO}_2$ are more than normally speculative because $1 \times \text{CO}_2$ is, at present, unreliable, although the accuracy of estimations is improving rapidly. At present, the error in water balance calculations employing GCM scenarios could easily be 100% or more.

The solution to these problems of estimation is to increase the number of long-term monitoring stations in unpopulated locations. This is contrary to the present trend, which is to reduce the number. Other needs are to better understand snow depths, densities and sublimation rates, and general precipitation patterns from storms. These can make use of contemporary technology employing remote sensing in the form of passive microwave sensing and radarsat and weather radar. There are promising developments in this direction but the need for standard long-term monitoring still remains. The overall goal should be to develop reliable methods of extrapolation and interpolation from a spatially limited climate network. Palaeoclimatic material should be exploited where possible to help generate some of the long-term data that do not exist for the region.

Hydrological

The need for accurate water balances for lakes, and particularly for wetland systems, has been reiterated several times in this paper. This involves a number of required inputs. Simple, reliable models for determining rates of evaporation from different wetland systems need further development. Water-holding capacities of reservoirs (soil, lake and river) under different permafrost and pedological conditions need documentation.

The thermal behaviour of wetland systems needs to be modelled. In lakes and rivers, this is especially closely related to dates of freeze and thaw and depths of freezing. For example, in a given environment,

at what depth does a pond become a lake? How does this relate to the thermal regime and the water balance? Basic information like this is essential for modelling the effect of a warmer world and it impinges on all aspects of the limnology of ponds and lakes. In peatlands the thermal regime operates in influencing permafrost active layer development, evapotranspiration and the water balance and the carbon budget.

The interrelationships between rivers with their basins through cold region processes is little understood. The example of the synergism of the Mackenzie Delta lakes with the river has been developed and this gives an example of the complexities of cold region hydrological systems. It is especially important with reference to the increasing demands to harness and divert north-flowing rivers for hydroelectric and other purposes. Even our limited contemporary knowledge indicates that the effects of diversions are major and mostly negative. They can also be compounded by climate change.

Limnological

Given the very large range in freshwater systems in region 2, our knowledge of the full limnological systems is very limited in spite of excellent local contemporary efforts. Two of the largest freshwater lakes in the world, Great Bear and Great Slave, are largely undocumented, in comparison to the Laurentian Great Lakes, for example, although palaeolimnological studies indicate some interesting trends (Stoermer *et al.*, 1990). They represent lakes dominated by cold region processes. Not only are they major ecosystems in their own right, but they also play a major role in the entire lower Mackenzie Basin, including the delta. Smaller lakes and ponds have been somewhat better documented in certain environments but freshwater systems in most of the regions have not been studied.

The carbon budget of freshwater systems is important on a global basis but is largely unknown. The obvious importance of peatlands is through the large carbon reservoir that they represent and the likelihood that they can readily change from sinks to sources of CO₂ and other forms of carbon, if this is not happening already. In this fashion, region 2 and other circumpolar cold lands can interact with the global atmosphere by enhancing the greenhouse effect in a positive feedback.

Multidisciplinary

Another way in which freshwater systems can influence the global climate system is through their freshwater input to the Arctic Ocean. The longevity of sea ice is intimately linked to the freshwater input from north-flowing rivers and responds to any changes in the volume of this input. The Arctic Ocean is, in turn, strongly linked to temperate oceans through deep oceanic circulations. The polar sea is also closely linked to the sun and the surface energy balance through its surface albedo. Thus, the water balance of freshwater systems in region 2 has effects that extend well beyond the immediate environments. There are basic research needs to measure, understand and model this much larger water and heat balance system. In such avenues the needs of the limnological, hydrological, atmospheric and marine scientific communities to understand more fully high latitude processes have become intertwined.

Basic long-term monitoring and interdisciplinary research is necessary in the little-studied environments of region 2. Only then can reliable models be developed and their validity on the regional scale be tested.

REFERENCES

- Andres, D. and Doyle, P. F. 1984. 'Analysis of breakup and ice jams on the Athabasca River at Fort McMurray, Alberta', *Can. J. Civil Eng.*, **11**, 444–458.
- Armentano, T. V. and Menges, E. S. 1986. 'Patterns of change in the carbon balance of organic soil-wetlands of the temperate zone', *J. Ecol.*, **74**, 755–774.
- Belland, R. J. and Vitt., D. H. 1995. 'Bryophyte vegetation patterns along environmental gradients in continental bogs', *Ecoscience*, **2**, 395–407.
- Benke, A. C. 1984. 'Secondary production of aquatic insects', in Resh, V. H. and Roserber, D. M. (Eds), *The Ecology of Aquatic Insects*. Praeger, New York. pp.289–322.
- Bliss, L. C. (Ed). 1977. *Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem*. University of Alberta Press, Edmonton. p. 714.

- Boer, G. J., McFarlane, N., Blanchet, J.-P., and Lazare, M. 1990. *Greenhouse gas induced climatic change simulated with the CCC second generation GCM*. Canadian Climate Centre, Atmospheric Environment Centre, Downsview, Ontario. 24 pp.
- Bradley, R. S. and Jones, P. D. 1993. 'Little Ice Age summer temperature variations, their nature and relevance to recent global warming trends', *The Holocene*, **3**, 367–376.
- Brett, J. R. and Groves, T. D. D. 1979. 'Physiological energetics', in Hoar, W. S., Randall, D. J., and J. R. Brett, J. S. (Eds), *Fish Physiology*, Vol. 8. Academic Press, New York. pp. 599–667.
- Brown, R. J. E. 1970. *Permafrost in Canada — its Influence on Northern Development*. University of Toronto Press, Toronto.
- Bryson, R. A. 1966. 'Air masses, streamlines and the boreal forest', *Geogr. Bull.*, **8**, 228–269.
- Bubier, J. L. and Moore, T. R. 1994. 'An ecological perspective on methane emissions from northern wetlands', *TREE*, **9**, 460–464.
- Burn, C. R. 1993. 'Permafrost, tectonics and past and future regional climate change, Yukon and adjacent Northwest Territories', *Can. J. Earth Sci.*, **31**, 182–191.
- Carpenter, S. R., Kitchell, J. F., and Hodgson, J. R. 1985. 'Cascading trophic interactions and lake productivity', *BioScience*, **35**, 634–639.
- Church, M. 1974. 'Hydrology and permafrost with reference to northern North America', in *Permafrost Hydrology*, Proceedings of Workshop Seminar 1974. Canadian National Committee for the International Hydrological Decade, Ottawa, Ontario. pp. 7–20.
- Cohen, S. J. 1993. *Mackenzie Basin Impact Study, Interim Report 1*. Environment Canada, Atmospheric Environment Service. Downsview, Ontario, Canada. 163 pp.
- Connell, J. H. 1978. 'Diversity in tropical rainforests and coral reefs', *Science*, **199**, 1302–1310.
- Deegan, L. A. and Peterson, B. J. 1992. 'Whole river fertilization stimulates fish production in an arctic tundra river', *Can. J. Fish. Aquat. Sci.*, **49**, 1890–1901.
- Desjardins, R. L., MacPherson, J. I., Schuepp, P. H., and Hayhoe, H. N. 1994. 'Airborne flux measurements of CO₂, sensible, and latent heat over the Hudson Bay Lowland', *J. Geophys. Res.*, **99**(D1), 1551–1562.
- Douglas, M. S. V. and Smol, J. P. 1993. 'Freshwater diatoms from high arctic ponds Cape Herschel, Ellesmere Island, N.W.T.', *Nova Hedwigia*, **57**, 511–552.
- Douglas, M. S. V. and Smol, J. P. 1994. 'Limnology of high arctic ponds Cape Herschel, Ellesmere Island, N.W.T.', *Arch. Hydrobiol.*, **131**, 401–434.
- Douglas, M. S. V., Smol, J. P., and Blake, W., Jr. 1994. 'Marked post-18th century environmental change in high Arctic ecosystems', *Science*, **266**, 416–419.
- Edlund, S. A. and Alt, B. T. 1989. 'Regional congruence of vegetation and summer climate patterns in the Queen Elizabeth Islands, Northwest Territories, Canada', *Arctic*, **42**, 3–23.
- Eisner, W. R. 1991. 'Palynological analysis of a peat core from Imnavit Creek, the North Slope, Alaska', *Arctic*, **44**, 279–282.
- Farley, D. W. and H. Cheng. 1986. 'Hydraulic impact of flow regulation on the Peace–Athabasca Delta', *Can. Water Res. J.*, **11**, 26–42.
- Forsberg, C. 1992. 'Will an increased greenhouse impact in Fennoscandia give rise to more humic and coloured lakes?', *Hydrobiologia*, **229**, 51–58.
- Gignac, L. D. and Vitt, D. H. 1994. 'Responses of northern peatlands to climatic change, effects on bryophytes', *J. Hattori Bot. Lab.*, **75**, 119–132.
- Goodison, B. E. 1981. 'Compatibility of Canadian snowfall and snow cover data', *Wat. Resour. Res.*, **17**, 893–900.
- Gorham, E. 1995. 'The biogeochemistry of northern peatlands and its possible responses to global warming', in Woodwell, G. M. and Mackenzie, F. T. (Eds), *Biotic Feedbacks in the Global Climate System: Will the Warming Feed the Warming?* Oxford University Press, New York. pp. 169–187.
- Gorham, E. and Janssens, J. 1992. 'The paleorecord of geochemist and hydrology in northern peatlands and its relation to global change', *Suo*, **43**, 117–126.
- Goyke, A. P. and Hershey, A. E. 1992. 'Effects of fish predation on larval chironomid *Diptera*, *Chironomidae* communities in an arctic ecosystem' *Hydrobiologia*, **240**, 203–211.
- Gray, D. M. and Prowse, T. D. 1992. 'Snow and floating ice', in Maidment D. R. (Editor-in-Chief), *The Handbook of Hydrology*. McGraw-Hill Publishing Co, N. Y., 631–653.
- Hamilton, J. D., Kelly, C. A., Rudd, J. W. M., Hesslein, R. H., and Roulet, N. T. 1994. 'Flux to the atmosphere of CH₄ and CO₂ from wetland ponds on the Hudson Bay Lowland', *J. Geophys. Res.*, **99**(D1), 1494–1510.
- Hanson, K. L., Hershey, A. E., and McDonald, M. E. 1992. 'A comparison of slimy sculpin *Cottus cognatus* populations in arctic lakes with and without piscivorous predators', *Hydrobiologia*, **240**, 189–201.
- Hare, F. K. and Thomas, M. K. 1979. *Climate Canada*, 2nd edn. John Wiley and Sons, Toronto. 230 pp.
- Hecky, R. E. and Guildford, S. J. 1984. 'The primary productivity of Southern Indian Lake before, during and after impoundment and Churchill River diversion', *Can. J. Fish. Aquat. Sci.*, **41**, 591–604.
- Hecky, R. E. and Hesslein, R. H. 1995. 'Contributions of benthic algae to lake food webs as revealed by stable isotope analysis', *J. North Am. Benth. Soc.*, **14**, 631–653.
- Hershey, A. E. 1990. 'Snail populations in arctic lakes: competition mediated by predation?', *Oecologia*, **82**, 26–32.
- Hershey, A. E. 1992a. 'Effects of experimental fertilization on the benthic microinvertebrate community of an arctic lake', *J. North Am. Benth. Soc.*, **11**, 204–217.
- Hershey, A. E. 1992b. 'Effects of predatory sculpin on the chironomid communities of an arctic lake', *Ecology*, **66**, 1131–1138.
- Hershey, A. E., Hiltner, A. L., Hullar, M. A. J., Miller, M. C., Vestal, J. R., Lock, M. A., Rundle, S., and Peterson, B. J. 1988. 'Nutrient influence on a stream grazer: *Orthocladus* microcommunities track nutrient input', *Ecology*, **69**, 1383–1392.
- Hesslein, R. H., Capel, M. J., Fox, D. E., and Hallard, K. A. 1991. 'Stable isotopes of sulfur, carbon and nitrogen as indicators of trophic level and fish migration in the lower Mackenzie River basin, Canada', *Can. J. Fish. Aquat. Sci.*, **48**, 2258–2265.
- Hiltner, A. L. and Hershey, A. E. 1992. 'Black fly response to phosphorus enrichment of an arctic tundra stream', *Hydrobiologia*, **240**, 259–265.

- 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.
- Hobbie, J. E. (Ed.) 1980. *The Limnology of Tundra Pond*. Dowden, Hutchinson and Ross, Stroudsburg, PA. 515 pp.
- Hobbie, J. E., Deegan, L. A., Peterson, B. J., Rastetter, E. B., Shaver, G. R., Kling, G. W., O'Brien, W. J., Chapin, F. S. T., Miller, M. C., Kipphut, G. W., Bowden, W. B., Hershey, A. E., and McDonald, M. E. 1995. 'Long-term measurements at the arctic LTER site', in Powell, T. M. and Steele, J. H. (Eds), *Ecological Time Series*. Chapman Hall Publ., New York. pp. 391–409.
- Hogg, E. H., Leiffers, V. J., and Wein, R. W. 1992. 'Potential carbon losses from peat profiles, effects of temperature, drought cycles and fire', *Ecol. Appl.*, **2**, 298–306.
- Irons, J. G., Oswood, M. W., Stout, R. J., and Pringle, C. M. 1994. 'Latitudinal patterns in leaf litter breakdown: is temperature really important?', *Freshwat. Biol.*, **32**, 401–411.
- Isaac, G. A. and Stuart, R. A. 1992. 'Temperature-precipitation relationships for Canadian Stations', *J. Climate*, **5**, 822–830.
- Jacoby, G. C., Jr., Cook, E. R., and Ulan, L. D. 1985. 'Reconstructed summer degree days in central Alaska and northwestern Canada since 1524', *Quat. Res.*, **23**, 18–26.
- Kane, D. L., Hinzman, L. D., Woo, M. K., and Everett, K. R. 1992. 'Arctic hydrology and climate change' in Chapin, F. S., III, Jeffries, R. L., Reynolds, J. F., Shaver, G. R., Svoboda, J., and Chu, E. W. (Eds), *Arctic Ecosystems in a Changing Climate: an Ecophysiological Perspective*. Academic Press, San Diego. pp. 35–57.
- Kling, G. W. 1995. 'Land-water linkages: the influence of terrestrial diversity on aquatic systems', in Chapin, F. S. and Korner, C. (Eds), *Arctic and Alpine Diversity*. Springer-Verlag, Berlin. pp. 295–308.
- Kling, G. W., Kipphut, G. W., and Miller, M. C. 1991. 'Arctic lakes and streams as gas conduits to the atmosphere: implications for tundra carbon budgets', *Science*, **251**, 298–301.
- Kling, G. W., O'Brien, W. J., Miller, M. C., and Hershey, A. E. 1992. 'The biogeochemistry and zoogeography of lakes and rivers in arctic Alaska', *Hydrobiologia*, **240**, 1–14.
- Koerner, R. M. 1991. 'Past climate changes as deduced from Canadian ice cores', in Woo, M. K. and Gregor, D. J. (Eds), *Arctic Environment, Past, Present and Future*. McMaster University, Hamilton. pp. 61–70.
- Lafleur, P. 1988. 'Leaf conductance of four species growing in a subarctic marsh', *Can. J. Bot.*, **66**, 1367–1375.
- Lafleur, P. M. 1993. 'Potential water balance response to climatic warming, the case of a coastal wetland ecosystem of the James Bay Lowland', *Wetland*, **13**, 270–276.
- Lafleur, P. M. and Rouse, W. R. 1995. 'Energy partitioning at treeline forest and tundra sites and its sensitivity to climatic change', *Atmos.-Ocean*, **33**, 121–133.
- Laine, J., Minkinen, K., Sinisalo, J., Savolainen, I., and Martikainen, P. J. 1997. 'Greenhouse impact of a mire after drainage for forestry', in Trettin, C. C., Jurgensen, M. F., Grigal, D. F., Gale, M. R., and Jeglum, J. K. (Eds), *Northern Forested Wetlands: Ecology and Management*, CRC Press.
- Leavesley, G. H., Turner, K., D'Agnesse, F. A., and McKnight, D. 1997. 'Regional delineation of North America for the assessment of freshwater ecosystems and climate change', *Hydrol. Process.*, **11**, this issue.
- Legendre, P. and Legendre, V. 1984. 'Postglacial dispersal of freshwater fishes in the Quebec peninsula', *Can. J. Fish. Aquat. Sci.*, **41**, 1781–1802.
- Lesack, L. F. W., Marsh, P., and Hecky, R. E. 1991. 'Ice cover growth and freeze-out of solutes in a Mackenzie Delta lake', in Prowse, T. D. and Ommanney, C. S. L. (Eds), *Northern Hydrology, Selected Perspectives*. Environ. Can., NHRI Symp. No. 6, July 1990, Saskatoon, pp. 219–236.
- Mackay, J. R. 1992. 'Lake stability in an ice-rich permafrost environment: examples from the western arctic coast', in Roberts, R. D. and Bothwell, M. L. (Eds), *Aquatic Ecosystems in Semi-Arid Regions: Implications for Resource Management*. NHRI Symp. Ser., No. 7, Saskatoon. pp. 1–26.
- Marsh, P. 1991a. 'Water flux in melting snow covers', in Corapcioglu, M. Y. (Ed.), *Advances in Porous Media*, Vol. 1, Elsevier, Amsterdam. pp. 61–124.
- Marsh, P. 1991b. 'Evaporation and ice growth in Mackenzie Delta lakes', in *Hydrology of Natural and Manmade Lakes, Proc., Vienna Symposium, IAHS Publ.*, **206**, 257–266.
- Marsh, P. and Hey, M. 1989. 'The flooding hydrology of Mackenzie Delta lakes near Inuvik, N.W.T., Canada', *Arctic*, **42**, 41–49.
- Marsh, P. and Lesack, L. F. W. 1996. 'Climate change and the hydrologic regime of lakes in the Mackenzie Delta', *Limnol. Oceanogr., Spec. Iss.*, **41**, 849–856.
- Marsh, P. and Ommanney, C. S. L. (Eds), 1991. *Mackenzie Delta, Environmental Interactions and Implications of Development*. Proc., Workshop on the Mackenzie Delta. National Hydrology Research Institute Symposium No. 4, Saskatoon. 195 pp.
- Marsh, P. and Prowse, T. D. 1993. 'Hydrology: hydrologic regime of the Mackenzie Basin, potential modelling approaches, and future research needs for addressing climate change issues', in *Mackenzie Basin Impact Study, Interim Report #1*, Cohen, S. J. (Ed.) Environment Canada, Downsview, Ontario, Canada. pp. 37–49.
- Marsh, P. and Schmidt, T. 1993. 'Influence of a Beaufort Sea storm surge on channel levels in the Mackenzie Delta', *Arctic*, **46**, 35–41.
- Marsh, P., Quinton, B., and Pomeroy, J. W. 1996. 'Hydrological processes and runoff at the Arctic treeline in northwestern Canada', *Proc. 10th Northern Research Basins*. IHP, Norway. 368–397.
- Martikainen, P. J., Nykanen, H., Alm, J., and Silvola, J. 1994. 'Change in fluxes of carbon dioxide, methane and nitrous oxide due to forest drainage of mire sites of different trophic', *Plant Soil*, in press.
- Maxwell, J. B. 1980. 'The climate of the Canadian Arctic Islands and adjacent waters', *Clim. Ser., No. 30*, Vol. 1. Environment Canada, Atm. Environ. Serv., Downsview, Canada. 531 pp.
- Maxwell, J. B. 1992. 'Arctic climate, potential for change under global warming', in Chapin, F. S., Jeffries, R. L., Reynolds, J. F., Shaver, G. R., and Svoboda, J. (Eds), *Arctic Ecosystems in a Changing Climate*. Academic Press. N. Y., pp. 11–34.
- McDonald, M. E. and Hershey, A. E. 1992. 'Shifts in abundance and growth of slimy sculpin in response to changes in the predator population in an arctic Alaskan lake', *Hydrobiologia*, **240**, 219–223.

- McDonald, M. E., Hershey, A. E., and O'Brien, W. J. 1992. 'Cost of predation avoidance in young-of-year lake trout (*Salvelinus namaycush*): growth differential in sub-optimal habitats', *Hydrobiologia*, **240**, 213–218.
- McDonald, M. E., Hershey, A. E., and Miller, M. C. 1996. 'Global warming impacts on trophic structure in arctic lakes', *Limnol. Oceanogr.*, **41**, 1102–1108.
- McKane, R. B., Rastetter, E. B., Shaver, G. R., Nadelhoffer, K. J., Giblin, A. E., Laundre, J. A., and Chapin, F. S., III. 'Effects of changes in CO₂ and climate on carbon storage in arctic tundra', *Ecology*, in press.
- Merrick, G. W., Hershey, A. E., and McDonald, M. E. 1991. 'Lake trout (*Salvelinus namaycush*) control of snail density and size distribution in an arctic lake', *Can. J. Fish. Aquat. Sci.*, **48**, 498–502.
- Merrick, G. W., Hershey, A. E., and McDonald, M. E. 1992. 'Salmonid diet and the size, distribution, and density of benthic invertebrates', *Hydrobiologia*, **240**, 225–233.
- Miller, M. C., Hater, G. R., Spatt, P., Westlake, P., and Yeakel, D. 1986. 'Primary production and its control in Toolik Lake, Alaska', *Arch. Hydrobiol. Suppl.*, **74**, 97–131.
- Miller, M. C., DeOliveira, P., and Gibeau, G. G. 1992. 'Epilithic diatom community response to years of PO₄ fertilization: Kaparuk River, Alaska', *Hydrobiologia*, **240**, 103–120.
- Mitchell, J. F. B., Manabe, S., Meleshko, V., and Tolioka, T. 1990. 'Equilibrium climate change and its implications for the future', in Houghton, J. T., Jenkins, G. J., and Ephraums, J. J. (Eds), *Climate Change. The IPCC Scientific Assessment*. Cambridge University Press, New York, pp. 135–164.
- Moore, T. R. and Kowles, R. 1989. 'The influence of water table levels on methane and carbon dioxide emissions from peatland soils', *Can. J. Soil Sci.*, **67**, 77–81.
- Moore, T. R. and Roulet, N. T. 1993. 'Methane flux, water table relations in northern wetlands', *Geophys. Res. Lett.*, **20**, 587–590.
- Nadelhoffer, K. J., Giblin, A. E., Shaver, G. R., and Laundre, J. A. 1991. 'Effects of temperature and organic matter quality on C, N, and P mineralization in soils from six arctic ecosystems', *Ecology*, **72**, 242–253.
- National Wetlands Working Group, 1988. *Wetlands of Canada. Ecological Land Classification Series*, No. 24. Sustainable Development Branch, Quebec, Environment Canada, Ottawa, Ontario, and Polyscience Publ. Inc., Montreal. 452 pp.
- Nicholson, B. J. 1994. 'Wetland development at Elk Island National Park, Alberta, Canada', *J. Paleolimnol.*, **12**, 19–34.
- Nicholson, B. J. and Gignac, L. D. 1996. 'Niche dimensions of peatland bryophyte indicator species along environmental and climatic gradients in the Mackenzie River Basin', *The Bryologist*, **98**, 437–451.
- Nogrady, T. and Smol, J. P. 1989. 'Rotifers from five high arctic ponds, Cape Herschel, Ellesmere Island', *Hydrobiologia*, **173**, 231–242.
- O'Brien, W. J., Buchanan, C., and Haney, J. F. 1979. 'Arctic zooplankton community structure: exceptions to some general rules', *Arctic*, **32**, 237–247.
- O'Brien, W. J., Hershey, A. E., Hobbie, J. E., Hullar, M. A., Kipphut, G. W., Miller, M. C., Moller, B., and Vestal, J. R. 1992. 'Control mechanisms of arctic lake ecosystems: a limnocorral experiment', *Hydrobiologia*, **240**, 143–188.
- Oechel, W. C. and Vourlitis, G. L. 1994. 'The effects of climate change on land-atmosphere feedbacks in arctic tundra regions', *TREE*, **9**, 324–329.
- Oechel, W. C., Hastings, S. J., Vourlitis, G., Jenkins, M., Riechers, G., and Grulke, N. 1993. 'Recent change of arctic tundra ecosystems from a net carbon dioxide sink to a source', *Nature*, **361**, 520–525.
- Oswood, M. W., Milner, A. M., and Irons, J. G., III. 1992. 'Climate change and Alaskan rivers and streams', in Firth, P. and Fisher, S. G. (Eds), *Global Change and Freshwater Ecosystems*. Springer-Verlag, New York. pp. 192–210.
- Payette, S. and Morneau, C. 1993. 'Holocene relict woodlands at the eastern Canadian treeline', *Quart. Res.*, **39**, 84–89.
- Peace-Anthabasca Delta Implementation Committee, 1987. *Peace Anthabasca Delta Water Management Works Evaluation*, Final Report. Peace-Anthabasca Delta Implementation Agreement, Canada/Alberta/Saskatchewan. 63 pp.
- Peterson, B. J., Hobbie, J. E., Hershey, A. E., Lock, M., Ford, T., Vestal, R., Hullar, M., Ventullo, R., and Volk, G. 1985. 'Transformation of a tundra river from heterotrophy to autotrophy by addition of phosphorus', *Science*, **229**, 1383–1386.
- Peterson, B. J., Deegan, L. A., Helfrich, J., Hobbie, J. E., Hullar, M. A. J., Moller, B., Ford, T. E., Hershey, A. E., Hiltner, A. L., Kipphut, G. W., Lock, M. A., Fiebig, D. M., McKinley, V. L., Miller, M. C., Vestal, J. R., Ventullo, R. M., and Volk, G. S. 1993. 'Biological responses of a tundra river to fertilization', *Ecology*, **74**, 653–672.
- Pienitz, R. 1993. 'Paleoclimate proxy data inferred from fresh water diatoms for the Yukon and Northwest Territories', *PhD Thesis*, Queen's University, Kingston, Ontario. 220 pp.
- Pienitz, R. and Smol, J. P. 1993. 'Diatom assemblages and their relationship to environmental variables in lakes from the boreal forest-tundra ecotone near Yellowknife, Northwest Territories, Canada', *Hydrobiologia*, **269/270**, 391–404.
- Pienitz, R., Walker, I. R., Zeeb, B. A., Smol, J. P., and Leavitt, P. R. 1992. 'Biomonitoring past salinity changes in an athalassic sub-arctic lake', *Int. J. Salt Lake Res.*, **12**, 91–123.
- Pienitz, R., Smol, J. P., and Birks, H. J. B. 1995. 'Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories, Canada', *J. Paleolimnol.*, **13**, 21–49.
- Pomeroy, J. W. and Gray, D. M. 1994. 'Sensitivity of snow relocation and sublimation to climate and surface vegetation', in Jones, H. G., Davies, T., Ohmura, A., and Morris, E. M. (Eds), *Snow and Ice Covers, Interactions with the Atmosphere and Ecosystems*, *IAHS Publ.*, **223**, 213–226.
- Prowse, T. D. 1994. Environmental significance of ice to streamflow in cold regions. *Freshwat. Biol.*, **32**, 241–259.
- Prowse, T. D. and Lalonde, V. 1996. 'Open, water and ice jam flooding of a northern delta, *Nord. Hydrol.*, **27**(1/2), 85–100.
- Prowse, T. D. and Stephenson, R. L. 1986. 'The relationship between winter lake cover, radiation receipts and the oxygen deficit in temperate lakes', *Atmos.-Ocean*, **24**, 386–403.
- Ramlal P. S., Hesslein, R. E., Hecky, R. E., Fee, E. J., Rudd, J. W. M., and Guilford, S. J. 1994. 'The organic carbon budget of a shallow, arctic tundra lake on the Tuktoyaktuk Peninsula, N.W.T., Canada'. *Biogeochemistry*, **24**, 145–172.
- Ritchie, J. C. 1984. *Past and Present Vegetation of the Far Northwest of Canada*. University of Toronto Press, Toronto.
- Roots, E. R. 1989. 'Climate change, high latitude regions', *Climatic Change*, **15**, 223–253.

- Roulet, N. T. and Woo, M.-K. 1986. 'Hydrology of a wetland in the continuous permafrost region', *J. Hydrol.*, **89**, 73–91.
- Roulet, N. T. and Woo, M.-K. 1988. 'Runoff generation in a low Arctic drainage basin', *J. Hydrol.*, **101**, 213–226.
- Roulet, N. T., Moore, T., Bubier, J., and Lafleur, P. 1992. 'Northern fens, methane flux and climatic change', *Tellus*, **44B**, 100–105.
- Roulet, N. T., Jano, A., Kelly, C. A., Klinger, L. F., Moore, T. R., Protz, R., Ritter, J. A., and Rouse, W. R. 1994. 'Role of the Hudson Bay Lowland as a source of atmospheric methane', *J. Geophys. Res.*, **99**(D1), 1439–1454.
- Roulet, N. T., Munro, S., and Morstich, L. 1997. 'Surface climate of wetlands', in Bailey, W., Rouse, W. R., and Oke, T. R. (Eds), *Surface Climates of Canada*. McGill-Queens Press, Montreal, Canada. In press.
- Rouse, W. R. 1993. 'Northern climates', in French, H. and Slaymaker, O. (Eds), *Canada's Cold Environments*. McGill-Queens Press. pp. 65–92.
- Rouse, W. R., Carlson, D. W., and Weick, E. J. 1992. 'Impacts of summer warming on the energy and water balance of wet tundra', *Climatic Change*, **22**, 305–326.
- Rublee, P. A. 1992. 'Community structure and bottom-up regulation of heterotrophic microplankton in arctic LTER lakes', *Hydrobiologia*, **240**, 133–142.
- Ruuhijärvi, R. 1983. 'The Finnish mire types and their regional distribution', in Gore, A. J. P. (Ed.), *Ecosystems of the World 4b. Mires, Swamp, Bog, Fen and Moor. Regional Studies*, Elsevier Science Publishers, New York. pp. 47–67.
- Schindler, D. W., Welch, H. E., Kalfi, J., Brunskill, G. J., and Kritsch, N. 1974. 'Physical and chemical limnology of Char Lake, Cornwallis Island (75°N Lat.)', *J. Fish. Res. Bd Can.*, **31**, 585–607.
- Schell, D. M. and Ziemann, P. J. 1983. 'Accumulation of peat carbon in the Alaska Arctic coastal plain and its role in biological productivity', in *Permafrost. Fourth International Conference*. National Academy Press, Washington, D.C. pp. 1105–1110.
- Schlesinger, D. A. and Regier, H. A. 1982. 'Climatic and morphoedaphic indices of fish yields from natural lakes', *Trans. Am. Fish. Soc.*, **111**, 141–150.
- Schlesinger, D. A. and Regier, H. A. 1983. 'Relationship between environmental temperature and yields of subarctic and temperate zone fish species', *Can. J. Fish. Aquat. Sci.*, **40**, 1829–1837.
- 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', *Freshwat. Biol.*, **32**, 261–275.
- Shaver, G. R., Billings, W. D., Chapin, F. S. III, Giblin, A. E., Nadelhoffer, K. J., Oechel, W. C., and Rastetter, E. B. 1992. 'Global change and the carbon balance of arctic ecosystems', *Bioscience*, **42**, 433–441.
- Sheath, R. G. 1986. 'Seasonality of phytoplankton in northern tundra ponds', *Hydrobiologia*, **138**, 75–83.
- Shurapli, N. J., Verma, S. B., Kim, J., and Afkebauer, T. J. 1995. 'Carbon dioxide exchange in a peat ecosystem', *J. Geophys. Res.*, **100**(D1), 14319–14326.
- Siegel, D. I., Reeve, A. S., Glaser, P. H., and Romanowicz, E. A. 1995. 'Climate-driven flushing of pore water in peatlands', *Nature*, **374**, 531–533.
- Skinner, W. R. and Gullet, D. W. 1993. 'Temperature trends in Canada', *Climatol. Bull.*, **27**, 63–77.
- Smol, J. P. 1988. 'Paleoclimate proxy data from freshwater arctic diatoms', *Verh. Int. Verein. Limnol.*, **23**, 837–844.
- Smol, J. P., Walker, I. R., and Leavitt, P. R. 1991. 'Paleolimnology and hindcasting climatic trends', *Verh. Int. Verein. Limnol.*, **24**, 1240–1246.
- Sommer, M. E. 1979. 'Role of zooplankton grazers in determining the composition and productivity of seston in arctic lakes and ponds', *MSc Thesis*, University of Cincinnati, Ohio.
- Spear, R. W. 1993. 'The palynological record of late Quaternary arctic treeline in northwestern Canada', *Rev. Paleobot. Palynol.*, **79**, 99–112.
- Stoermer, E. F., Schelske, C. L., and Wolin, J. A. 1990. 'Siliceous microfossil succession in the sediments of McLeod Bay, Great Slave Lake, Northwest Territories', *Can. J. Fish. Aquat. Sci.*, **47**, 1865–1874.
- Sweeney, B. W. 1984. 'Factors influencing life-history patterns of aquatic insects', in Resh, V. H. and Rosenberg, D. M. (Eds), *The Ecology of Aquatic Insects*. Praeger, New York. pp. 56–100.
- Szeicz, J. M. and MacDonald, G. M. 1995. 'Dendroclimatic reconstruction of summer temperatures in northwestern Canada since A.D. 1638 based on age-dependent modeling', *Quat. Res.*, **44**, 257–266.
- Van Everdingen, R. O. 1974. 'Groundwater in permafrost regions of Canada', *Permafrost Hydrol.: Proc. Workshop Seminar, Can. Nat. Comm., The IHD*, pp. 83–93.
- Veres, A., Pienitz, R., and Smol, J. P. 1995. 'Lake water salinity and periphytic diatom succession in three subarctic lakes, Yukon Territory, Canada', *Arctic*, **48**, 63–70.
- Verry, E. S. 1988. 'The hydrology of wetlands and man's influence on it', in *Int. Symp. Hydrol. Wetlands in Temperate and Cold Regions*, Vol. 2. Suomen Akatemian Julkaisuja, Joensuu, Finland. pp. 41–61.
- Watt, W. E. (Editor-in Chief), 1989. *Hydrology of Floods in Canada: a Guide to Planning and Design*. N.R.C., Ottawa, Canada. 245 pp.
- Wein, R. W. 1983. 'Fire behavior and ecological effects in organic terrain', in Wein, R. W. and MacLean, D. A. (Eds), *The Role of Fire in Northern Circumpolar Ecosystems*. John Wiley & Sons, Toronto. pp. 81–95.
- Welch, H. E. and Bergman, M. A. 1985. 'Water circulation in small arctic lakes in winter', *Can. J. Fish. Aquat. Sci.*, **43**, 506–520.
- Welch, H. E. and Legault, J. A. 1986. 'Precipitation chemistry and chemical limnology of fertilized and natural lakes at Saqvagjuak', N.W.T., *Can. J. Fish. Aquat. Sci.*, **43**, 1104–1134.
- Wells, E. D. and Hirvonen, H. E. 1988. 'Wetlands of Atlantic Canada', in *Wetlands of Canada. Ecological Land Classification Series*, No. 24. Sustainable Development Branch Quebec. Environment Canada, Ottawa, Ontario, and Polyscience Publ. Inc., Montreal. pp. 251–303.
- Whalen, S. C. and Cornwell, J. C. 1985. 'Nitrogen, phosphorus, and organic carbon cycling in an arctic lake', *Can. J. Fish. Aquat. Sci.*, **42**, 797–808.
- Woo, M.-K. 1986. 'Permafrost hydrology in North America', *Atmos.-Ocean*, **24**, 201–234.

- Woo, M.-K., Heron, R., Marsh, P., and Steer, P. 1983. 'Comparison of weather station snowfall with winter snow accumulation in high arctic basins', *Atmos.-Ocean*, **21**, 312–325.
- 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.
- Zoltai, S. C. 1993. 'Cyclic development of permafrost in peatlands of northwestern Alberta, Canada', *Arctic Alp. Res.*, **25**, 240–246.
- Zoltai, S. C. and Vitt, D. H. 1990. 'Holocene climatic change and the distribution of peatlands in western interior Canada', *Quart. Res.*, **33**, 231–240.