

POTENTIAL EFFECTS OF CLIMATE CHANGES ON AQUATIC SYSTEMS: LAURENTIAN GREAT LAKES AND PRECAMBRIAN SHIELD REGION

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ABSTRACT

The region studied includes the Laurentian Great Lakes and a diversity of smaller glacial lakes, streams and wetlands south of permanent permafrost and towards the southern extent of Wisconsin glaciation. We emphasize lakes and quantitative implications. The region is warmer and wetter than it has been over most of the last 12 000 years. Since 1911 observed air temperatures have increased by about 0.11°C per decade in spring and 0.06°C in winter; annual precipitation has increased by about 2.1% per decade. Ice thaw phenologies since the 1850s indicate a late winter warming of about 2.5°C. In future scenarios for a doubled CO₂ climate, air temperature increases in summer and winter and precipitation decreases (summer) in western Ontario but increases (winter) in western Ontario, northern Minnesota, Wisconsin and Michigan. Such changes in climate have altered and would further alter hydrological and other physical features of lakes. Warmer climates, i.e. 2 × CO₂ climates, would lower net basin water supplies, stream flows and water levels owing to increased evaporation in excess of precipitation. Water levels have been responsive to drought and future scenarios for the Great Lakes simulate levels 0.2 to 2.5 m lower. Human adaptation to such changes is expensive. Warmer climates would decrease the spatial extent of ice cover on the Great Lakes; small lakes, especially to the south, would no longer freeze over every year. Temperature simulations for stratified lakes are 1–7°C warmer for surface waters, and 6°C cooler to 8°C warmer for deep waters. Thermocline depth would change (4 m shallower to 3.5 m deeper) with warmer climates alone; deepening owing to increases in light penetration would occur with reduced input of dissolved organic carbon (DOC) from dryer catchments. Dissolved oxygen would decrease below the thermocline. These physical changes would in turn affect the phytoplankton, zooplankton, benthos and fishes. Annual phytoplankton production may increase but many complex reactions of the phytoplankton community to altered temperatures, thermocline depths, light penetrations and nutrient inputs would be expected. Zooplankton biomass would increase, but, again, many complex interactions are expected.

Generally, the thermal habitat for warm-, cool- and even cold-water fishes would increase in size in deep stratified lakes, but would decrease in shallow unstratified lakes and in streams. Less dissolved oxygen below the thermocline of lakes would further degrade stratified lakes for cold water fishes. Growth and production would increase for fishes that are now in thermal environments cooler than their optimum but decrease for those that are at or above their optimum, provided they cannot move to a deeper or headwater thermal refuge. The zoogeographical boundary for fish species could move north by 500–600 km; invasions of warmer water fishes and extirpations of colder water fishes should increase. Aquatic ecosystems across the region do not necessarily exhibit coherent responses to climate changes and variability, even if they are in close proximity. Lakes, wetlands and streams respond differently, as do lakes of different depth or productivity. Differences in hydrology and the position in the hydrological flow system, in terrestrial vegetation and land use, in base climates and in the aquatic biota can all cause different responses. Climate change effects interact strongly with effects of other human-caused stresses such as eutrophication, acid precipitation, toxic chemicals and the spread of exotic organisms. Aquatic ecological systems in the region are sensitive to climate change and variation.

Assessments of these potential effects are in an early stage and contain many uncertainties in the models and properties of aquatic ecological systems and of the climate system. © 1997 by John Wiley & Sons, Ltd.

Hydrological Processes, vol. 11, 825–871 (1997)

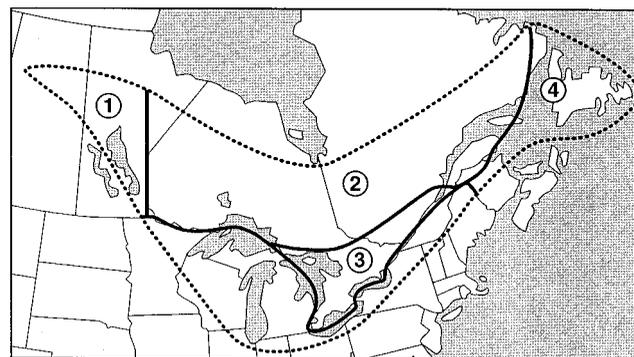
(No. of Figures: 20 No. of Tables: 3 No. of Refs: 222)

KEY WORDS Laurentian Great Lakes; Precambrian Shield; climate change; aquatic systems; north temperate glacial lakes; hydrology; paleoclimates; lake ice; water level; physical limnology; chemical limnology; phytoplankton; zooplankton; fish; terrestrial-aquatic linkages; interaction with other stresses; heterogeneity in response; biogeochemistry

INTRODUCTION

The Laurentian Great Lakes and Precambrian Shield Region extends from the southern edge of the permafrost line to the southern extent of the Wisconsin glaciation (between 40–50°N) (Figure 1). Much of the current character of the region was shaped by geological and glacial processes, especially by the retreat of the Wisconsin glaciation beginning about 12 000 years ago. This water-rich region has low relief, cool to cold winters and warm to cool summers. A multitude and diversity of aquatic resources dominates the landscape, including the Laurentian Great Lakes, smaller glacial lakes, streams and wetlands.

The Great Lakes system has a surface area of 244 000 km² and a volume of 23×10^{15} litres, 20% of the world's fresh surface water. Lake Superior is the world's largest freshwater lake in surface area, while Huron is fifth and Michigan is sixth. Lake Ontario is the fourth deepest and fourteenth largest lake in the world. About 30 million people live in the Great Lakes Basin, including 9% of the total population of the US and 29% of that of Canada. The Great Lakes play an important role in the region's economy, supplying water for domestic uses, agriculture, power generation and industry; providing a vital inland shipping route for a variety of products; and supporting important recreational and commercial fisheries. The region includes high concentrations of smaller inland lakes. Over 376 000 lakes greater than 1 ha in area (about 18 000 000 ha total) occur in south-eastern Canada south of 52°N and east of 90°W. Similar high densities of lakes occur in the upper mid-western states of Wisconsin, Michigan and Minnesota. For example,



.... Laurentian Great Lakes and Precambrian Shield Region

Canadian Climatic Regions

- ① Northwestern Forest
- ② Northeastern Forest
- ③ Great Lakes/St. Lawrence
- ④ Atlantic

Figure 1. Major climatic areas of Canada used for analysis of temperature and precipitation trends

Wisconsin alone has 12 500 natural lakes covering 140 000 ha (Wisconsin Department of Natural Resources, 1995), or, on a smaller scale, nearly 2500 lakes occur in Vilas and Oneida Counties, Wisconsin, where they cover about 12% of the landscape. Wisconsin also contains about 2 000 000 ha of wetlands and perhaps 53 000 km of streams. These are important components of the landscape that are strong attractors for humans.

The physical, chemical and biological processes and attributes of these systems are sensitive to climate change as are the values placed on these aquatic systems by humans. Two overarching considerations shaped our thoughts; first, the wide array of limnological processes and phenomena expected to be influenced by climate changes; and, secondly, the heterogeneity or differences in responses expected among water bodies. Our interests were also drawn to quantitative estimates over qualitative ones. Our review builds on general overviews of the potential changes in aquatic ecosystems related to climatic warming (J. B. Smith, 1991; Carpenter *et al.*, 1992; Arnell *et al.*, 1996). We address potential changes in the climate itself; physical limnology, including ice phenologies, water temperatures and mixing regimes; hydrology, with respect to water levels, runoff, weathering and residence times; light availability, with respect to changes in water clarity; chemical limnology, such as dissolved organic carbon concentrations, nutrient availability and deep water oxygen concentrations; and distribution, growth and persistence of the fauna and flora. Watershed- and lake-specific factors were identified as being key in determining the heterogeneity of response between waters. Even adjacent lakes can respond differently owing to differences in morphology and position in the hydrological flow system.

PRESENT CLIMATE

The Laurentian Great Lakes and Precambrian Shield Region (Figure 1) contains a suite of climates; conditions range from the cold winters and cool summers of the boreal areas; to the eastern remnant of the prairies in Manitoba; to the warm, humid summers and cold winters of the south-western Great Lakes region; to the maritime influence in Newfoundland (Table I). This diversity reflects the latitudinal and longitudinal extent of the region, as well as the other climatic controlling factors of topography, proximity to water bodies, continentality and large-scale atmospheric circulation.

Most of the region lies in the zone of westerlies, where migrating cyclones and anticyclones predominate. In winter, storms travel from the west and south-west into the Great Lakes area and along the St Lawrence River valley, while in summer, they follow a more northerly route above Lake Superior and through Hudson Bay, northern Quebec and Labrador. Seasonal changes in the position of the polar jet stream affect the route of storm tracks and the predominant air masses. In winter, the more southerly extent of the jet stream allows cold, dry Arctic air to penetrate south, while in summer, the more northerly position of the jet stream allows warm, moist air from the Gulf of Mexico to intrude. Mean monthly and annual air temperatures generally decrease with increasing latitude, reflecting latitudinal differences in intensity and duration of solar radiation. Mean annual temperatures range from -1.1 to $+2.2^{\circ}\text{C}$ in the north, to $+2.3$ to $+9.1^{\circ}\text{C}$ near the Great Lakes, to 0.0 to $+4.8^{\circ}\text{C}$ on the east coast (Table I). The difference between mean January and July temperatures is greatest near Winnipeg, Manitoba (40°C), least near St. John's, Newfoundland (19°C), and intermediate near Windsor in southern Ontario (27°C) (Phillips, 1990). The southernmost limit of discontinuous permafrost coincides approximately with the -1.0°C mean annual air temperature (Mortsch, 1990). Scattered discontinuous permafrost occurs near James Bay; no permafrost is present in the Great Lakes basin and Newfoundland. The number of freeze-free days ranges from 140 in the north to 230 in the south. Most small lakes freeze over completely; the Great Lakes attain maximum ice cover in February or March but usually do not freeze over completely (Superior 75%, Michigan 45%, Huron 68%, Erie 90% and Ontario 24%; Assel *et al.*, 1983). Depending on flow, size and location, rivers may or may not freeze over. Hudson Bay and James Bay offer little warmth or moderating influence to the surrounding region because ice-out occurs in late June. Annual precipitation increases from west to east at a rate of approximately 40 mm every 100 km, from about 400 mm per year in Winnipeg, Manitoba, to 1400 mm on the eastern

Table I. Current climate statistics for sites in, or somewhat north of, the Great Lakes and Laurentian Shield Region. Data are from Atmospheric Environment Service (1982a–f) and McIver and Isaac (1989)

Climate station	Location	Mean annual daily temp. (°C)	Mean January temp. (°C)	Mean July temp. (°C)	Mean annual freeze-free days (days)	Mean annual growing season (days)	Mean annual growing degree-days (°C)	Total annual precip. (mm)	Total annual snowfall (cm)	Total January precip. (mm)	Total July precip. (mm)
Manitoba											
Winnipeg Int'l A	49°54'N 97°14'W	2.2	-19.3	19.6	170	159	1784.9	525.5	125.5	21.3	75.9
Ontario											
Moosonee	51°16'N 80°39'W	-1.1	-20.4	15.3	139	123	1107.4	727.7	239.3	40.7	95.9
Thunder Bay A	48°22'N 89°19'W	2.3	-15.4	17.6	161	147	1425.4	711.8	213.0	40.9	75.4
Warton	44°45'N 81°06'W	6.0	-7.1	18.5	141	N/A	1821.0	964.7	352.6	97.0	75.1
Windsor A	42°16'N 82°58'W	9.1	-4.9	22.2	231	213	2533.3	848.8	117.4	55.0	83.4
Quebec											
Sept-Isles A	50°13'N 66°16'W	1.1	-14.0	15.2	158	135	1015.6	1124.9	426.9	95.5	97.0
Newfoundland											
St John's A	47°37'N 52°45'W	4.8	-3.9	15.5	189	169	1196.1	1513.6	359.4	155.8	75.3
Goose (Bay) A	53°19'N 60°25'W	0.0	-16.4	15.8	151	135	1021.9	946.1	445.2	74.4	105.1

shore of Newfoundland (Phillips, 1990). Precipitation exceeds 1000 mm in the lee of the Great Lakes, along the St Lawrence River and in Newfoundland.

The mid-continental location of the Great Lakes Basin contributes to large seasonal air temperature contrasts between the warm summers and cold winters. The Atlantic Ocean cannot exert a significant moderating influence because air flow is primarily from the west. The polar jet stream is often located near or over the basin and is the focal point for the genesis and development of low pressure storm systems that are characterized by cloudy skies, windy conditions and precipitation. The frequent passage of these low pressure systems results in the day to day variability in weather conditions.

The Great Lakes are large heat reservoirs that moderate the surrounding climate. This moderation delays the onset of spring because large lakes are a heat sink, with water temperatures cooler than the surrounding land. The autumn is extended and first frost is delayed because the warmer waters slowly release stored heat. 'Lake effect' snowbelts occur along the leeward sides of the lakes. During late autumn and winter, when the water is still open, outbreaks of cold, dry Arctic air pass over the warm, moist waters of the Great Lakes and convective snowfall develops (Phillips and McCulloch, 1972; Kunkel *et al.*, 1993).

Newfoundland and Labrador have a maritime climate although the influence of the Labrador Sea and the Atlantic Ocean is minimal because the prevailing westerly winds are offshore. In spring and summer, winds can be onshore and the cold Labrador Current moderates temperatures and causes fog and low clouds. Newfoundland can be influenced occasionally by tropical cyclones.

PALAEOCLIMATES

A variety of palaeotechniques reveal a pattern of continuous climate change and variation over the last 12 000 years (Figure 2) (see also Grimm and Jacobson, 1992). A coarse scale interpretation is that climates were cooler than the present from 12 000 to 7000 BP and again from 3000 to 300 BP; a period of warmer climates existed from about 7000 to 3000 BP (Figure 2a). Temperatures were up to 7°C cooler and 3°C warmer. Precipitation at present is high relative to the last 12 000 years; only the years around 9000 BP were wetter than present (Figure 2b). Precipitation was up to 40 mm greater and 180 mm lower than at present. Below, we discuss the palaeoclimates and palaeolimnology for the three Canadian climate regions relevant to the Laurentian Great Lakes and Precambrian Shield Region (Figure 1).

Laurentian Great Lakes/St Lawrence

The earliest lacustrine and bog sediment records from the Laurentian Great Lakes and Precambrian Shield Region date to *ca.* 14 500 BP, with the development of glacial Lake Maumee in the Lake Erie basin, from where the Wisconsin ice sheet first waned northwards (Calkin and Feenstra, 1985). Most lake sediment records north of Lake Ontario and east of Lake Huron began somewhat later, *ca.* 12 000 to 11 500 BP, when the Wisconsin ice sheet retreated. Sediments of much longer duration exist only in a few cases; a sediment record from Ile de la Madeleine, Quebec, dates at least as far back as the Sagamonian climatic optimum (89–110 ka), and contains pollen suggesting a warmer climate than at any time during the Holocene (Dredge *et al.*, 1992). Climatic and vegetational trends were not synchronous throughout the Great Lakes region during the early postglacial period. Trends were initiated earlier in the south and later in the north as the ice retreated northwards and the Champlain Sea disappeared in approximately 11 000 BP (Anderson, 1987).

Pollen and lake level data, and the climatic estimates inferred from them, indicate that the greatest climatic changes took place between 12 000 and 9000 BP (Webb *et al.*, 1987). The initial vegetation following deglaciation was herb–shrub tundra, interspersed with open stands of spruce, poplar, juniper and shrub birch and alder (Anderson, 1987). This vegetation developed along the southern Great Lakes from shortly after deglaciation until about 11 200 BP, and persisted to the north of the Champlain Sea until about 10 000 BP (Anderson, 1987). Pollen transfer functions infer mean July temperatures ranging from 11 to 14°C during this period at Tonawa Lake (44°51'N, 77°11'W) near Bancroft, Ontario (McAndrews and Campbell, 1993), which are much lower than the present temperatures of about 19°C.

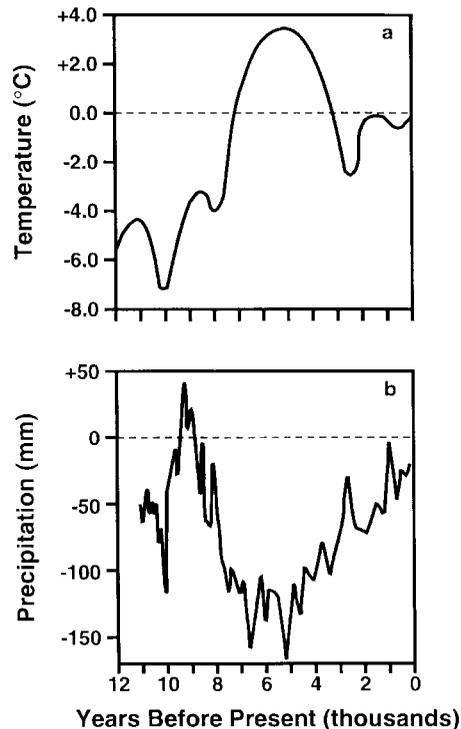


Figure 2. Mean annual palaeotemperature (a) for south-eastern Canada (modified from Terasmae, 1961) and precipitation estimates (b) from pollen data at Kirchner Marsh in Minnesota (modified from Webb *et al.*, 1987)

About 11 000 BP an open canopy spruce forest developed along the Great Lakes and migrated northwards with the margin of the Laurentian Ice Sheet, reaching the Precambrian Shield in the Ottawa Valley by about 10 200 BP (Anderson, 1987), and north of Sudbury, Ontario just after 10 000 BP (Liu, 1990). The spruce forest spread as climatic conditions warmed, but the climate remained cooler and wetter than today (Webb *et al.*, 1987). Pollen-inferred mean July temperatures ranged from 14 to 17°C in southern Ontario, and slightly cooler to the north (McAndrews and Campbell, 1993). The spruce period persisted for about 1000 years until birch and pine arrived from the south.

Up until the end of the spruce period, lake diatom assemblages usually consisted of benthic taxa dominated by *Fragilaria* sp. (Sreenivasa and Duthie, 1973; Smol and Boucherle, 1985; Hall, 1993). Precise inferences of limnological conditions are difficult because similar species occur today from oligotrophic to eutrophic conditions. The general absence of planktonic forms suggests that the lakes were ice covered for extended periods during summer and that thermal stratification did not develop. Apparently benthic diatoms were restricted largely to nearshore, ice-free moats in shallow margins of the lakes (Smol and Boucherle, 1985; Smol, 1982).

Pollen and lake level data indicate that 12 000 and 9000 BP were considerably cooler and wetter than the present (Terasmae, 1961; Webb *et al.*, 1987) (Figure 2). Seasonal differences in insolation and temperature were pronounced. The Laurentide Ice Sheet created unique climatic conditions that do not exist today. Mean annual temperatures warmed between 12 000 to 11 000 BP and again between 10 000 to 8000 BP, and generally ranged from 8–4°C below those at present.

Localized climatic shifts adjacent to the Laurentian Great Lakes were caused by the retreats and readvances of the ice sheet; this altered patterns of inflow and outflow to and from the lakes, as well as water levels, surface water temperatures and local climates (Lewis and Anderson, 1989; Anderson and Lewis,

1992). Lake Agassiz discharged cold glacial meltwater eastwards through the Great Lakes and the Gulf of St Lawrence during two distinct periods, 11 000–10 500 and 9600–8300 BP, when the Laurentide Ice Sheet migrated northwards (Teller and Thorliefson, 1983; Teller, 1985). Cold meltwater flowing into the Great Lakes most likely increased several-fold, cooled surface waters (Lewis and Anderson, 1989), cooled local climates and reduced the growing season around the upper Great Lakes and Gulf of St Lawrence (Lewis and Anderson, 1989, 1992).

Pollen assemblages and, thus, climatic and edaphic conditions, became largely synchronous everywhere in the Great Lakes/St. Lawrence area after 9500 BP, when a closed pine forest developed in response to a warmer and drier climate (Anderson, 1987). In southern Ontario, pollen-inferred July temperatures averaged 19–21°C, similar to those of today (McAndrews and Campbell, 1993). The warmer temperatures probably extended the growing season of phytoplankton in the deep water regions of lakes (Smol and Boucherle, 1985), and permitted planktonic diatom and chrysophyte communities to develop. Lake nutrient concentrations were low because watershed nutrient release was low from the immature pine forest.

The Hypsithermal, or mid-Holocene warm period, occurred between 8000 and 4000 BP. The pollen–climate transfer functions of Bartlein and Webb (1985) and Bartlein and Whitlock (1993, in Yu and McAndrews, 1994) indicated mean July temperatures 1–2°C warmer, and precipitation 10–20% less than at present. These conditions permitted hemlock, beech and thermophilous hardwood taxa (including maple, elm and oak) to migrate into southern Ontario. By 7500 BP, a forest similar to the present Great Lakes/St Lawrence forest became established in the southern parts of the region (Rowe, 1977). Independent evidence from stable isotopes (Edwards and Fritz, 1988) and lower lake levels (Webb *et al.*, 1987; Yu and McAndrews, 1994) also indicated a warm/dry climate between 7400 and 4000 BP.

About 3500 BP, during the Neoglacial cooling, the climate became cooler and moister (Anderson, 1989). Palaeoecological evidence for this cooling is not straightforward in the Great Lakes/St Lawrence region. Pollen-inferred temperatures did not decline at this time in southern Ontario (McAndrews and Campbell, 1993) but palaeolimnological evidence indicates that water levels rose in Rice Lake, which is attributable to cooler and wetter conditions as well as continued isostatic uplift (Yu and McAndrews, 1994). Perhaps the best evidence for Neoglacial cooling comes from sites farther north in the boreal forest, where the ecotonal boundary shifted southwards (see below).

Campbell and McAndrews (1991, 1993) presented pollen stratigraphical evidence of the Little Ice Age cooling between 1450 and 1850 AD; beech pollen declined at its northern limit just south of Lake Nipissing, and the climate optimum for white pine shifted 100–140 km southwards. Pollen transfer functions inferred that mean July temperatures declined by about 0.5°C during this period at Tonawa Lake, near Bancroft, Ontario.

North-eastern forest

A steep climatic gradient and ecotonal boundary between the boreal and Great Lakes/St Lawrence forest exists between Lake Huron and James Bay (Liu, 1990). Its position is controlled by continent-scale atmospheric circulation that determines the position of the arctic front. Thus, the boundary shifted markedly with postglacial climatic changes (Liu, 1990); climatic shifts did not occur synchronously across the entire area.

Lake sedimentation began after 10 000 BP, later than in the Great Lakes/St Lawrence area, because the glacier retreated later. Spruce forests began about 9500 BP near the southern edge of the area (Nina Lake, 46°36'N, 81°30'W; Liu, 1990) and was delayed until about 7500 BP 220 km farther north (Lake Six, 48°24'N, 81°19'W). The pine forest was also delayed relative to more southern sites. Pollen profiles near Sudbury and Sault Ste. Marie inferred relatively rapid increases in mean July temperatures, from 16 to 19°C, in the pine period (McAndrews and Campbell, 1993). Jack pine forest development occurred later at sites farther north, beginning about 9000 BP at Nina Lake, and not until about 7000 BP at Lake Six (Liu, 1990). The period of jack pine forest was shorter at more northern sites, as white pine became established and dominant everywhere by about 7000 BP (Liu, 1990).

Hypsithermal warming caused a marked northward migration of the boundary between the boreal and Great Lakes forests. By 7400 BP this ecotone had migrated north of Sudbury (Nina Lake). By 3000 BP the boundary advanced to its northernmost position of the entire postglacial period, i.e. 140 km north of its present position (Liu, 1990). Southward movement of the boundary in the area north of Sudbury provides strong evidence for Neoglacial cooling (Liu, 1990). The boundary migrated past Lake Six (to the north) about 4000 BP and Nina Lake (to the south) about 2500 BP. Pollen-inferred mean July temperature dropped about 0.5–1°C both at Lake QC (46°50'N, 80°42'W) near Sudbury and R Lake (54°18'N, 84°34'W) near the north-western edge of James Bay (McAndrews and Campbell, 1993).

Atlantic

The timing and nature of climatic and vegetational shifts in eastern maritime Canada were somewhat different from Quebec and Ontario, possibly owing to oceanic influences and different soil development. Sediment records in New Brunswick and Nova Scotia began just before 12 500 BP (Wilson *et al.*, 1993). Pollen stratigraphies indicated that the region was initially colonized by herb–shrub tundra. Prior to 11 000 BP, spruce trees became established, but appeared unable to colonize sites with direct exposure to oceanic weather, i.e. Brier Island Bog Lake (Wilson *et al.*, 1993). Pollen profiles typically showed a decline in spruce abundance and an increase in tundra-like vegetation (Mott *et al.*, 1986) in the cool Younger Dryas (*ca.* 11 000–10 000 BP). Based on reconstructions using chironomid assemblages, Wilson *et al.* (1993) approximated midsummer water temperatures at 17–20°C prior to the Younger Dryas (before 11 000 BP) at Brier Island Bog Lake, Nova Scotia, and at Splan Lake, New Brunswick. During the Younger Dryas midsummer, water temperatures dropped to 13–16°C, and subsequently increased after 10 000 BP to 20–24°C (Wilson *et al.*, 1993). Diatom assemblages indicated that the lakes supported seasonally ice-free, open water, and possibly turbulent, wind-mixed conditions during the Younger Dryas (Wilson *et al.*, 1993).

In Labrador, initial vegetation developed between 10 500 and 9500 BP, and consisted of an open tundra dominated by sedges, grasses, herbs and shrubs (Engstrom and Hansen, 1985). The climate was cold, but generally warmer than present day tundra. From 9500 to 8000 BP, shrub taxa, including birch and alder, increased, creating a vegetation similar to the shrub tundra that exists today. Continuous vegetation changes occurred from 8000 to 6000 BP owing to the sequential rise and replacement of Labrador's major tree species. White spruce arrived at *ca.* 8000 BP, substantially later relative to sites farther south along the Gulf of St Lawrence where spruce appeared between 10 000 and 9000 BP (Engstrom and Hansen, 1985). This shift was attributed to progressive changes in soil conditions, towards more waterlogged peat, rather than to climatic factors.

A relatively stable pollen assemblage characteristic of the present boreal forest has persisted in Labrador from 6000 BP to present. However, pollen and geochemical evidence indicated a regional shift to colder conditions after 4000 BP, resulting in decreased tree density and thinner soil humus (Engstrom and Hansen, 1985). Interior sites were more strongly affected than coastal ones. This cooling, which began between 4000 and 3000 BP, corresponds with the period of Neoglacial cooling detected at a number of sites in the Laurentian Great Lakes and Precambrian Shield Region.

RECENT CLIMATE TRENDS

Four climatic regions delineated for analysis of the Canadian climate include portions of the Laurentian Great Lakes and Precambrian Shield Region; these are the North western Forest, the North eastern Forest, the Great Lakes/St Lawrence and the Atlantic (Figure 1). Daily temperature and precipitation (Mekis and Hogg, 1997) and monthly temperature and precipitation (Gullett *et al.*, 1992) data sets were developed to analyse climate trends across Canada. The daily data were a contribution to the 1995 Intergovernmental Panel on Climate Change (IPCC) report and the monthly data comprise the Historical Canadian Climate Database (HCCD). Daily precipitation data were corrected for under catch from wind and other factors,

wetting loss, trace value correction and instrumentation changes (Mekis and Hogg, 1997; Metcalfe *et al.*, 1994). Monthly precipitation data were not corrected. Monthly temperature data were adjusted to account for discontinuities or 'inhomogeneities' from changes in observing programme, instrumentation, site conditions and other non-climatic effects (Gullet *et al.*, 1992; Skinner and Gullet, 1993). For both data sets, methodologies were developed for joining observation records of nearby stations to extend the time-series. Missing values were estimated (Gullet *et al.*, 1992; Mekis and Hogg, 1997). Monthly temperature and daily precipitation data were selected to provide the most reliable time-series. The 83 years from 1911 to 1993 generally comprised the daily precipitation time-series, while 1895–1993 were used for temperature time-series. In addition, for major Great Lake basins, we examined precipitation and temperature trends from 1900 to 1990. Two primary hydrometeorological variables affecting the Great Lakes/St Lawrence River Basin ecosystem are precipitation and air temperature. Monthly precipitation data (Croley and Hunter, 1994) were based on US Lake Survey District, Corps of Engineers areally weighted 'precipitation districts' for 1900–1929 (Quinn and Norton, 1982); a modified Thiessen approach using a 5-km grid for 1930–1947 (Quinn and Norton, 1982); and a Thiessen weighting approach using a 1-km grid and daily data for 1948–1990 (Croley and Hartmann, 1985). Air temperature data were an update of Bolsenga and Norton (1993) from gridded data of quality controlled land stations for the Great Lakes Basin. Primary sources were the Carbon Dioxide Information Analysis Center and the Canadian Climate Centre.

Annual and seasonal temperature and precipitation trends for each Canadian climate region (Figure 1) within the Laurentian Great Lakes and Precambrian Shield, are summarized in Table II. Both the Great Lakes/St Lawrence and North eastern Forest areas show temperature and precipitation trends (Figure 3). An analysis of the linear trend in the temperature time-series for the Great Lakes/St Lawrence area indicates an increase of 0.6°C from 1895 to 1993. Weak oscillations are suggested from visual inspection, with the values peaking near 1950. For the North eastern Forest, temperature increased 0.4°C from 1895 to 1993; virtually all of the warming had occurred by 1940. Examination of seasonal data reveals that most of the increase in both areas was during the spring. The most significant temperature increases occurred in spring and winter. Across the Great Lakes basin as a whole the long-term trend in annual temperature is weak and inconsistent over time (Figure 4). However, spring air temperatures over the basin have warmed persistently, summer temperatures have a slow downward trend since the 1940s, autumn temperatures have declined since the 1960s and winter temperatures have been lower since the late 1950s (Bolsenga and Norton, 1993).

Precipitation trends are more variable in both the Great Lakes/St Lawrence (1911–1993) and the North-eastern Forest (1918–1993) (Figure 3, bottom). Annual precipitation increased 2.0 mm per decade, or 2.1% per decade, for the Great Lakes and 2.4% per decade for the North eastern Forest, corresponding to an increase of 21–24% per century. These two areas demonstrate the largest absolute rate of change of the 11 Canadian climatic regions. Scrutiny of both time-series (Figure 3, bottom) reveals that precipitation peaked in the late 1960s to early 1970s and has been declining since then.

Table II. Linear temperature and precipitation trends within climatic regions of the Great Lakes and Laurentian Shield Region. Data are from Climate Change Detection, Atmospheric Environment Service, Environment Canada

Climatic area	Temperature change (°C) 1895–1993					Precipitation (% over 10 years) 1911–1993				
	Annual	Spring	Summer	Autumn	Winter	Annual	Spring	Summer	Autumn	Winter
North-western Forest*	1.4	2.3	1.1	0.4	1.7	1.4	−0.9	2.5	2.4	−2.9
Northeastern Forest†	0.4	0.9	0.5	0.0	0.5	2.4	2.8	1.8	2.4	2.9
Great Lakes/St Lawrence	0.6	0.8	0.1	0.3	1.1	2.1	1.5	2.3	2.9	1.5
Atlantic	0.2	0.2	0.8	−0.1	0.2	1.0	0.8	0.5	0.8	1.5

* Precipitation period 1937–1993.

† Precipitation period 1918–1993.

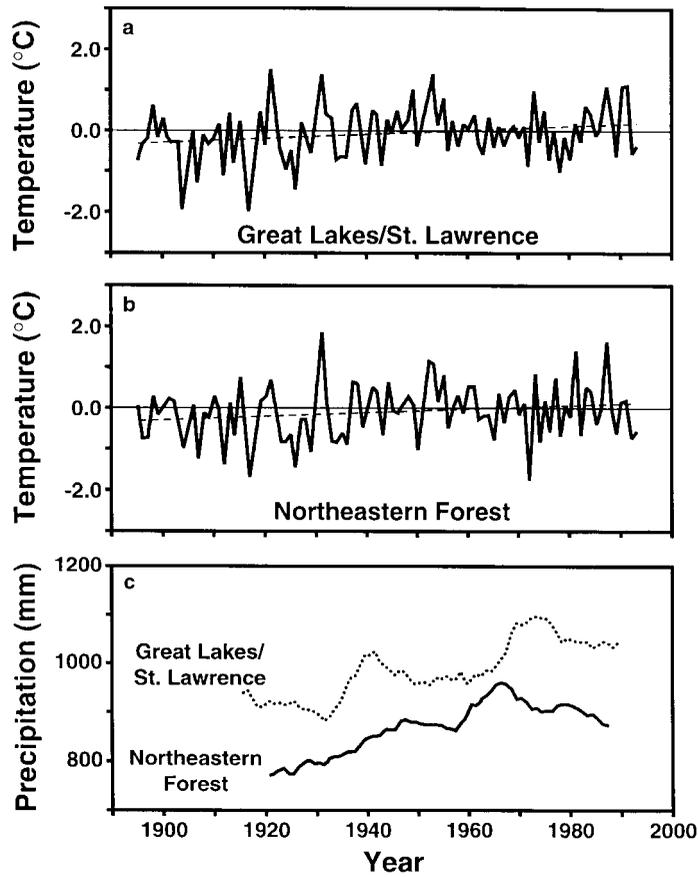


Figure 3. Departure from 1951–1980 average temperature (solid line) and linear trends (dashed lines) for: (a) Great Lakes Basin/ St Lawrence lowlands; and (b) North-eastern Forest. (c) Annual precipitation (9-year running mean) amount for these two regions

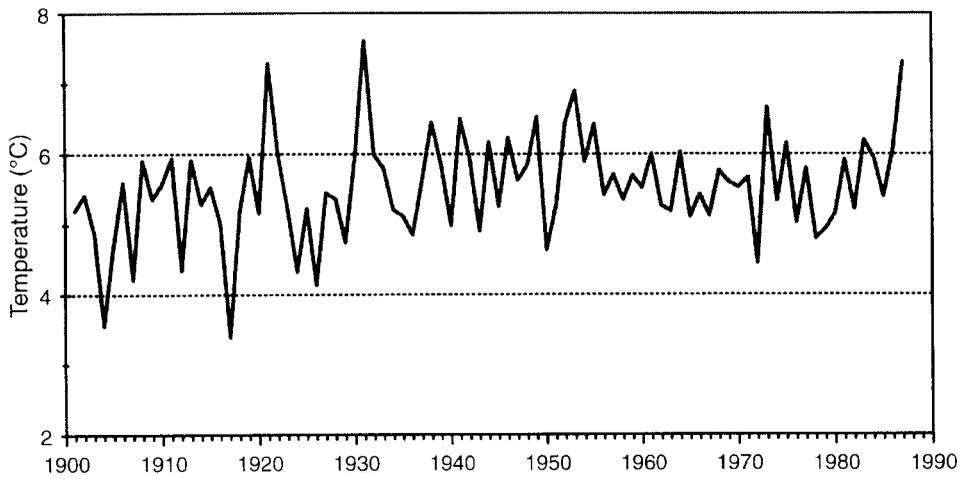


Figure 4. Annual temperatures for the Great Lakes Basin (1960–1990)

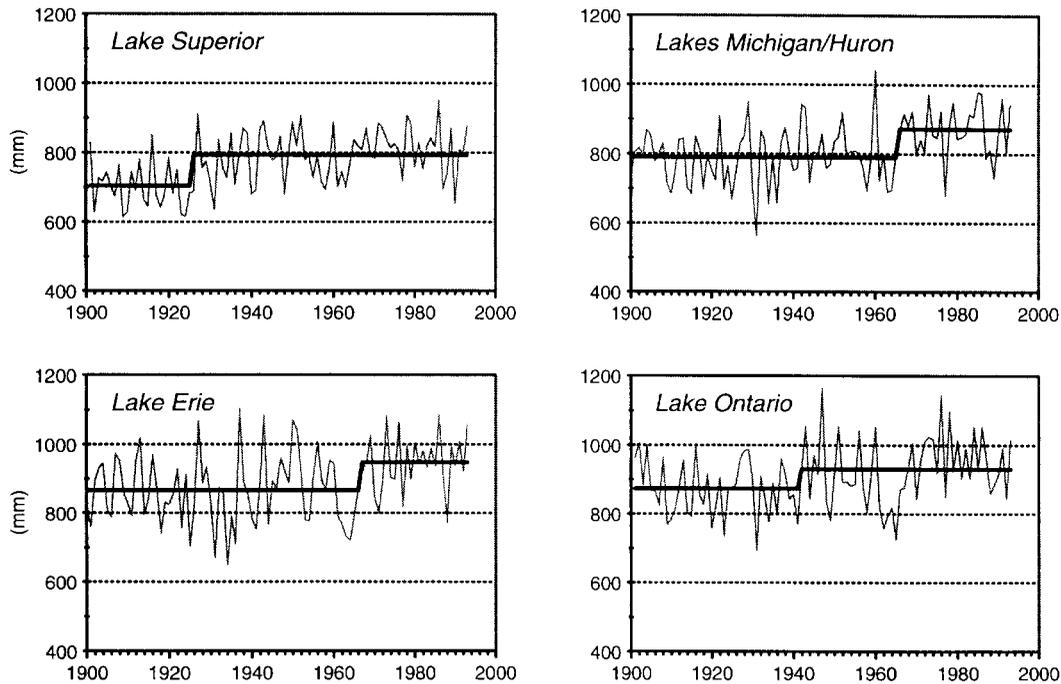


Figure 5. Annual precipitation and trends for Superior, Michigan/Huron, Erie and Ontario lake basins from early 1900s to the present. Heavy lines mark the time of step changes

Based on an update by Quinn (1981), several patterns emerge in seasonal and annual precipitation for each Great Lake basin. Annual precipitation time-series (Figure 5) indicate two distinct regimes for the Lake Michigan–Huron and Erie basins; a low precipitation regime from 1900 to about 1966 and a significantly higher precipitation regime from 1967 to the present. For the Lake Superior basin, a sudden increase in precipitation occurred in the late 1920s and was followed by a relatively stable period from 1930 to the present. The increase in precipitation around 1929 may be an artefact related to the number of stations in existence or to a change in the precipitation estimation methodology rather than a true change in regime. Lake Superior precipitation increased in all seasons from approximately 1930 (again, this may be an artefact), but during the 1980s, precipitation was lower for winter and spring in the Lake Superior Basin. For the Lake Ontario Basin, a low precipitation regime until the early 1940s was followed by a high precipitation regime. The increases in precipitation for Michigan and Huron, Erie, and Ontario (Figure 5), were primarily in summer and autumn.

Slivitsky and Mathier (1993) applied a variety of parametric and non-parametric time-series approaches to individual lake basins within the Great Lakes Basin using climate data from 1900 to 1988 for temperature, and 1990 to 1991 for precipitation. Most of the time-series contained statistically significant shifts in the mean during the century, suggesting that the changes were described well as steps or shifts rather than as linear trends.

CLIMATE CHANGE SCENARIOS

In this review, four general circulation models (GCMs) are used in various simulations of effects of increased greenhouse gases on climate. The Canadian Climate Centre general circulation model 2 (CCC GCMII) is discussed below in some detail. The others are the Goddard Institute for Space Studies model (GISS) (Hansen *et al.*, 1988), the Geophysical Fluid Dynamics Laboratory model (GFDL) (Manabe and Stouffer,

1980) and the Oregon State University model (OSU) (Schlesinger and Zhao, 1988). None of these models included the influence of aerosols and all were implemented with a step change from present to doubled CO₂ concentrations in the atmosphere (1 × CO₂ climates to 2 × CO₂ climates) rather than with a ramped change to doubled CO₂. Including such enhancements would most likely have reduced the magnitude of the simulated climate changes and their effects (Houghton *et al.*, 1996).

The second-generation atmospheric general circulation model from the Canadian Climate Centre of Environment Canada (CCC GCMII) was selected to illustrate a climate change scenario with an 'enhanced' greenhouse effect (Mortsch and Quinn, 1996). The CCC GCMII is a three-dimensional atmospheric GCM coupled to a mixed-layer ocean model that incorporates a thermodynamic sea ice component and allows a realistic simulation of the ocean surface temperature distribution and ice boundaries. Other improvements include greater horizontal resolution (3.75 degrees latitude by 3.75 degrees longitude), interactive cloudiness parameterization, more sophisticated radiative transfer treatment, including full diurnal and annual cycles, and incorporation of soil and vegetation information into land surface processes and hydrology (McFarlane *et al.*, 1992).

The CCC GCMII was used to test the sensitivity of the climate system to increased greenhouse gas concentrations in a 2 × CO₂, or doubled carbon dioxide, equilibrium response experiment (Boer *et al.*, 1992; Atmospheric Environment Service, 1994). First, a current climate simulation (1 × CO₂) was initiated where the average global carbon dioxide level was set at the present level; this model was run until a stable climate was produced. Secondly, the carbon dioxide gas component of the GCM was doubled and the model was run again until it reached a new equilibrium. The difference between the results of the 1 × CO₂ and the 2 × CO₂ runs provided an estimate of climate system sensitivity to a doubling of carbon dioxide. Although GCMs are the most advanced and most physically based tool for assessing the response of the climate system to significant increases in greenhouse gases, the results should not be interpreted as a prediction of climate change, but as a scenario. Climate scenarios provide a range of possible futures — 'what if' situations for exploring the implications of a changed climate.

The CCC GCMII 2 × CO₂ simulated a global mean surface temperature increase of 3.5°C; this is in the middle range of other GCM simulations (McFarlane, 1991; Boer *et al.*, 1992). The greatest warming was at high latitudes in winter. Precipitation increased by 3.8% over the globe and was statistically significant over 20% of the globe. The largest precipitation increase occurred over the oceans. Evaporation increased, soil moisture decreased by approximately 6.6% and summer dryness was enhanced in northern mid-latitudes. A major decrease in the area (53%) and mass (66%) of sea ice was simulated.

With scenarios for the Laurentian Great Lakes and Precambrian Shield Region, contours for increases in mean air temperature across the region ranged from +2 to +5°C in summer and +4 to +8°C in winter (Figure 6a and b). Contours for precipitation changes across the region ranged from -20 to +10% in summer and -10 to +20% in winter (Figure 6c and d). The predominant trend was for increased precipitation. Subregional differences in four scenarios for the Great Lakes Basin (CCC GCMII, GISS, GFDL and OSU) generally resulted in greater increases in temperature to the north in winter and to the west and south in summer, and greater increases in precipitation to the north-west in winter and to the north and east in spring (Mortsch and Quinn, 1996).

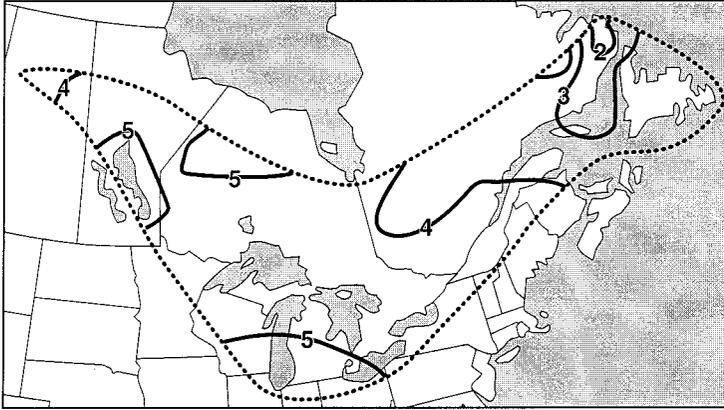
HYDROLOGY AND LAKE LEVELS

Climate changes influence the hydrological flows into and out of lakes, net basin water supplies and water levels. Thus, hydrological systems are potentially very sensitive to climate changes and can, in turn, influence many aspects of lake and stream ecosystems (Arnell *et al.*, 1996).

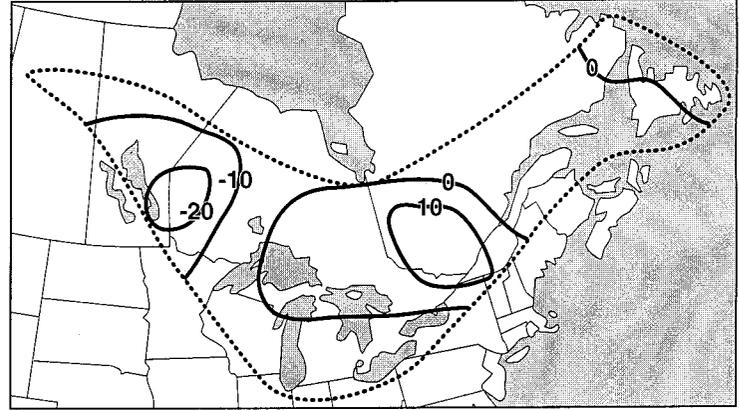
Laurentian Great Lakes

Historically, water levels of the Laurentian Great Lakes have fluctuated over a relatively small range, with approximately 1.8 m between record lows and highs. The Great Lakes system is naturally well regulated

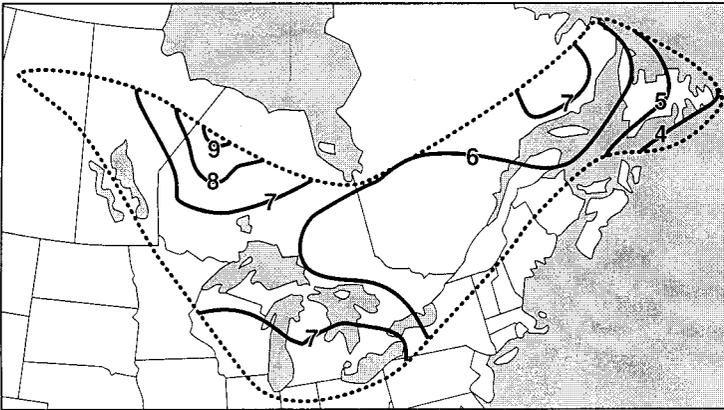
a) Summer Air Temperature Change (°C)



c) Summer Precipitation Change (%)



b) Winter Air Temperature Change (°C)



d) Winter Precipitation Change (%)

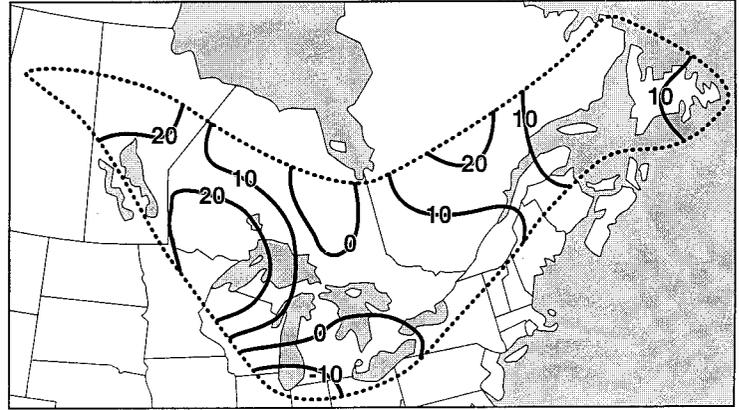


Figure 6. Changes in winter and summer mean air temperature (a,b) and winter and summer precipitation (c,d), comparing $2 \times \text{CO}_2$ with $1 \times \text{CO}_2$ scenarios

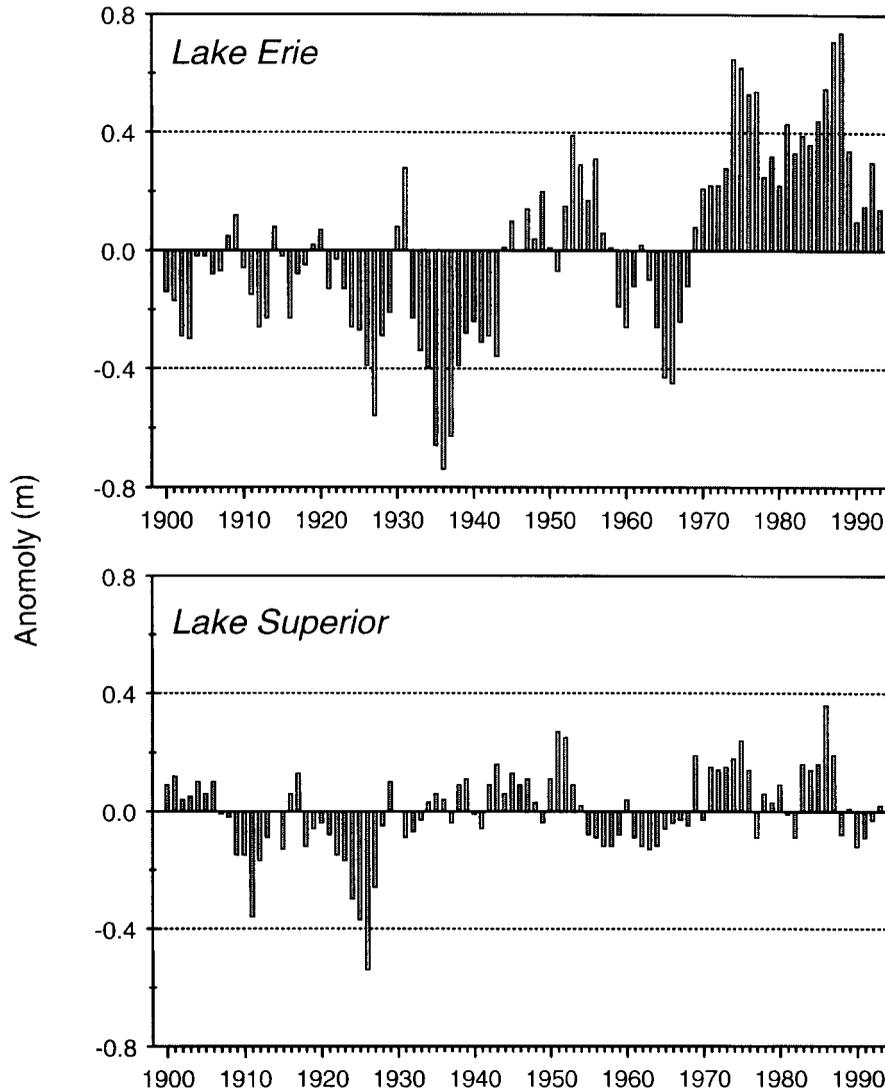


Figure 7. Water level anomalies (m) for lakes Erie and Superior

because it is large, has constructed outlet channels and two of the lakes (Superior and Ontario) have regulated outflows. The lakes have been in a high water-level regime since the late 1960s, culminating in record highs in 1986. A major decline in levels occurred in response to the 1987–1990 drought, but levels have continued to remain above the long-term mean for Michigan, Huron and Erie, and have been near or slightly below long-term mean levels for Superior. As examples, anomalies from the 1901–1989 long-term mean are shown for Erie and Superior (Figure 7). These above-average lake levels resulted from high water supplies beginning in the late 1960s.

In contrast to the general increases in water level over the last century, GCM scenarios for a doubling of CO_2 produced marked declines in water levels and outflows (Croley, 1990, 1993; Hartman, 1990; Mortsch and Quinn, 1996). Summaries of the hydrological model results by Mortsch and Quinn (1996) indicated declines from -0.23 to -2.48 m in water levels among all lakes and scenarios (CCC, GFDL, GISS and OSU). The greatest declines were for Michigan–Huron (-0.99 to -2.48 m among scenarios); the smallest

Table III. Average, annual, steady state Great Lakes Basin hydrology under base ($1 \times \text{CO}_2$), transposition and $2 \times \text{CO}_2$ scenarios. Values in italics are the percentage change from the base case

Scenario	Overland precipitation (m ³ /s)	Evapotranspiration (m ³ /s)	Basin runoff (m ³ /s)	Over lake precipitation (m ³ /s)	Over lake evaporation (m ³ /s)	Net basin supply (m ³ /s)
Base case — $1 \times \text{CO}_2$	13855	7814	6206	6554	4958	7803
Transposition scenarios:						
#1 $6^\circ\text{S} \times 10^\circ\text{W}$	14643 +6%	10201 +31%	4674 -25%	6767 +3%	7394 +49%	4048 -48%
#2 $6^\circ\text{S} \times 0^\circ\text{W}$	17167 +24%	11198 +43%	6154 -1%	8169 +25%	6615 +33%	7708 -1%
#3 $10^\circ\text{S} \times 11^\circ\text{W}$	16236 +17%	11563 +48%	4877 -21%	7379 +13%	8699 +75%	3556 -54%
#4 $10^\circ\text{S} \times 5^\circ\text{W}$	20095 +45%	13907 +78%	6308 +2%	9482 +45%	8364 +69%	7426 -5%
$2 \times \text{CO}_2$ scenarios						
CCC*	13637 -2%	7727 +22%	6090 -32%	6499 0%	5352 +32%	7237 -46%
GISS†	13871 +2%	9317 +21%	4658 -24%	6747 +4%	6821 +27%	4584 -37%
GFDL‡	13725 +1%	9176 +19%	4714 -23%	6501 0%	7685 +44%	3530 -51%
OSU§	14438 +6%	9204 +19%	5438 -11%	6903 +6%	6745 +26%	5596 -23%

* Canadian Climate Centre GCM (Croley, 1993).

† Goddard Institute for Space Studies GCM (Croley, 1990).

‡ Geophysical Fluid Dynamics Laboratory GCM (Croley, 1990).

§ Oregon State University GCM (Croley, 1990).

decline was for Superior (-0.23 to -0.47 m among scenarios); and Erie, Ontario and the St Lawrence River at Montreal were intermediate at about -1.3 m. Mean annual outflows also declined for all lakes; Lake Superior declined only -8% while the others ranged from -20 to -40% among scenarios, with a mean of about -30% . These declines in water level and outflows resulted from the simulated declines in inflows of -2 to -54% among lakes and scenarios. Greatest declines were for the Lake Erie Basin (-19 to -54%); smallest declines were for the Lake Superior Basin (-2 to -12%); and Michigan, Huron and Ontario were intermediate with declines ranging from -7 to -38% .

The seasonal pattern of hydrological parameters did not shift in the $2 \times \text{CO}_2$ simulations, nor were seasonal amplitudes accentuated a great deal (Croley, 1990; Hartman, 1990). However, compared with base conditions, runoff, temperature and evaporation were higher, and net basin supply was lower, in the $2 \times \text{CO}_2$ scenarios in all months. Net basin supply was highest in March and April when runoff was maximum and temperature and evaporation were low, and was lowest in August–October when runoff was low, and temperatures and evaporation were high.

To test further the sensitivity of the Laurentian Great Lakes hydrology, transposition climate scenarios were developed to introduce a change in both the mean and the variability of temperature and precipitation (Croley *et al.*, 1994, 1995; Mortsch and Quinn, 1996). Four climate regimes, selected from areas a few degrees south and west of the Great Lakes, were transposed to the Great Lakes Basin (Table III). Scenario 1 is warm and dry ($6^\circ\text{S} \times 10^\circ\text{W}$); scenario 2 is warm and wet ($6^\circ\text{S} \times 0^\circ\text{W}$); scenario 3 is very warm and dry ($10^\circ\text{S} \times 11^\circ\text{W}$); and scenario 4 is very warm and wet ($10^\circ\text{S} \times 5^\circ\text{W}$). Areal averages of the transposed climatic elements for 121 watersheds and over lake surfaces were derived by Thiessen weighting of daily data. The areally averaged transposed data were input to the hydrological models by the method used by Croley (1990, 1993). In these transposition scenarios, air temperature increased by $+4$ to $+11^\circ\text{C}$ and precipitation ranged from -20 to $+70\%$ of the current regime. Changes in Great Lakes water supplies resulting from the transposition were compared with the base case or current conditions and hydrology was expressed as total flows from all lake basins (Table III). Net basin supply declined by -1 to -54% ; the decline was about 50% under the westernmost scenarios (1 and 3) because evaporation and evapotranspiration tended to be higher and precipitation lower than in the easternmost scenarios (2 and 4), where net basin supplies were close to the base case. For comparison, corresponding results are shown for four GCM scenarios (Table III).

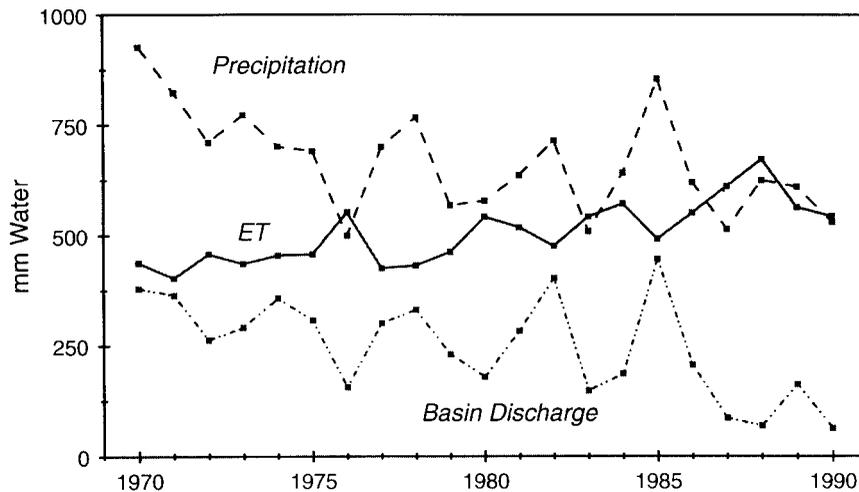


Figure 8. Hydrological changes observed for the Lake 240 basin during the 20-year period of warmer and drier conditions at ELA (adapted from Schindler *et al.*, 1996a)

Small inland lakes and streams

Comparable hydrological models for small lakes in the region have not been undertaken, but Mortsch and Quinn (1996) suggested that their water supplies would be expected to decline as well. They simulated changes in hydrological parameters (air temperature, precipitation, basin runoff and total basin moisture storage) for 121 sub-basins draining to the Laurentian Great Lakes. Moisture storage declined substantially in the doubled CO₂ scenarios, even though precipitation increased in the northern sub-basins; the declines occurred because temperature and evapotranspiration increased. Declines in basin runoff were greatest where simulated increases in temperature and declines in precipitation were greatest, namely in the southern half of the basin. Such reductions in tributary flow and soil moisture would affect the hydrology and related limnological properties and processes of groundwater, wetland, stream and lake systems.

The sensitivity of the water levels of small inland lakes to climatic changes is apparent from the observed responses to recent droughts. During the 1987–1990 drought in Wisconsin, water levels of lakes at the North Temperate Lakes Long-Term Ecological Research (LTER) site declined by up to 1 m. Lake level declines were largest in seepage lakes that were high in the landscape and received most of their water inputs from direct precipitation (Webster *et al.*, 1996). In contrast, declines of only a few cm were observed for drainage lakes low in the landscape, which received substantial inputs of both surface and groundwater.

Substantial hydrological shifts were also observed during the 20-year period of warmer and drier conditions in the 1970s and 1980s at the Experimental Lakes Area (ELA) in north-western Ontario. There, increased evaporation and decreased runoff resulted in the lengthening of water retention times in many lakes by a factor of about four over 20 years (Figure 8) (Schindler *et al.*, 1996a) at a rate of increase ranging from one to seven years per decade. Streams in the ELA also showed significant hydrological responses to drought; the number of days that first-order streams were dry during summer increased from less than 10 days per summer to about 140 days during the 20-year drought (Schindler *et al.*, 1996a).

The most dramatic effect of climate change will be the disappearance of lakes as a result of increased evaporation relative to precipitation. Short of this, salinities and nutrient concentrations would increase as lake volumes shrink while the sizes of drainage basins remain unchanged. In lakes with increased water renewal times, pollutant concentrations would rise even if inputs remained at present levels. Accompanying these abiotic changes would be a general shift towards species characteristic of eutrophic, saline and contaminated lakes.

Human adaptation and costs

Changes in lake levels, recently observed or simulated in $2 \times \text{CO}_2$ climate change scenarios, exceed those observed or simulated for sea level changes (Arnell *et al.*, 1996). Human responses to such large changes would be costly, particularly those related to shipping, dredging and replacement or refurbishing of shoreline structures in the Great Lakes (J. B. Smith, 1991). Changes in ice cover also influence shipping costs. In addition, higher demand and usage of water from the Laurentian Great Lakes would probably occur following a decrease in net basin water supplies.

For shipping at simulated water levels, 0.5–1.5 m lower than base levels, dredging costs would be incurred or ships would have to carry lighter loads (Keith *et al.*, 1989). If lighter loads were carried, costs per ton transported in $2 \times \text{CO}_2$ scenarios increased from 1.6 to 33% depending on the harbour (Duluth/Superior, Two Harbors and Whitefish Bay on Lake Superior, and Toledo, Cleveland and Buffalo on Lake Erie) and the scenario (GISS, GFDL and OSU). Cargoes would have to be reduced by 1.6–27% to get into the harbours without additional dredging. Dredging costs can be high, ranging from \$0.0–31 million per harbour among harbours and scenarios without including the costs associated with shipping-related facilities. For the 101 km Illinois shoreline of Lake Michigan, including Chicago, \$138–312 million would be needed over a 50-year period for dredging harbours to compensate for a 1.25–2.5 m decline in lake level (Changnon *et al.*, 1989). The cost of sheeting and bulkheads, slips and docks was estimated at an additional \$113–203 million. Taken together these shipping costs for the Illinois shoreline total \$251–515 million over a 50-year period. Increased dredging activities would also have implications for destruction of benthic habitats and resuspension of toxics in harbour sediments.

Keith *et al.* (1989) observed that, even with lighter loads, the same goods could be shipped over a season if the ice-free season were longer (see section on ice, below). For Buffalo, an increase in the shipping season of 99 days would be sufficient to compensate for the need for lighter loads with a 1.5 m decline in water level; simulated increases in the ice-free period more than compensated for the need for lighter loads in two (GISS and OSU) of the three scenarios. For Lake Superior ports, a slightly shorter increase in the ice-free season would be sufficient, a value achieved in all GCM scenarios. The bottom line projection for shipping costs for ports on Lakes Superior and Erie, as a consequence of reduced water levels plus the longer shipping season apparent in $2 \times \text{CO}_2$ scenarios, was 1–7.5% above present costs or about one-half of the increases in costs from water level reductions taken alone.

Additional costs, unrelated to shipping, have been estimated for the Illinois shoreline of Lake Michigan by Changnon *et al.* (1989) for $2 \times \text{CO}_2$ scenarios. These included costs to extend water intake structures for city water supplies (\$16–17 million), to relocate beach facilities (\$1–2 million) and to extend and modify storm water outfalls (\$2–4 million). These costs are less than those associated with shipping. Historical responses to lower water in the Chicago area include relocation and encroachment to take advantage of the new beach areas; damage to these structures was extensive when water levels returned to higher levels.

Generation of electricity from hydroelectric facilities in the Great Lakes Basin would also be reduced in a drier and warmer climate. Presently, the capacity of the Great Lakes electric generation system is about 3.2 million kW for Ontario, 1.7 million kW for Quebec and 3.1 million kW for New York (Melo, 1989). The costs of replacing the hydroelectric power generated at Niagara and along the St Lawrence River following a 0.6 m decline in water level in Lakes Erie and Ontario is high. Long-term annual costs of replacing this capacity with nuclear or fossil fuel plants were estimated to be in the range of US \$160 million in 1988 for New York (Crissman, 1989), and Can \$1 billion for Ontario (Melo, 1989). The output from these hydropower facilities is of the same magnitude as that of the Tennessee Valley Authority.

ICE COVER

Ice cover on lakes and streams is not only a robust indicator of climate change and variation (Robertson *et al.*, 1992), but also represents a limnological response to climate change that influences the ecology of

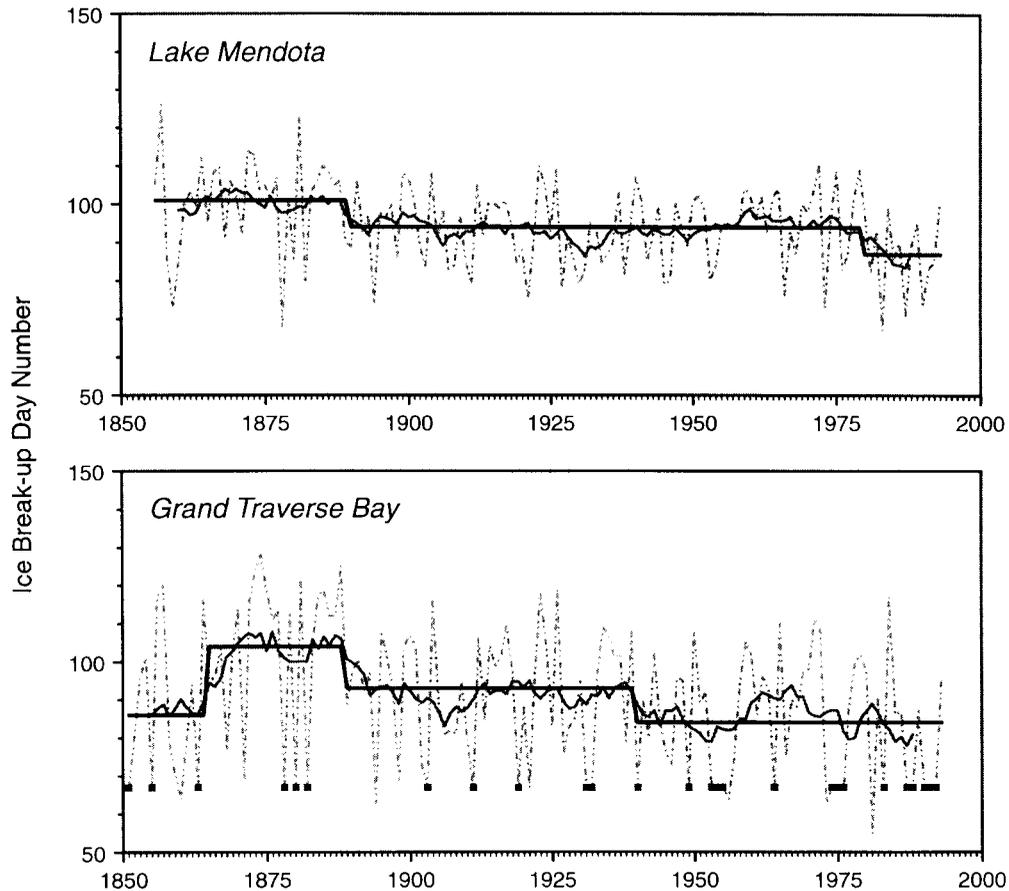


Figure 9. Ice-off dates for Lake Mendota and Grand Traverse Bay between 1851 and the present (dashed line) (adapted from Assel and Robertson, 1995). Heavy solid lines mark step changes in the long-term average, while the lighter solid line is a centred 10-year moving average. Years in which Grand Traverse Bay did not freeze over are marked by a solid square on 8 March

aquatic systems (Vanderploeg *et al.*, 1992). Ice phenologies, i.e. dates of freezing over (ice-on) and break-up (ice-off), are especially useful because shoreline residents and early navigators of lakes and streams have recorded these events longer and in more locations than other climatic data. Ice phenologies can also be measured by analysis of satellite images over large regions where there are no weather stations (Wynne and Lillesand, 1993).

Past trends in ice phenology

In general, the average duration of ice cover has decreased in a series of step changes in the Laurentian Great Lakes and Precambrian Shield Region over the last century or so, indicating early and late winter warming of 1.5–2.7°C. Continuous lake ice phenologies date back to 1823 in the Laurentian Great Lakes and 1855 for Lake Mendota, Wisconsin. Analyses of Lake Mendota and Grand Traverse Bay, Lake Michigan (*ca.* 320 km apart), indicated later ice-on dates and earlier ice-off dates (Figure 9) (Assel and Robertson, 1995). A step change of eight days (Mendota) and 12 days (Grand Traverse) in average ice-on date occurred in about the 1888–1889 winter in both systems, representing an increase of about 1.5°C in early winter air temperatures. Two step changes in average ice-off dates, totalling 14 days (Mendota) and 20 days (Grand Traverse), have occurred since the 1870s representing an increase in late winter air temperatures of

2.2°C (Mendota) and 2.7°C (Grand Traverse). The first step changes were coincident for both sites, *ca.* 1888–1889, while the second occurred in 1939–1940 (Grand Traverse) and 1979–1980 (Lake Mendota). The transition to later average ice-on and earlier average ice-off dates in the late 1800s corresponded with the end of the Little Ice Age.

For the Great Lakes, we simulated annual maximum ice cover averaged by decade from 1900 to 1990 using a regional winter air temperature model for annual maximum ice cover of the combined surface areas (Assel *et al.*, 1985). Average November–February monthly air temperatures were used from Duluth, Minnesota; Sault Ste. Marie, Michigan; Detroit, Michigan; and Buffalo, New York. Average ice cover decreased from approximately 61% maximum coverage for the decades ending in 1910 and 1920, to near 50% for the decades ending in 1940, 1950 and 1960. Ice cover then increased over the next two decades [1970 (61%) and 1980 (64%)] before declining again in the 1980s [1990 (55%)]. These trends are consistent with simulations from degree-day ice cover models developed for Lakes Erie and Superior (Assel, 1990). The later models suggested that decadal midwinter ice cover averaged about 10–25% greater for both 1900–1925 and 1960–1983 than for the intervening years (1926–1959). Contemporary midwinter ice cover averages 90% for Lake Erie and 56% for Lake Superior (Assel *et al.*, 1983).

For the shallow shore zones of the Great Lakes, the timing of ice-on, ice-off and percentage of lake area covered by ice are comparable to those of smaller inland lakes. However, because the Great Lakes have greater thermal inertia and longer wind fetch than the smaller lakes (Assel, 1986), ice forms later and is more dynamic in midlake areas than inshore areas or in the smaller lakes. Ice usually forms in shallow bays and over most of Lake Erie in December and January. Ice forms in the deeper embayments and in midlake areas in February, reaches its maximum extent in February or March and is usually lost by the end of April (Assel *et al.*, 1983). The Great Lakes do not freeze over completely because of their large heat storage capacity, the action of winds and their exposure to relatively moderate winter temperatures, particularly towards the south. During mild winters, midlake areas remain relatively ice free (Assel *et al.*, 1985) and annual maximum ice cover is typically less than 35%. During severe winters midlake ice can form as early as January, can last into May and can cover 80% of the combined surface area of the Great Lakes (Assel *et al.*, 1996).

Changes and variations in ice-off dates were coherent between lakes across the Laurentian Great Lakes/Precambrian Shield Region. The recent change to earlier ice-off dates for Lake Mendota was consistent with data from 19 other Wisconsin lakes (Anderson *et al.*, 1996) and with Lake 239 in north-western Ontario (Schindler *et al.*, 1990, 1996a). Rates of change were 0.7–8.4 (mean = 4.3) days per decade for northern Wisconsin, 0.6–12.2 (mean = 8.1) days per decade in southern Wisconsin and 7.6 days per decade for Lake 239. Locations around the Laurentian Great Lakes from Chequamegon Bay (Lake Superior), Grand Traverse Bay (Lake Michigan) and Buffalo (Lake Erie) also showed an earlier ice-off during the same 21 years (Assel *et al.*, 1995), and earlier ice-off dates were apparent in inland Canadian lakes from western Manitoba to central Quebec (Reycraft and Skinner, 1993). Ice-on dates, however, had no obvious trend over the same 21 years (Robertson *et al.*, 1992; Reycraft and Skinner, 1993; Assel *et al.*, 1995; Schindler *et al.*, 1996a).

In contrast to the apparent coherence in general trends of lake ice phenologies in Wisconsin and across the region, Wynne *et al.* (1996) found low average coherence in inter-year patterns among 62 inland lakes spanning a wide range of latitudes in the western part of the region. Using satellite-derived ice-off dates from 1987 to 1994, they measured coherence as the correlation coefficient between the time-series for each lake pair. In this analysis, two lakes with quite different mean ice-off dates could still be coherent, *i.e.* have the same inter-year pattern in ice-off dates. While some lake pairs were highly coherent ($r = +0.9996$) others were negatively coherent ($r = -0.89$), and average coherence was low ($r = +0.45$) for the area as a whole. There was a geographical pattern to the coherence. First, adjacent lakes tended to be coherent. More interestingly, lakes tended to be more coherent if their mean ice-off dates were more similar. Furthermore, lakes that were not close but had high coherence tended to be at similar latitudes; for example, lakes in southern Wisconsin were highly coherent with those in eastern South Dakota. These results were interpreted to mean that lakes at the same location or latitude with similar ice-off dates, integrated the same seasonal weather, while those that were neither close nor at the same latitude, integrated different seasonal weather.

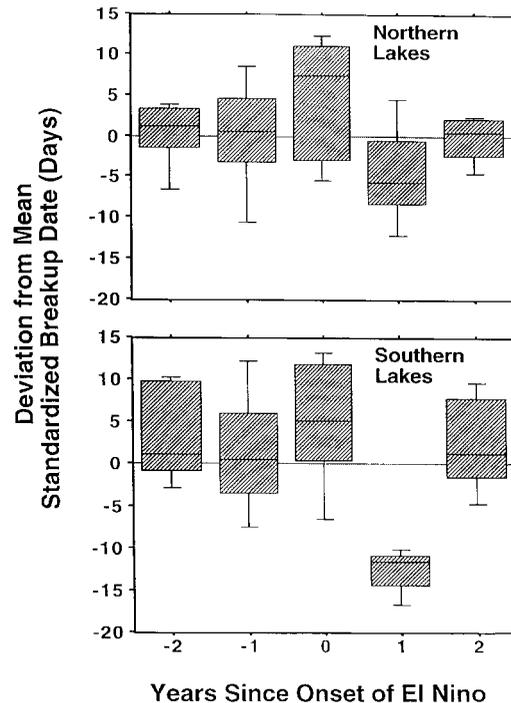


Figure 10. Effect of El Niño events on ice break-up dates for lakes in northern and southern Wisconsin (modified from Anderson *et al.*, 1996)

This point was also made by Assel and Robertson (1995) when comparing Grand Traverse Bay and Lake Mendota and by Anderson *et al.* (1996) when comparing El Niño effects on ice-out for Wisconsin lakes (Figure 10); lakes freezing or thawing on different dates integrate different climate windows and thus can have different inter-year patterns of ice phenologies. This suggests that lakes at different latitudes can be used to represent finer seasonal time-scales than, simply, early winter for ice-on or late winter for ice-off.

Ice formation and break-up are dependent on many climatic forcing variables, such as air temperature, solar radiation, wind and snow depth. Yet, air temperature alone often provides a reasonable prediction of ice phenologies. Using a moving average of air temperatures, McFadden (1965) observed that large lakes in central Canada and Lake Mendota in Wisconsin, froze when the 40-day average reached 0°C and broke up when it exceeded $+5^{\circ}\text{C}$. Using a sensible heat transfer model developed by Robertson *et al.* (1992), Assel and Robertson (1995) found that ice-on changed by 5.3 and 8.4 days and ice-off changed by 6.4 and 7.1 days per 1°C change in air temperature for Lake Mendota and Grand Traverse Bay, respectively; conversely, air temperature increased by 0.18 and 0.12°C for each day change in ice-on date and by 0.15 and 0.14°C for each day change in ice-off date.

A more complete process model for lake ice phenologies was developed recently by Vavrus *et al.* (1996), patterned after a thermodynamic sea ice model (Maykut and Untersteiner, 1971; Parkinson and Washington, 1979). Inputs to the model are mean lake depth, air temperature and moisture, wind speed, solar radiation, snowfall and cloudiness; energy transfers between the air–snow, or air–ice, snow–ice and ice–water are included. When driven with hourly meteorological data, the model simulated the annual ice-on and ice-off dates for Lake Mendota between 1961 to 1990 with a median absolute error of two days (ice-on) and four days (ice-off). In the model, ice-on and ice-off dates responded strongly to changes in mean annual air temperature, ice-off was more sensitive to temperature changes than was ice-on and both events were more sensitive to climate warming than to climate cooling.

The model developed by Vavrus *et al.* (1996) was also sensitive to changes in snowfall. A 50% increase in snowfall increased ice-off by six days and a 50% decrease in snowfall decreased ice-off by four days; a no-snow scenario, however, again increased ice-off by one day. Snowfall was also an important factor in the spatial analyses of the satellite-derived time-series discussed above (Wynne *et al.*, 1996). The model of Wynne *et al.*'s (1996) ($R^2 = 0.93$) was:

$$\text{Ice-off date} = (4.47 \times \text{latitude}) + (0.5 \times \text{snowfall in cm}) - 112$$

Simulations of changes in ice phenologies with climate warming predicted the occurrence of ice-free years for Wisconsin's Long-Term Ecological Research (LTER) lakes, which, historically, have had ice cover every year (Robertson *et al.*, 1992; DeStasio *et al.*, 1996). For Lake Mendota, in southern Wisconsin, a 1°C warming would shorten ice duration by about 11 days (Robertson *et al.*, 1992); a 4°C warming would result in frequent thawing and refreezing events; a 5°C warming would reduce mean ice cover by 64 days and result in no ice cover in 1 out of every 15–30 years. Robertson's model was parameterized for three lakes in northern Wisconsin (Crystal, Sparkling and Trout) and phenologies calculated with temperature increases for 2 × CO₂ scenarios; ice did not form in 33% of 27 runs (DeStasio *et al.*, 1996). The 27 runs were for three model scenarios (GFDL, GISS and OSU), three lakes and three base climates (a cool, intermediate and warm year). Using the same analysis for Lake Mendota in southern Wisconsin, ice did not form in 89% of the nine simulations. For the northern Wisconsin lakes, even when the lakes were simulated to freeze, the ice-free season was increased by 16–64 days.

For Lakes Erie and Superior, ice phenologies were simulated with a single 1 × CO₂ scenario over a 30-year base (1951–1980), and with 2 × CO₂ scenarios for the same years from three GCMs (GFDL, GISS and OSU) (Assel, 1991). With the 1 × CO₂ scenario ice cover formed every year for Lake Superior and for 29 of the 30 years for Lake Erie. With the 2 × CO₂ scenarios, ice-free winters appeared with the GFDL scenarios for Lake Erie in 17% of the 30 years and for Lake Superior in 43% of the years; with the other two scenarios the simulations were, for GISS, 10% (Superior) and 3% (Erie) and, for OSU, 7% (Superior) and 0% (Erie). Average ice cover duration for the 1951–1980 base period (1 × CO₂) ranged from 13 to 16 weeks. Ice duration with 2 × CO₂ scenarios was reduced to 5 to 13 weeks; midlake areas were ice free in most 2 × CO₂ winters.

PHYSICAL LIMNOLOGY, WATER CLARITY AND DISSOLVED OXYGEN

Lake and stream temperatures are responsive to climate warming in the Laurentian Great Lakes and Precambrian Shield Region. Lake mixing and stratification would be altered directly by the warming, and indirectly by changes in water clarity, responding to decreased inputs of dissolved organic carbon (DOC) or changes in trophic state. Physical changes would in turn influence the dissolved oxygen availability in the deep stratified waters, with many biological and biogeochemical consequences. Refuges from the warmer temperatures may be available in lakes that have an oxygenated hypolimnion and in some smaller streams that receive significant groundwater and shading from riparian vegetation.

Lakes

Lake thermal regimes respond to climate change because they are controlled by solar radiation, wind velocity, air temperature and humidity. McCormick (1990) (see Figure 11 for Lake Michigan); Hondzo and Stefan (1991, 1993); Stefan *et al.* (1993a,b, 1996); and DeStasio *et al.* (1996) used several GCMs (CCC, GISS, GFDL, OSU) to simulate the effects of a doubling of CO₂ on physical limnology. Their simulations predicted temperature changes of 1–7°C warmer in surface mixed waters (epilimnion), of 8°C warmer to a surprising 6°C cooler in deep hypolimnetic waters; sharper thermoclines, from 4 m shallower to 3.5 m deeper; longer durations of summer stratification; and decreased durations of ice cover or frequencies of winters with ice cover (see section on ice phenology above).

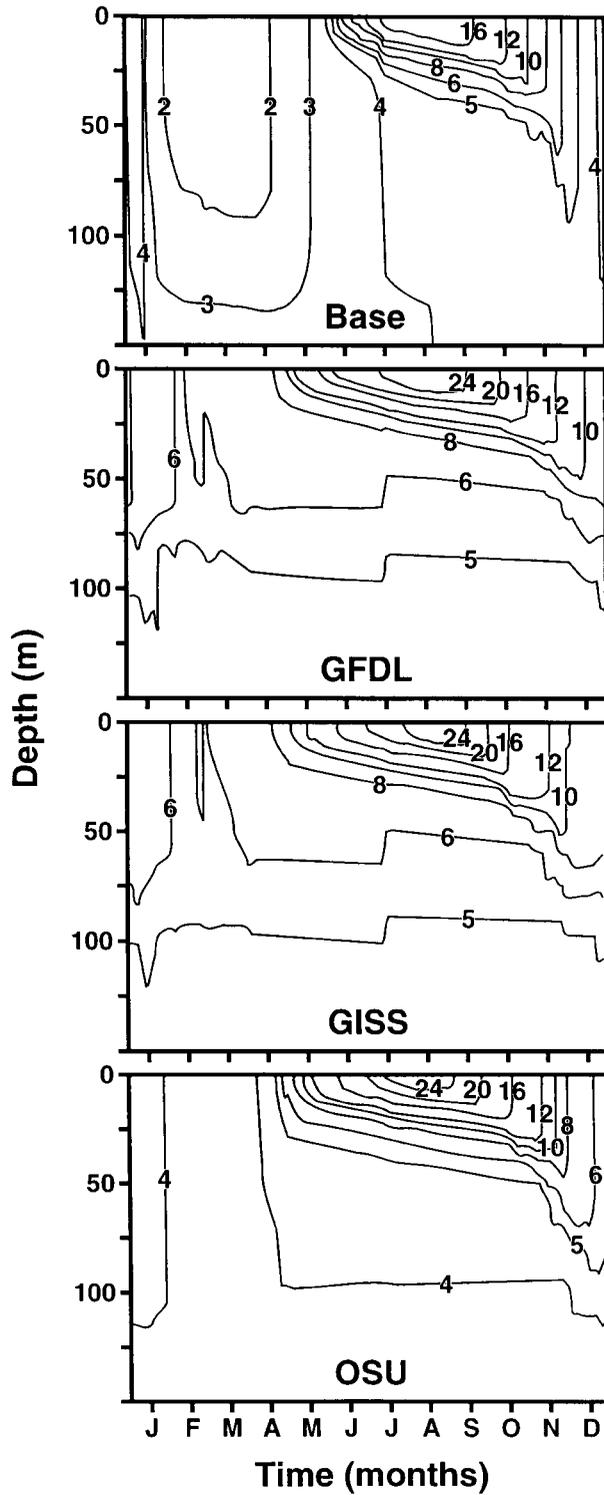


Figure 11. Simulated temperature isotherms (°C) for Lake Michigan under base and 2 × CO₂ scenarios from three global climate models (modified from McCormick, 1990)

The simulated changes varied among scenarios and lakes; differences in simulated responses were generally greater among GCMs than between lakes or base year, at least for the four Wisconsin lakes (Crystal, Sparkling, Trout and Mendota) used by DeStasio *et al.* (1996). Simulated increases in surface temperatures of four Wisconsin lakes averaged +4.2 to +4.8°C across four GCMs with a cool, intermediate and warm base climate. However, temperature simulations for bottom waters were more variable, +0.8 to +4.6°C, among the four lakes (DeStasio *et al.*, 1996). For 27 Minnesota lake classes (three maximum depths, three surface areas and three water clarities) 25-year averages of surface temperatures simulated with the GISS GCM were about 3°C warmer, compared with a 4.4°C air temperature rise (Hondzo and Stefan, 1993); increases in hypolimnetic temperatures ranged up to +3°C (Stefan *et al.*, 1996). The largest changes in water temperature occurred in spring and autumn.

Warming also would alter the mixing regimes of lakes. In the southern part of the region, lakes switching from ice covered to open in winter would become monomictic; i.e. they would mix in autumn, winter and spring, and stratify in summer. In the northern part, some lakes that are presently monomictic and mix only during summer, would stratify in summer and become dimictic, mixing in spring and autumn. Some large deep lakes, like Lake Michigan, that are dimictic would be less likely to mix completely (Figure 11) (McCormick, 1990).

Inter-lake differences in depth and transparency often have a greater influence on measured and simulated bottom temperatures or thermocline depths than does simulated climate warming (Stefan and Fang, 1995; DeStasio *et al.*, 1996; Fee *et al.*, 1996). Surface temperatures simulated with $1 \times \text{CO}_2$ climates changed little with lake depth or transparency (Hondzo and Stefan, 1993; DeStasio *et al.*, 1996), but bottom temperatures and thermocline depth did. For shallow lakes, bottom and surface temperatures were the same; for lakes 10 m deep bottom temperatures were less than half the surface temperatures; for those greater than 20 m deep, bottom temperatures were less than one-quarter of the surface temperatures. Simulations for less transparent lakes showed cooler hypolimnia and shallower thermoclines with $1 \times \text{CO}_2$ climates than they did for more transparent lakes.

Biogeochemical processes that alter lake transparency during warmer conditions may override the influence of physical factors on thermocline depths in many lakes. Because DOC is an important control on the transparency of many lakes in the region (Scully and Lean, 1994; Fee *et al.*, 1996), decreased DOC concentrations related to lower DOC export rates from catchments during warmer and drier conditions result in higher transparencies and thus deeper thermoclines (Figure 12) (Schindler *et al.*, 1996a), which is the opposite response to that predicted by some physically based models. Fee *et al.* (1996) suggested that for many lakes in the Experimental Lakes Area in north-western Ontario the expected magnitude of thermocline deepening related to changes in transparency was the same as the shallowing predicted by $2 \times \text{CO}_2$ scenarios. In fact, thermoclines deepened in a small ELA lake over a 20-year period when epilimnion temperatures rose by $>2^\circ\text{C}$ and DOC concentrations declined (Schindler *et al.*, 1990). Thermocline deepening in this small lake was probably affected by local forest fires (the basin was burned twice during the period of study) which increased the mean wind speed over the lake during the same period.

The effects of transparency and wind speed on thermocline depth are likely to be more important in small lakes than in large lakes. Epilimnion depth was, in general, positively related to lake area across a wide range of lake sizes (Fee *et al.*, 1996). Transparency was an important influence in those lakes smaller than 500 ha. Thus, the influence of increased transparency, driven by decreased DOC during warmer climates, may override other physical factors in smaller lakes. In contrast, decreased DOC concentrations in large lakes would probably be too small to modify significantly the mixing depth (Fee *et al.*, 1996). In addition, the over-water wind speed in large lakes would not be affected significantly by changes of the surface roughness of the watershed related to fires or land use modification.

Changes in temperature, stratification and light would be expected to alter the availability of dissolved oxygen in lakes. Longer summer stratification would increase the likelihood that deep hypolimnetic waters would be depleted of oxygen. Simulations with $2 \times \text{CO}_2$ scenarios for Lake Erie (Blumberg and Di Toro, 1990) predict summer oxygen declines of 1 mg/l in upper layers and 1–2 mg/l in deeper layers, as well as the

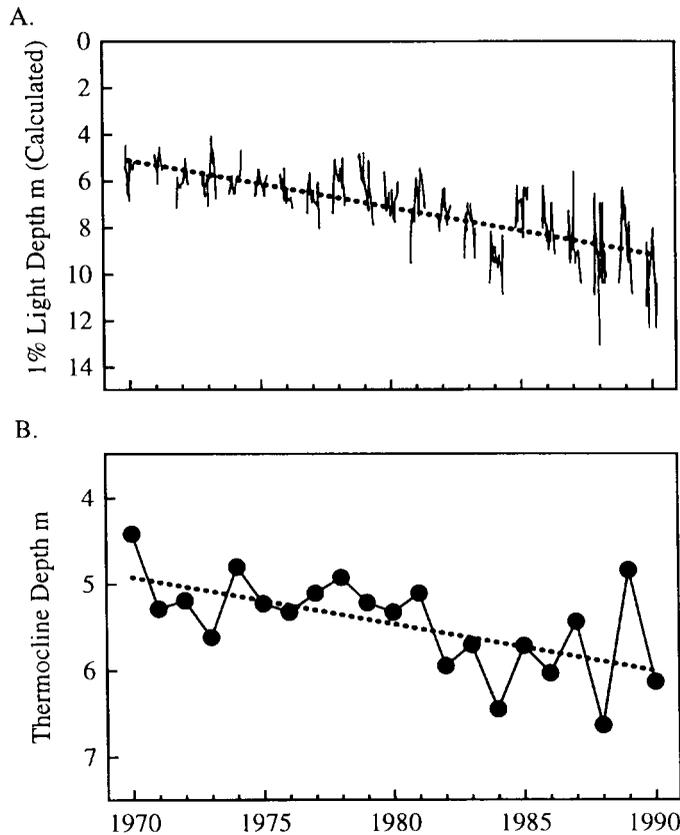


Figure 12. (a) Changes in penetration of photosynthetically active radiation (PAR) in Lake 239 as the depth of the isopleth representing 1% of surface light (equivalent to photic zone depth) (modified from Schindler *et al.*, 1996a); (b) changes in thermocline depth in Lake 239

development of a more extensive area of anoxia. In these simulations, warmer temperatures increased bacterial activity in deep waters and sediments; a change in thermocline depth was not the cause. Similar responses were obtained for smaller Minnesota lakes in model simulations by Stefan *et al.* (1993a), Stefan and Fang (1995) and Stefan and Fang (1994). Oxygen concentrations declined by 2 mg/l in surface waters and by as much as 8 mg/l in deep hypolimnetic waters, while summer oxygen depletion lasted up to two months longer compared with base climate scenarios. These oxygen declines occurred more rapidly and were longer lasting in eutrophic, compared with oligotrophic, lakes. In winter, shorter ice cover durations would decrease the likelihood of winter kill resulting from oxygen depletion in shallow lakes, although this may be countered by predicted declines in lake level and volume, which would lower the total content of dissolved oxygen available at ice-on.

Streams

Mean weekly temperatures tracked air temperatures closely in six Minnesota streams (Stefan and Preud'homme, 1993) according to the relationship:

$$T_w(\text{week}) = 2.85 + 0.866T_a(\text{week})$$

where $T_w(\text{week})$ is the weekly mean water temperature in °C and $T_a(\text{week})$ is the weekly mean air temperature in °C. The regression slopes for individual rivers ranged from 0.669 for the Vermillion River to

1.026 for the Roseau River; intercepts ranged from 1.40°C for the Straight River to 4.49°C for the Mississippi River at St. Paul. The relationship for daily data was similar but had a larger standard deviation and a time lag of 1–4 days:

$$T_w(\text{day}) = 4.90 + 0.733T_a(\text{day})$$

The regression slopes for individual rivers in Minnesota ranged from 0.604 for the Vermillion River to 0.874 for the Roseau River; intercepts ranged from 3.96°C for the Straight River to 7.37°C for the Mississippi River at St. Paul.

Other factors besides air temperature influence stream temperatures, such as solar radiation, relative humidity, wind speed, water depth, groundwater inflow, artificial heat inputs and the thermal conductivity of the sediments. Of these, radiation is the most important (Sinokrot and Stefan, 1993); thus, diel variation and shading from riparian vegetation are important. Deterministic models including shading and wind sheltering can simulate water temperatures with a standard deviation of about 1°C, which is considerably smaller than the above regressions, but such models have much greater data demands; approximations can be achieved rapidly with the regressions (Stefan and Preud'homme, 1993).

A modified version of the MNSTREM model was used to simulate the potential affects of doubling atmospheric CO₂ for five Minnesota streams (Stefan and Sinokrot, 1993). Stream temperatures were projected to increase 2.4–4.7°C with scenario inputs from four GCMs (GISS, GFDL, UKMO and OSU) and 2 × CO₂ climates. If there was no riparian shading, additional increases up to 6°C were projected.

Increases in groundwater temperatures with climate warming are expected to be about the same magnitude as that predicted for mean annual air temperatures (Meisner *et al.*, 1988). As a result, the cooling effect of groundwater on streams would be reduced, indirectly contributing to stream warming. The combined effect of an increase in groundwater temperature of 4.8°C, with the direct effects of warmer air temperatures, on stream waters in south-central Ontario were simulated to decrease the length of headwater trout streams that remained below 24°C during July and August by 30 and 40%, respectively (Meisner, 1990). For one stream, the increase in water temperature was almost equally attributable to groundwater inputs and to air temperatures; in the other stream, nearly all of the increase in temperature was accountable by groundwater inputs. The effect of climate change on stream temperatures below dams will be more pronounced where the water release is from the reservoir epilimnion rather than the hypolimnion. Cold hypolimnetic water release is felt as far as 48 km downstream in small, shaded Minnesota streams. This distance is projected to be shortened by 25–50% under a 2 × CO₂ climate scenario (Sinokrot *et al.*, 1995).

BIOGEOCHEMISTRY

Effects of climate change on chemical properties of lakes are a function of the alteration of hydrological flows and subsequent changes in lake volume and water level, inputs of solutes and increases in hypolimnetic anoxia and summer stratification. Inferences are made primarily from a 20-year period of increasingly warm and dry weather at the Experimental Lakes Area (ELA) in north western Ontario and a late 1980s drought at the North Temperate Lakes LTER site in Wisconsin.

During the 1970s and 1980s at ELA, mean annual air temperatures increased by about 2°C, precipitation generally declined and evaporation increased (Schindler *et al.*, 1990, 1996a). As a result, stream flow and the flushing rates of lakes underwent a more or less continuous decline over the 20 years. While the cause of these climatic trends is unknown, the magnitude and rate of warming are similar to what might be expected from a doubling of CO₂. Thus the record provides an interesting glimpse of how climate change may affect small lakes in boreal regions of the Precambrian Shield. The effects of increased forest fires on lake chemistry during the period, an indirect effect of climate warming, were also important. Forest fires increased dramatically in Canada as the weather warmed, precipitation declined and evapotranspiration increased. Not surprisingly, a 1974 forest fire burned the eastern half of the Lake 239 catchment, including

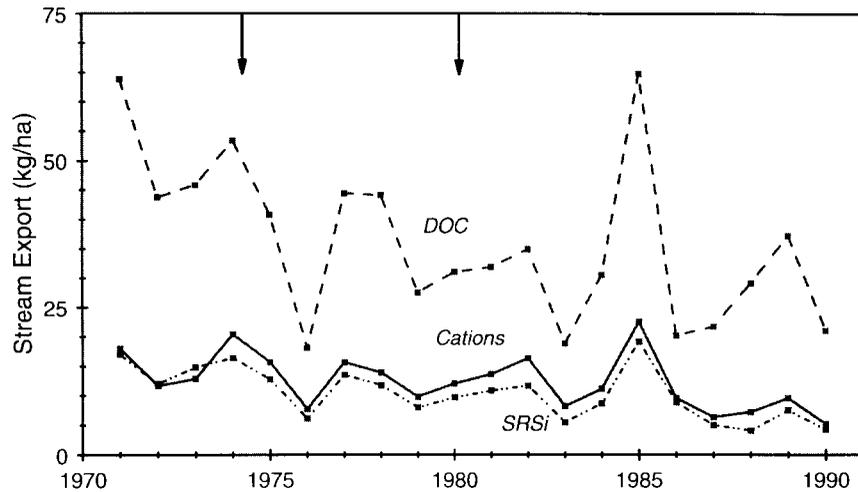


Figure 13. Annual exports of base cations (Ca + Mg + Na + K), silica and DOC from the catchment of Lake 239 (from Schindler *et al.*, 1996a). Rates of decrease are all significantly different from zero. Arrows indicate when major fires occurred

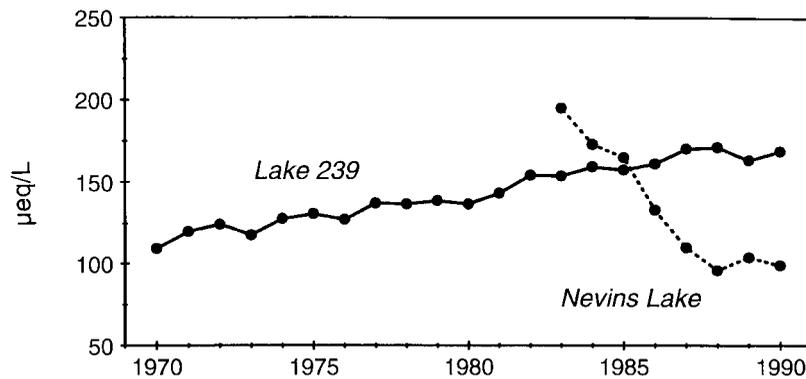


Figure 14. Temporal patterns in calcium in Lake 239 and Nevins Lake during drought. Data for Lake 239 are from Schindler *et al.* (1990) and for Nevins Lake are adapted from Webster *et al.* (1990)

the subbasins of two first-order streams, and a 1980 fire burned a third stream basin as well as the same sub-basins again.

During these warmer and drier conditions, inputs of silica, DOC, base cations and phosphorus from streams to ELA lakes generally declined (Figures 13 and 14) (Bayley *et al.*, 1992a; Schindler *et al.*, 1996a). The decreased yields of soluble reactive silica from the east subbasin of Lake 239, which contains fairly deep soils, suggested a reduction in weathering caused by drier conditions. Despite decreased inputs, concentrations of most inorganic solutes increased and lakes became more alkaline (Schindler *et al.*, 1990, 1996a), a trend that appears to be continuing. The increased concentration of more conservative solutes was driven by the large increases in water retention time, which effectively increased the loading rate of solutes (Schindler, 1997). For example, as the water renewal time of Lake 239 reached 20 years, it would take 60 years to attain 95% of a new steady state if no further changes occurred in water or chemical inputs. In contrast to this accumulation effect, longer water retention times increased the importance of consumptive in-lake processes such as biotic assimilation and sulfate reduction. Consequently, concentrations of more bioactive solutes, such as silica, total dissolved phosphorus and DOC, declined in Lakes 239 and 240 and alkalinity-generating processes, such as sulfate reduction, increased (Schindler *et al.*, 1996a). Internal sulfate

reduction caused sulfate:cation ratios to decline rather quickly, despite long water residence times. This, plus the return of base cations from sediments, caused the alkalinity to increase by 30–50% and pH to increase a few tenths of a unit (Schindler *et al.*, 1990, 1996a). Total dissolved nitrogen increased in Lake 240 and initially in Lake 239, with subsequent declines presumably related to changes in in-lake processes (Schindler *et al.*, 1990, 1996a).

A less extensive drought in northern Wisconsin from 1987 to 1990 also altered the hydrological pathways of water and solute flow to lake ecosystems. In contrast to the ELA drainage lakes set in thin soils (<0.5 m in thickness), the Wisconsin lakes are a mixture of seepage and drainage systems set in thick sandy outwash till deposited by receding glaciers. Many chemical, biological and physical attributes of the Wisconsin lakes are related to their position in the groundwater flow system, ranging from precipitation-dominated lakes high in the landscape to groundwater-dominated lakes low in the landscape (Kratz *et al.*, 1997). Changes in the cations, Ca and Mg, during drought were related to lake landscape position (Webster *et al.*, 1996). Cation concentrations increased during drought as observed for the ELA lakes, but differences in the direction of change in cation mass, which accounts for the effect of evapoconcentration, were related to lake landscape position. This suggests that lakes may diverge in their long-term response to warmer and drier conditions. Increases in cation mass for lakes low in the landscape during drought were attributed to proportionately high inputs of groundwater from deeper flow paths (which are more cation rich) and to a lessening of the diluting effect of precipitation. In contrast, cation mass declined for lakes high in the landscape as transient groundwater inflows were interrupted during drought. Such differences among lakes are apparent in long-term calcium data on Lake 239 at ELA and Nevins Lake in the upper peninsula of Michigan (Figure 14). In Nevins, cation and silica concentrations, alkalinity and pH rapidly declined during the same drought (Webster *et al.*, 1990). This lake has a short water retention time (<2 years) compared with other seepage lakes and its chemistry is extremely responsive to changes in groundwater inputs driven by climate (Krabbenhoft and Webster, 1995).

In addition to responses to altered inputs of solutes, the biogeochemical cycling of nutrients and other ions in lake ecosystems will be influenced greatly by the oxygen conditions in a lake's deep waters. Many compounds, such as iron phosphates, are more soluble under anoxic conditions; their availability to the water column from nutrient-rich sediments would be increased with increased anoxic conditions. Thus, recycling of nutrients from the sediments to the water column would be enhanced by climate warming in thermally stratified lakes during summer. This would be countered to an unknown extent by reductions in hydrological flow and associated nutrient export from the catchments.

Climate conditions also influence retention and cycling of solutes in peatlands. Pulsed exports of sulfate, acidity and cations occurred from a minerotrophic swamp located near Dorset (LaZerte, 1993) and from a peatland draining into Lake 239 at ELA (Bayley *et al.*, 1992a) after dry summers when accumulated sulfur was exposed and oxidized. The strength of these acid pulses was related to deposition history; under conditions of higher acid loading and, thus, increased storage of sulfur, the potential for acidification events at downstream sites is enhanced (Bayley *et al.*, 1986). The cycling of solutes, particularly carbon, within peatlands is a function of groundwater flow patterns, which, in turn, are influenced by climate (Siegel *et al.*, 1995). In a northern Minnesota peatland, groundwater flow advected dissolved organic compounds into deeper peat layers during wet periods, stimulating methanogenesis, while during dry periods a discharge regime dominated and organic compounds were advected upwards, limiting methanogenesis to the more refractory carbon of the peat itself (Siegel *et al.*, 1995).

The biogeochemical responses of small lakes, streams and peatlands to climate change reveal an intricate interaction between weather, catchments and lakes, and between physical, chemical and biological effects. Biological factors on the land and geomorphological legacies influence how aquatic ecosystems respond to climate change. For example, standing trees on the shoreline affect wind exposure and lake thermal properties; DOC export from catchments influences light penetration and mixing depth; and position in the hydrological flow system influences changes in solute concentrations. Biogeochemical responses are also a function of lake water retention time and the biological reactivity of a given solute.

AQUATIC ECOLOGY

Responses to the diverse changes in the physicochemical environments induced by changes in climate can occur in individual organisms, in populations of organisms, in communities of interacting species and in the structure of interactions between biotic and abiotic components of entire aquatic ecosystems, including the landscape in which the lakes, streams and wetlands are imbedded. Our review treats these responses for the phytoplankton, zooplankton, benthos and fishes. The phytoplankton are the microscopic algae that live in the water column and, through their photosynthetic production of new organic matter, form the major base for the food-web in lakes. The zooplankton are microscopic animals that live in the water column and, functionally, are either herbivores on the phytoplankton or predators on smaller zooplankton. The benthos are organisms that live on bottom substrates of lakes, wetlands and streams; they include a wide range of plants and animals, from large-rooted plants and algal mats to immature insects, clams and snails and bottom-dwelling fishes. The fishes are generally long lived and mobile; they can be herbivores, predators or omnivores; they play important structuring roles in aquatic communities; and they are valued for sport, food and biological diversity.

Phytoplankton

Increased epilimnion temperatures are unlikely to affect rates of phytoplankton primary production directly, but species composition would change, annual production would increase and phytoplankton diversity and biomass might increase. The phytoplankton community consists of hundreds of species with simple life cycles. Even though rates of photosynthesis of nutrient-sufficient algal cultures increase exponentially with increasing temperature (Eppley, 1972), the realized rate of photosynthesis in lakes is virtually independent of temperature for several reasons.

1. Algae rapidly adapt to the temperature at which they are grown; thus, realized rates of photosynthesis, even in isolated species, are either partially or fully independent of temperature (Davison, 1991).

2. In freshwater, *in situ* phytoplankton photosynthesis is typically either nutrient (phosphorus, nitrogen, silica) or light limited, especially during midsummer when the greatest temperature increases are expected (Schindler, 1977; Healey and Hendzel, 1980); these primary limitations prevent phytoplankton from achieving temperature-determined physiological limits (Fee *et al.*, 1987).

3. Some phytoplankton species are favoured by lower temperatures, while others are favoured by higher temperatures. Because life cycles are short, competition soon results in a community capable of photosynthesizing optimally at any temperature.

Results from a long-term study of phytoplankton photosynthesis in seven Canadian Shield lakes, ranging in size from 30 to 34 600 ha (Fee *et al.*, 1992), clearly support these ideas.

1. As in most unperturbed temperate zone lakes, variations of chlorophyll concentration and phytoplankton production were highest in the spring and lowest in midsummer; i.e. the inverse of variations of temperature but precisely the pattern of variation of nutrient availability.

2. Interannual variations of phytoplankton production were unrelated to epilimnion temperatures (which varied by $> 3.0^{\circ}\text{C}$; i.e. similar to the range of the mean temperature rise predicted for a $2 \times \text{CO}_2$ climate), but were significantly and positively related with total rainfall, which is the main nutrient source to remote shield lakes (Fee *et al.*, 1994).

Clearly, nutrients, not temperature, are the factors of greatest importance in determining phytoplankton growth and abundance in shield lakes (Hecky and Kilham, 1988). This conclusion is supported by 24 years of phytoplankton community composition data at the species level from a variety of lakes in the Experimental Lakes Area, where year to year changes of community composition correlated strongly with chemical variables (pH, DOC, nutrients, total cations) but not at all with water temperature (Kasian *et al.*,

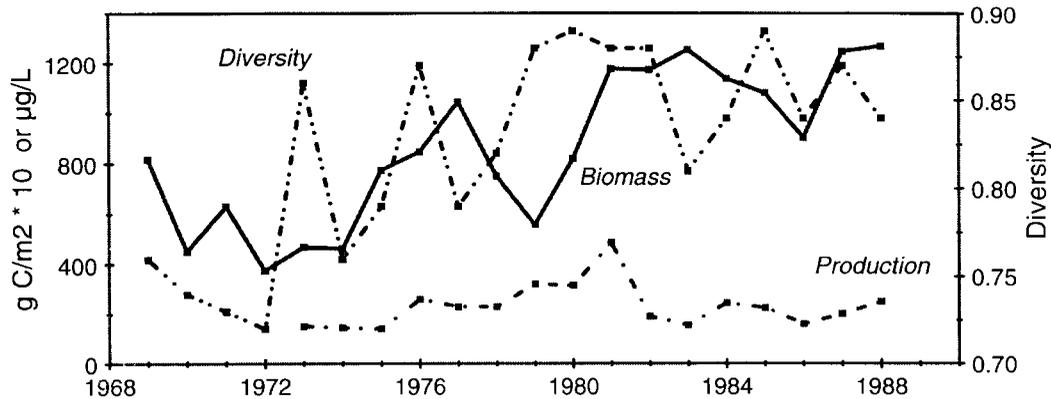


Figure 15. Change in phytoplankton biomass and diversity in Lake 239 (from Schindler *et al.*, 1990) and total and subepilimnetic production in lakes 239 and 240 (adapted from Schindler *et al.*, 1996a)

in press). The implication is that the new phytoplankton communities that are almost certain to appear in a $2 \times \text{CO}_2$ climate will be only secondarily related to elevated temperatures.

Although the direct effects of increased epilimnion temperatures on phytoplankton photosynthesis (primary production) will be minimal, some indirect effects are not so easily dismissed. Agreement is close between the temperature vs growth performance of major algal groups in cultures (Allen and Stanier, 1968; Canale and Vogel, 1974) and the phytoplankton community composition in lakes: blue-green algae dominate at the highest temperatures, and are succeeded by green algae, then flagellates and then diatoms as the temperature drops. Warmer epilimnia will thus favour blue-greens and greens at the expense of chrysophytes and diatoms. These climate-altered phytoplankton communities will have different trophic efficiencies than the present ones (Schindler, 1977), and ecosystemic effects could be profound. As Smayda (1980) points out, while there may be general temperature/growth tendencies in major taxonomic groups, detailed attempts to model seasonal succession of phytoplankton based on the temperature optima of individual species measured in isolation have not been successful. He concludes that the regulatory variable is not temperature *per se* but something strongly correlated with it.

Phytoplankton biomass and diversity did increase slightly during the 20-year period of increasing temperature at ELA (Schindler *et al.*, 1990, 1996a). However, consistent with the above, phytoplankton productivity did not appear to be related to climatic trends (Figure 15), and production below the thermocline did not increase, owing to the parallel deepening of the thermoclines and the euphotic zone.

Shallower epilimnia and sharper thermoclines from climate warming scenarios would cause epilimnetic phytoplankton to be more severely nutrient limited; shallowness by reducing light limitation and the residence time of particles in the mixed layer, sharpness by reducing the upward flux of hypolimnetic nutrients to the mixed layer (Fee *et al.*, 1994). While this may not affect phytoplankton productivity in shield lakes that are already nutrient limited (Guildford *et al.*, 1994), it would affect the elemental composition of phytoplankton and thus their food value to consumers (V. H. Smith, 1991; Sterner *et al.*, 1993), and consequently rates of bioaccumulation of organochlorines in the food web (Swackhamer and Skoglund, 1991) and the toxicity of contaminants to phytoplankton (Twiss and Nalewajko, 1992).

The expected decrease in DOC and increase in light transmission would have two important effects on phytoplankton. First, algal populations that are now light limited would grow faster. In contrast to epilimnetic phytoplankton that are rarely light limited (Fee *et al.*, 1992), phytoplankton that thrive deeper in the water column almost always are (DeNoyelles *et al.*, 1980; Shearer *et al.*, 1987), and would increase in productivity if water clarity increased. The influence of this potential increase might not affect the productivity of higher trophic levels because the characteristic species have large cells or are colonial (Fee, 1976); they may be too large for filter-feeding zooplankton to process.

Annual phytoplankton production would be expected to increase for lakes, provided that there were no large increases in cloudiness. Phytoplankton production in shield lakes was proportional to the length of the ice-free season (Fee *et al.*, 1992), i.e. a 25% increase from six to eight months resulted in 25% more phytoplankton production under an assumption that all other features of the lakes were unchanged. Obviously, this will only occur in lakes that are currently ice covered for part or all of the year. Other studies by Regier *et al.* (1990a), using analyses of empirical relations that removed the statistical influence of the morphoedapic index, also indicated that annual primary production increased with temperature with a Q_{10} of 3.7. However, annual primary production is markedly reduced by cloudy days at the North Temperate Lake LTER site in Wisconsin (Adams *et al.*, 1990).

Zooplankton

Zooplankton production or biomass may well be influenced by climate warming. Regier *et al.* (1990a), in an analysis of comparative lake data that statistically removed the influence of the morphoedapic index, observed an increase in lake zooplankton biomass with temperature, with a Q_{10} of 4.0. DeStasio *et al.* (1996) simulated differences in the vertical spatial overlap between zooplankton and zooplanktivorous fishes using a dynamic programming approach for two Wisconsin lakes and a $2 \times \text{CO}_2$ warming with four GCMs (CCC, GISS, GFDL and OSU). Results were mixed for Sparkling Lake, a small oligotrophic lake with a cold water zooplanktivore in northern Wisconsin; overlap in vertical distributions increased as much as 37% and decreased as much as 26% among GCM scenarios, but three of the four simulations were for decreased overlap. For Lake Mendota, a eutrophic lake with warm water zooplanktivores in southern Wisconsin, overlap consistently increased from 20 to 27% among the four GCM scenarios. The explanations for the difference between the two lakes were: (1) for Sparkling Lake, the fish were more restricted to the deeper cold waters as the surface waters warmed and the *Daphnia* could seek refuge in the warm epilimnion; and (2) for Lake Mendota, the warm water fish experienced an increase in warm waters and forced a portion of the *Daphnia* to seek refuge in the anoxic hypolimnion.

Temperature is the cue that stimulates the production of overwintering stages for zooplankton and their release from dormancy (Stirling and McQueen, 1986; Chen and Folt, 1996; Hairston, 1996). Warming events could alter the timing or occurrence of resting eggs in autumn, potentially leading to a loss of a cohort or of numbers in the 'seed bank'. For example, resting eggs hatch prematurely with a 12°C temperature increase in autumn (Chen and Folt, 1996). Local extinctions would be more likely when warm summer temperatures and anoxia reduce the hypolimnetic refuge required by particular species (Stemberger *et al.*, 1996).

Benthos

Although benthic algal photosynthesis has been widely reported to be no more than a few per cent of phytoplankton photosynthesis, even in small shield lakes (Schindler *et al.*, 1973), recent stable isotope evidence indicates that benthic algae are an important energy source for aquatic animals in lakes of all sizes and in many climates (Hecky and Hesslein, 1996). Either the methods used to measure photosynthesis in phyto-benthos and phytoplankton do not yield comparable results, or benthic production is transferred to higher trophic levels much more efficiently than is planktonic production. Whatever the cause, it is important in the context of climate change because benthic photosynthesis in shield lakes is limited by dissolved inorganic carbon (Turner *et al.*, 1994), and should increase in response to a doubling of atmospheric CO_2 . Phytoplankton photosynthesis, on the other hand, is not carbon limited (Schindler and Fee, 1973) and thus will not be directly affected by increased CO_2 .

Benthic invertebrate species have fixed temperature thresholds for egg development and/or generation times that are a function of degree-days (Giberson *et al.*, 1991). Effects of temperature increases on benthic and other invertebrates were reviewed in Arnell *et al.* (1996); increased temperatures cause: faster life stage development and shorter generation times; greater rates of reproduction, ingestion, growth and respiration; lower rates of mortality, smaller body size and more generations per year. Given the high natural dispersal capability of benthic insects, rapid colonization of waters that are presently too cold for egg development can

be expected. Furthermore, many insect species would mature more rapidly in waters that they already inhabit (e.g. in one year instead of two). These effects would not occur in species that inhabit the profundal zone of deep lakes, because temperatures there are expected to change little.

Fishes

Reviews and information on the potential effects of climate warming on fishes have been published recently in Arnell *et al.* (1996), Everett *et al.* (1996), Regier *et al.* (1996) and Wood and McDonald (1996). Useful earlier reviews include Coutant (1981), Meisner *et al.* (1987) and Magnuson *et al.* (1989) and the Regier *et al.* (1990b) symposium.

Thermal niche. Fishes are ectothermic heterotherms whose body temperatures track the habitat in which they live. Fry (1947, 1971) classified environmental factors, including temperature, by their effects on fishes as lethal, controlling and directive. Thus, while temperature can be lethal, it controls many physiological rates and behaviours within the lethal limits. Various rates are optimized at intermediate temperatures. Fishes are mobile and seek out their preferred temperatures that typically include these optima, provided those temperatures are available within their habitat. The thermal niche of a fish can be described in terms of lethal, controlling and directive effects on the particular species (Figure 16) (Magnuson *et al.*, 1979; Magnuson and DeStasio, 1996; Regier *et al.*, 1996). Warming of aquatic habitats would produce changes in fish species composition and productivity because fishes differ in their response to temperature depending on whether they are adapted for cold or warm waters.

The thermal niche was defined in terms of a directive factor as the final temperature preferendum $\pm 2^\circ\text{C}$ or $\pm 5^\circ\text{C}$ by Magnuson *et al.* (1979). Fish occupy temperatures within the 4°C range 67% of the time in laboratory temperature preference tanks, and all of the time within the 10°C range. These preferred temperatures grade continuously from low to high among species, but reasonable examples are near $10\text{--}15^\circ\text{C}$ for cold water fishes, 21°C for a cool water fish and 30°C for a warm water fish (Figure 16) (Hokanson, 1977; Magnuson *et al.*, 1979). The adapted range of temperature is broader for survival, basal metabolism and digestion than for growth, egg development and active metabolism. Typically, species preferences and the thermal optima they include are near the warm edge of their lethal limits (Lin, 1995; Regier *et al.*, 1996); for example, the final temperature preferendum is about $5\text{--}10^\circ\text{C}$ below the upper lethal

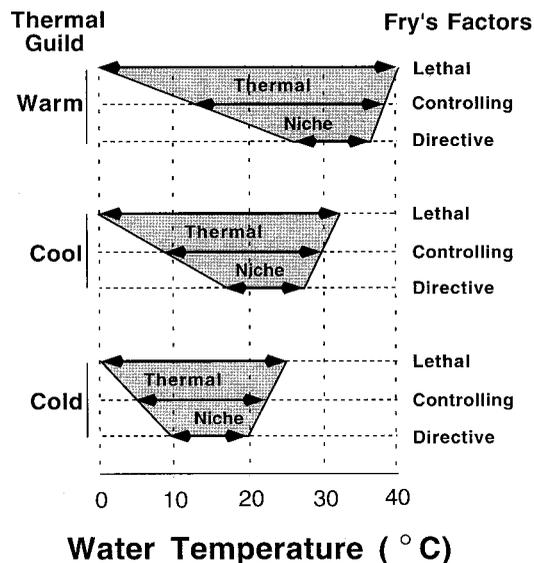


Figure 16. Niche dimension diagram for temperature showing Fry's factors for different thermal guilds

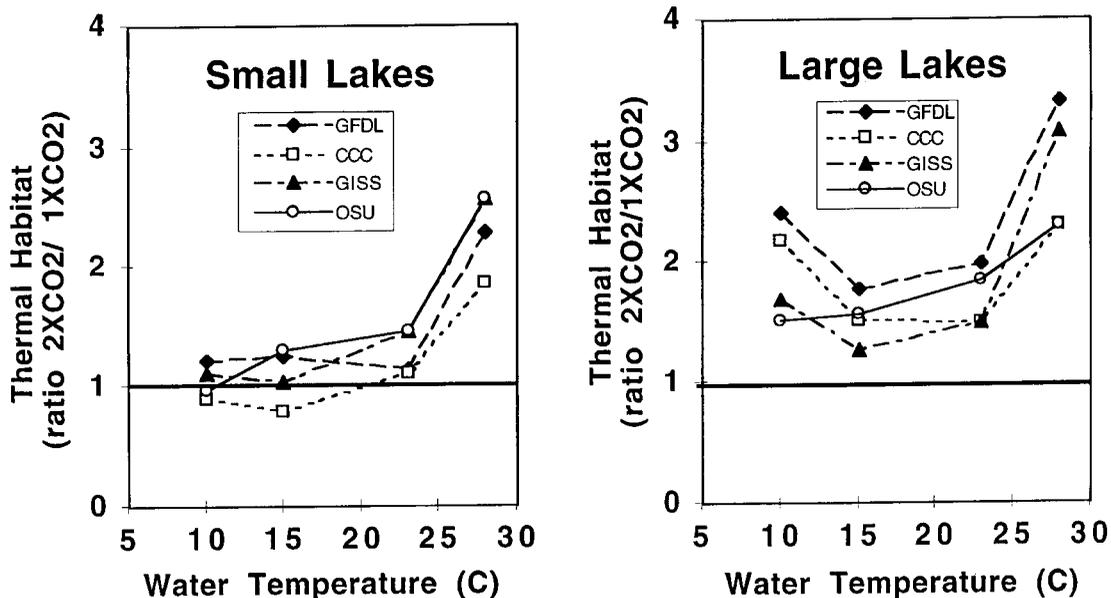


Figure 17. Simulated changes in thermal habitat in small (Crystal and Sparkling) and large (Michigan, Mendota and Trout) stratified temperate lakes for cold, cool and warm water fish under a $2 \times \text{CO}_2$ with four GCMs (adapted from Magnuson and DeStasio, 1996)

temperature. Regier *et al.* (1996) sum this up by stating that 'these ectotherms seem to have evolved to live dangerously but not too dangerously'.

The thermal niche, measured as habitat preferences under laboratory conditions, is the fundamental or non-interactive niche (Magnuson and DeStasio, 1996), but in field situations the fish occupy their realized or interactive niche. *A priori*, fish would be expected to occupy their non-interactive niche if other environmental factors were benign and if preferred temperatures existed in the lake or stream. However, other factors are not necessarily benign; e.g. anoxia can develop in the hypolimnion or under the ice in shallow lakes and displace fishes to less than optimum temperatures. Also, temperatures within the non-interactive thermal niche often do not exist in an ecosystem at a particular season or latitude. Thus, the scenarios of climate change effects on fish thermal habitat must consider other factors influenced by global warming such as anoxia, stream flow and water clarity, as well as geographical location and date.

In global warming ($2 \times \text{CO}_2$) scenarios for deep, thermally stratified lakes, thermal habitat (non-interactive thermal niche) typically increased, not only for warm-water fishes, but also for cool- and cold-water fishes (Figure 17) (Magnuson *et al.*, 1990; DeStasio *et al.*, 1996; Magnuson and DeStasio, 1996). For large and medium size lakes, habitat increased for all thermal guilds with four GCM scenarios (CCC, GISS, GFDL and OSU); for small lakes it increased for cool- and warm-water fishes in all scenarios, but for cold-water fishes it stayed about the same. The increases occurred because the length of the growing season was extended and because fish could move to deeper, cooler waters when surface waters exceeded preferred temperatures. Deep water refuges were maintained in model projections over large latitudinal ranges (McLain *et al.*, 1994). These scenarios of increased thermal habitat did not include the consequences of expected increase in anoxia in the hypolimnion. In Lake Erie scenarios, cold water refuges would not be available because the waters would be expected to be anoxic. Cold water habitat did decrease in small ELA lakes over 20 years of warming weather because the thermocline deepened and the anoxic zone at the bottom increased slightly (Schindler *et al.*, 1990, 1996a). Lake trout stopped reproducing in Lake 239 during the 1970s. Farther south, in Ohio ponds, cool bottom water habitat for northern pike was constricted in warmer years by lower dissolved oxygen and resulted in summer weight loss and reduced development (Headrick and Carline, 1993).

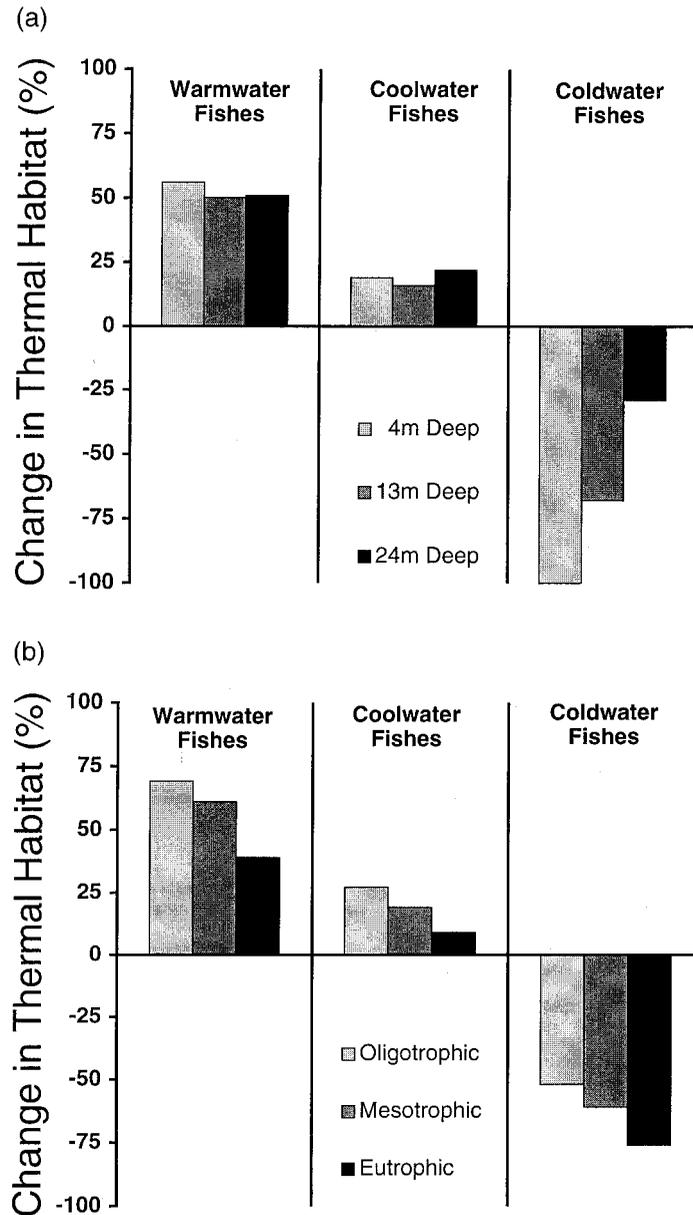


Figure 18. Changes in thermal habitat under $2 \times \text{CO}_2$ scenarios for warm, cool and cold water fishes in (a) lakes of different depths and (b) lakes of different trophic status (data from Stefan *et al.*, 1995)

Comprehensive warming scenarios for fish thermal niche in Minnesota lakes, including both temperature and dissolved oxygen, were developed for a wide range of lake maximum depths, from shallow (4 m) to deep (23 m); trophic status, from oligotrophic (Secchi depth 1.2 m) to eutrophic (Secchi depth 4.5 m); and area, from small (0.2 km²) to large (10 km²) (Stefan *et al.*, 1995). Temperatures that controlled growth of cold-, cool- and warm-water fishes were used to define changes in the favourable habitat. The simulations indicated that a loss of thermal habitat for cold-water fishes occurred across all lake types, but was progressively greater in shallow compared with deep lakes, and in eutrophic compared with oligotrophic lakes (Figure 18).

Thermal habitats increased for warm- and cool-water fishes across all lake types, but increases were progressively greater from eutrophic, to mesotrophic, to oligotrophic lakes (Figure 18).

Shallow ponds and streams would not have the possibility of the thermal refugia associated with the deep stratified waters of some lakes, thus, warming would be more likely to reduce fitness or even be lethal in shallow than in deep lakes. Even in thermally stratified lakes, simulated surface temperatures exceeded lethal levels even for warm-water fishes in some scenarios for selected Wisconsin lakes (DeStasio *et al.*, 1996). Simulations for stream fishes were conducted by Eaton and Scheller (1996) using simulated increases in the mean July, August and September air temperatures of 4.0–5.5°C, including 10 states at the southern part of our region. Based on their results, about 70% of the sites would become unsuitable for the cold-water rainbow trout and the cool-water white sucker, but the number of suitable sites for the warm-water largemouth bass appeared to about double. In two headwater streams with significant groundwater input in southern Ontario, a thermal refuge for cold-water fishes survived a $2 \times \text{CO}_2$ climate scenario, but they were reduced in size by 34 and 40% (Meisner, 1990).

Populations and production. The production of fishes in lakes would be expected to increase with warming. Maximum sustainable fishery yields increased with temperature ($Q_{10} = 2.6$) in a statistical analysis of 43 lakes, many in our region (Regier *et al.*, 1990a). Yields of cold- and cool-water species were correlated with the size of the thermal habitat (non-interactive niche) in 21 large north temperate lakes (Christie and Regier, 1988).

Under $2 \times \text{CO}_2$ climates, process models that included temperature dependence of all life history stages produced increases in population size and productivity of smallmouth bass along cooler shorelines of the Laurentian Great Lakes (analyses by Shuter in Magnuson *et al.*, 1989). Warmer climate scenarios resulted in a longer adult growing season, younger age of maturity, longer young-of-year growing season, greater young-of-year winter survival, greater year-class strengths and larger fishable populations. The ratios between $2 \times \text{CO}_2 : 1 \times \text{CO}_2$ for year-class strengths and fishable populations were greatest for northern Lake Superior, intermediate for Lake Huron and almost zero for Lake Erie. The smallmouth bass has a thermal biology at the boundary between cool- and warm-water fishes. Similar responses would be expected for other species. Temperature increases hatching success and growth of sea lamprey (Holmes, 1990), but expansion of the sea lamprey would be a problem rather than a benefit to human users of fishery resources. Simulated growth rates of cold-, cool- and warm-water fishes all increased in $2 \times \text{CO}_2$ scenarios along warm, cool and cold shorelines of the Great Lakes (Hill and Magnuson, 1990). Growth rates increased and age of smoltification decreased in $2 \times \text{CO}_2$ simulations for Atlantic salmon in eastern Canada (Minns *et al.*, 1995). While this would increase the production of salmon, associated scenarios of river runoff decreased the area of fluvial habitat for juvenile salmon by an average of 4% (range –40 to +16%).

Since climate scenarios indicate greater warming in winter than summer, it is important to consider factors that affect fish populations in winter. On the one hand, warmer winter temperatures would increase winter survival of warmer water species (Johnson and Evans, 1990), those subject to winterkill from anoxic conditions in shallow lakes (Tonn, 1990) and those exposed to low pH and elevated aluminium (Leino and McCormick, 1993). Alternatively, warmer winters would reduce the reproductive success of species that require a cold period for normal gonadal development (Jones *et al.*, 1972), or of autumn-spawning species that have higher overwinter egg survival with ice cover (Taylor *et al.*, 1987). The white perch invasion of the Great Lakes seemed to have been enhanced by higher winter survival of young-of-the-year fishes in warm winters (Johnson and Evans, 1990). Reductions in the duration or the complete absence of ice cover would reduce or prevent anoxic conditions from forming in shallow lakes and backwaters of rivers. In shallow northern Wisconsin lakes, fish communities dominated by central mudminnow, a species tolerant of low dissolved oxygen, would become dominated by northern pike or largemouth bass, species intolerant of low oxygen (Magnuson *et al.*, 1989; Tonn *et al.*, 1990). Only moderate increases in acidity and aluminium affect the electrolyte balance of juvenile largemouth bass at winter temperatures (Leino and McCormick, 1993). The spring-spawning yellow perch require a winter cold period for normal egg development (Jones *et al.*,

1972); the highest percentages of viable eggs produced were 93% after overwintering at 4°C; at 6°C only 65% were viable and at 8°C only 31%. In Grand Traverse Bay, Lake Michigan, year classes of lake whitefish were smaller by an order of magnitude in years without ice cover than in years with ice cover, apparently because eggs on the bottom were dislodged from favourable substrates by the increased turbulence and currents without ice cover (Taylor *et al.*, 1987; Freeberg *et al.*, 1990; Brown and Taylor, 1993).

Species near the northern limits of their range have good years of recruitment and growth that are positively related to summer temperatures (Pereira *et al.*, 1995a,b). Such relationships were observed for freshwater drum, walleye, sauger and possibly for smallmouth bass in long-term data from Minnesota. These growth and recruitment events related to summer temperatures provide another example that fish populations would be sensitive to warming scenarios.

Many fish species, but not all, would grow faster, become more productive and disperse northwards. The ability of young-of-year fishes to reach a sufficient size to overwinter successfully explains the present northern limit of smallmouth bass and yellow perch across our region and other areas of Canada (Shuter and Post, 1990). Simulations of a new northern limit under $2 \times \text{CO}_2$ climate scenarios using this criterion resulted in a potential northward dispersal of about 500 km. Simulations for a doubling of CO_2 from an empirical analysis of fish distributions in Ontario watersheds produced similar potentials for a northward dispersal for smallmouth bass and carp, *ca.* 500–600 km (Minns and Moore, 1995). Thus, warming would be expected to accelerate greatly the northward dispersal of fishes following the Wisconsin glaciation.

In open systems like the Great Lakes and in north/south rivers, as successively warmer species were favoured, changes in species composition, abundance and overall production would occur; other warm-water species would invade through connecting rivers and canals (Mandrak, 1989). Such changes would also be expected to extend north of the Laurentian Great Lakes, with the Great Lakes serving as new sources of colonists. With an air temperature increase of 4.5–5.5°C, simulated increases in species richness ranged from 12 to 60 species per tertiary watershed in Ontario using empirical statistical models (Minns and Moore, 1995). At an individual lake level, the mean scenario was for three new species per lake, which, when compared with the present richness of 3–6 species per lake across much of Ontario, is a large increase; the changes in community structure and dynamics would be dramatic. Dispersal of 33 species already occurring in Ontario but with distributions bounded by temperature, differ across the province (Figure 19); fewer invasions would occur to the north owing to temperature limitations even after the warming scenario, and fewer would occur to the south because many of the species already occur there. In more closed aquatic systems both in Ontario and across the region, such as seepage lakes without inlets or outlets or stream reaches above impassable waterfalls or dams, the arrival of warm-water fauna would also be inhibited. At the same time, to the south, especially in shallow habitats, cold- and even cool-water species would find themselves in progressively suboptimal environments and their populations would be expected to decline progressively from the south. Within the geographical region now inhabited by cold- and cool-water species, local geomorphological, hydrological and anthropogenic factors such as lake depth, groundwater inflow and waste heat loadings would result in populations disappearing in a salt and pepper fashion over broad regions, as simulated by Eaton and Scheller (1996).

IMPLICATIONS OF TERRESTRIAL–AQUATIC LINKAGES

Although the potential effects of climate change on terrestrial environments and aquatic systems have been discussed extensively in the literature, less is known about the interactions between terrestrial and aquatic environments with respect to a changing climate. Interactions among the atmospheric (chemistry and climate), terrestrial (vegetation and soils) and aquatic (flowing water, wetlands and lakes) biomes are complex (Figure 20). Climate (and thus climate change) affects atmospheric chemistry, vegetation, soils, hydrology and aquatic ecosystems; the converse is also true. Included among the terrestrial processes that would directly or indirectly affect aquatic systems in a warming climate are increased rates of fire and drought, changes in the physical and chemical properties of soils and altered hydrology in both space and

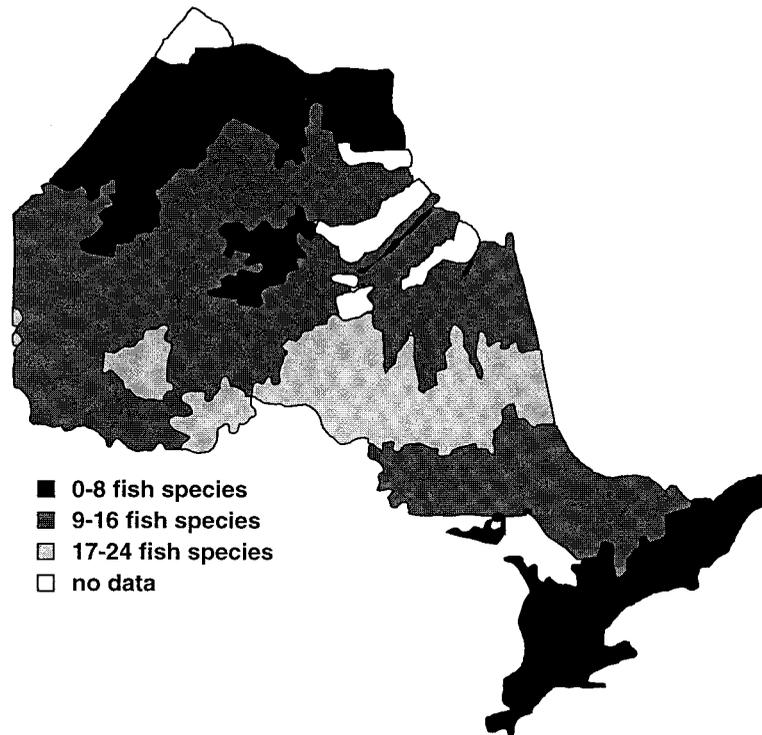


Figure 19. Tertiary watersheds in Ontario where 0–8, 9–16 and 17–24 of the 33 freshwater fish species with temperature-determined boundaries are predicted to be able to invade following climate warming of 4.5–5.5°C (modified from Minns and Moore, 1995)

time. Increased CO₂ concentrations will indirectly affect the terrestrial ecosystem through increased rates of photosynthesis, evapotranspiration, and respiration at higher temperatures. The effects of rising temperature on respiration may overwhelm the direct effects of rising CO₂ on photosynthesis and growth (Drake, 1992), although increases in CO₂ can reduce plant respiration (Bunce, 1994). Since plant metabolism and stomatal control of water loss depend on other climatic factors such as humidity and wind, an increase in evapotranspiration cannot necessarily be assumed (Rosenberg *et al.*, 1990 as cited by Poff, 1992).

Climate-related changes in precipitation, runoff and soil moisture will alter redox potentials and most likely cause declines in wetland coverage, both spatially and temporally. These changes will influence DOC production and export (Hemond, 1990; Sedell and Dahm, 1990) and the cycling of sulfur, phosphorus, nitrogen and metals (Devito and Dillon, 1993a,b), and will affect detrimentally the fauna that rely on wetlands for habitat. For example, the storage of sulfate and/or the oxidation of stored reduced sulfur usually occurs during dry seasons (Dillon and LaZerte, 1992), or in dry years when the water table recedes. At the beginning of the next season, or in a wet year, the stored sulfate is released back into the outflowing waters. The implication is that sulfur inputs to streams and lakes will be affected by climate change long after anthropogenic reductions in sulfate deposition occur. Decreased export of DOC from terrestrial to aquatic environments is expected to occur with climate warming and drying. DOC originates from the forest canopy, the forest floor, the mineral soil, wetlands and groundwater (Cronan, 1990). The quality of the DOC varies with source material and the chemical composition of the water leaching through it (Hynes, 1975; Wetzel, 1992). Higher carbon content in the terrestrial system might lead to higher DOC concentrations in mineral soils, which could counter, in part, the observed decreases in catchment export. Alternatively, soil warming could result in accelerated respiration of soil organic matter, which would otherwise be transported to streams as DOC, and thus decrease DOC inputs (Meyer and Pulliam, 1992).

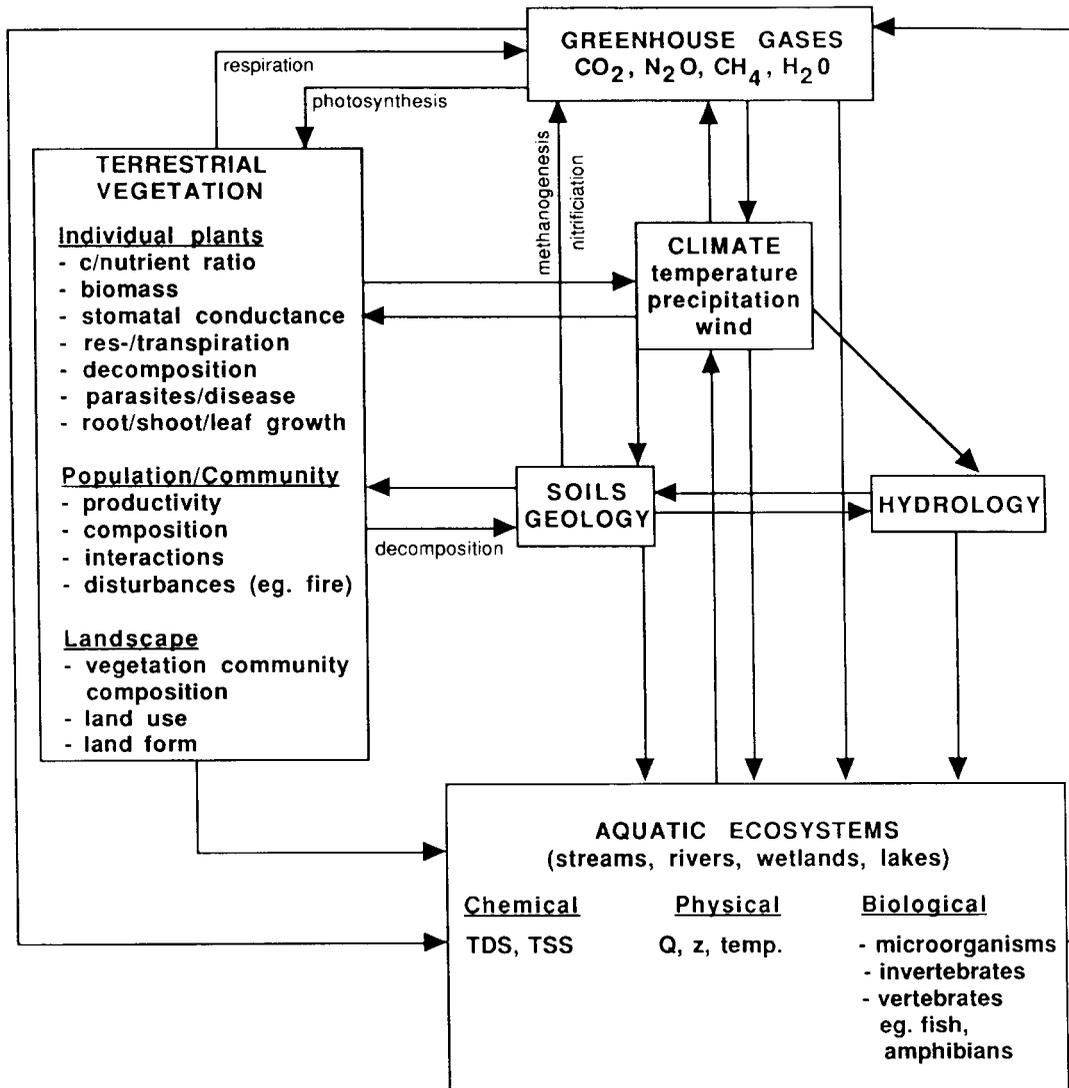


Figure 20. Terrestrial and aquatic linkages influenced by climate change

Other terrestrial effects relevant to freshwater ecosystems could result from changes in the ranges of plant species and species composition at a regional scale (Bazzaz, 1990). Rizzo and Wilken (1992) forecast that much of the moist boreal forest will be replaced by transitional grasslands and cool temperate forests. Northward range migrations of several tree species are projected (Peters, 1990). Unfortunately, while substantial changes in terrestrial vegetation patterns are predicted, the exact response differs between scenarios (Lenihan and Neilson, 1994). Changes to the terrestrial riparian zones of streams will affect exports of inorganic and organic matter to streams and lakes. Changes in plant species composition, decreases in foliar N content and increases in C:N ratios would affect the quality of the leaf litter both on the forest floor and in the streams. Increased production and transfer of plant biomass to the roots might affect nutrient uptake and the amount available to be leached from the soil. Finally, more fire and drought could increase the rate at which forests are 'opened up' for new trees, and thus short circuit the slower process of forest-gap overturn

through old age mortality (Overpeck *et al.*, 1990). Inputs of woody debris to streams would increase, gaps left by fallen trees would undergo succession and the litter contributed by successional species would increase. In small streams, heavy litter accumulation from a longer dry season may cause deoxygenation (Hynes, 1975), which could affect transport of nutrients, DOC and metals.

The effect of climate change on carbon storage in the terrestrial ecosystem depends on plant species composition, soil water holding capacity and C:N dynamics. While most predict that, at least in the short term, carbon storage will increase because of higher productivity and C:N ratios (Post *et al.*, 1992; Rastetter *et al.*, 1992), rising temperatures might increase forest ecosystem respiration sufficiently for terrestrial ecosystems to become a source and not a sink for CO₂ (Drake, 1992). These predictions are complicated by expected increases of *ca.* 40% in the frequency and intensity of fires in boreal regions with global warming (Flannigan and Van Wagner, 1991, cited in Kasischke *et al.*, 1995). In the short term, the combined effects of changes in climate and fire regime would influence net carbon storage in the boreal forest through increases of 20–50% in the area burned, an increase in forest flammability and a decrease in carbon storage in the ground layer (Kasischke *et al.*, 1995). Over the long term (150–200 years), shifts in forest species composition to more deciduous trees would result in more carbon storage as living biomass and a decrease in forest flammability (Kasischke *et al.*, 1995).

INTERACTIONS WITH OTHER STRESSES

Lakes integrate the combined effects of human activities in their catchments and airsheds. Thus, they can be sensitive indicators of the added perturbations from climate warming. Many anthropogenic perturbations, already affecting aquatic systems in the Laurentian Great Lakes and Precambrian Shield Region, would interact with the potential effects of climate change. Climate change effects are not independent of other human stresses on the system, nor are the effects of these stresses independent of climate change effects. Interacting stresses include atmospheric deposition of acids and toxic organic chemicals; discharges of agricultural, industrial, and domestic wastes; forest fires and clear cutting; urbanization; pipeline and reservoir construction; mining; dredging; invasion of exotics; and so on. What most of these stresses have in common is that they change the fluxes of water and dissolved and suspended materials, leading to the generic problems of eutrophication and contamination. Thus, the stresses that we have been dealing with may be accentuated, or in some cases countered, by the added effects of climate change. Below we discuss some of the potential interactions between climate warming and these other human-caused stresses on aquatic systems, especially lakes.

Eutrophication

Regier *et al.* (1990a) made the case that the thermal effects of climate warming would superficially resemble those of eutrophication. Their empirical relations indicated that annual primary production of phytoplankton, zooplankton biomass and maximum sustained fishery yields all increased with temperature. Increased anoxia of the deep hypolimnetic waters, a feature of eutrophication, also increased in climate warming scenarios for both Lake Erie (Blumberg and DiToro, 1990) and small inland lakes scenarios (Stefan *et al.*, 1993a, 1995; Stefan and Fang, 1994). Faster growth rates for fishes in the Great Lakes were simulated in warming scenarios, provided adequate prey were available to fuel higher metabolic rates (Hill and Magnuson, 1990). So, superficially, the effects of eutrophication appear to parallel those of climate warming.

The influence of climate change on nutrient dynamics is less certain and more contradictory. Because climate change models predict lower runoff and, thus, a decline in nutrient export from catchments to lakes, a reduction in eutrophication might result. However, increases in the water residence time of lakes, as observed for many ELA lakes during warmer conditions (Schindler *et al.*, 1996a), may counteract the decreased inputs, potentially causing an overall increase in the effective loading rate. In addition, the increased frequency of severe weather events might result in higher pulsed inputs of nutrients during flooding and runoff events in agricultural and urban catchments, or at construction sites. The greater duration and

extent of hypolimnetic anoxia would forecast an increase in recycling of nutrients from the sediments to the water column and increased blooms during spring and autumn mixis during the erosion of the thermocline in late summer and early autumn, and possibly in the metalimnion and hypolimnion of lakes that became even clearer owing to the decrease in DOC induced by climate change.

Acid precipitation and toxic substances

Climate warming interacts with acid deposition in complex ways. Alkalization of lakes, related to the increased importance of in-lake alkalinity-generation processes and decreased sulfate:cation ratios, was observed at ELA during the 20-year warming period (Schindler *et al.*, 1996a). In contrast, both episodic and long-term acidification of lakes and streams have been attributed to drought. Dry conditions expose the littoral zones of lakes and wetlands and enhance the oxidation of stored sulfur (Bayley *et al.*, 1992b; LaZerte, 1993; Yan *et al.*, 1996). Subsequent wet conditions then flush sulfate, cations and acidity into lakes and streams in pulsed acidification events. The acidity of these pulses is related to the deposition history; sites receiving higher acid loads export more acid waters (Bayley *et al.*, 1986; LaZerte, 1993). During drought, inputs of solute-rich groundwater to precipitation-dominated seepage lakes decrease (Anderson and Cheng, 1993; Wentz *et al.*, 1995), with the potential for rapid acidification (Webster *et al.*, 1990). A set of headwater, acid-sensitive lakes monitored in northern Minnesota, Wisconsin and Michigan failed to show a consistent increase in acid-neutralizing capacity (ANC) or pH as acid deposition rates declined in the region from 1983 to 1994 (Webster and Brezonik, 1995). General declines of SO_4^{2-} in the lakes were, instead, often associated with a decline in cations linked to decreased loading from deposition and decreased inputs of groundwater late in the 1980s.

Acidity, DOC and temperature changes related to climate warming could influence the transport and biological availability of a variety of toxic substances. The increased acidity of flow from certain landforms would have the potential for higher transport of metals, which become more soluble at lower pH levels. Decreases in DOC concentrations could reduce the chemical binding capacity of waters and cause the biotic effects of the toxins to increase (Connel and Miller, 1984; Moore *et al.*, 1995, 1997; Schindler *et al.*, 1996a). Increased transparency related to decreases in DOC could also increase the penetration of harmful UV-B radiation in lakes (Schindler *et al.*, 1996b; Yan *et al.*, 1996). Warming of lakes could increase the accumulation of methyl mercury in fishes; the ratio of methylation to demethylation increases with temperature and a high proportion of the variation in mercury content of fishes was associated with warmer temperatures (Bodaly *et al.*, 1993). Conversely, hydrological shifts that decrease the export of solutes from wetlands may likewise reduce the transport of mercury to lakes and streams; methyl mercury concentrations in lakes show a positive relationship with DOC and wetland area in the catchment (Mierle and Ingram, 1991; St. Louis *et al.*, 1994; Watras *et al.*, 1995). Heavy metal and pesticide accumulation increase at warmer water temperatures (Reinert *et al.*, 1974; Wood and McDonald, 1996). Zinc becomes more toxic to bluegill under conditions of reduced dissolved oxygen concentrations (Pickering, 1968), which are likely to accompany higher lake and stream temperatures. Acute exposure (24 h) of the fathead minnow to a synthetic pyrethroid pesticide reduced its tolerance to both lethally high and low environmental temperatures (Heath *et al.*, 1994). Thus, toxic substances might be more problematic in some systems in a warmer and drier climate.

Exotic organisms

Climate warming and drying influence the movement of exotic organisms by: (1) providing warmer habitats that could favour invading rather than native organisms (Mandrak, 1989); (2) potential management actions to augment the communities of isolated lakes and stream sections by moving warmer water organisms northwards (Arnell *et al.*, 1996); and (3) reducing the connectivity of headwater lakes that can become more isolated as connecting streams or wetlands dry up (see Lodge, 1993). The poleward movement of freshwater communities in response to climate warming is expected to be just as dramatic as the poleward movement of terrestrial vegetation (Arnell *et al.*, 1996). Thus, many waters would become host to new species or 'exotics'. The northwards dispersal of organisms observed following the retreat of the Wisconsin glaciation would

occur at a much faster rate. Twenty-seven fish species residing in the Great Lakes area have the potential to invade the Laurentian Great Lakes with climate warming, dramatically altering present Great Lakes fish communities (Mandrak, 1989). For isolated lakes and streams with barriers to dispersal from adjacent waters, pressures for the managed northwards dispersal would most likely be high, especially for game fishes and any threatened or endangered species. Such movements could have two positive features; increasing the productivity of a too-warm system occupied by species adapted for cooler waters, and saving a species about to be extirpated or become extinct. Alternatively, there are several disadvantages: reductions in the population viability of native species at a faster rate than that owing to climate change alone owing to species interactions with exotics, increasing rates of extirpation and increasing rates of species turnover, making species structure more chaotic and difficult to manage for human goals (see Magnuson, 1976; Regier *et al.*, 1996).

HETEROGENEITY IN RESPONSE AMONG WATER BODIES

Finally, we believe it is important to repeat what must be obvious from this article. Not only are lakes and other aquatic systems in the Laurentian Great Lakes and Precambrian Shield Region strong responders to climate change and variability, but also differences in response are paramount both across the region and among adjacent waters. Differences in morphometry or hydrology of lakes, streams and ponds can result in changes that are in opposite directions. Some responses differ within a lake or a stream, others are only apparent in comparisons among different lakes or streams; still others only are apparent in a network of lakes and streams or in analyses of large geographical regions. Changes in the edaphic, climatic, anthropogenic and morphological factors that typify the typologies of lakes all influence how the physical, chemical and biological limnology plays out in a warmer and drier climate. Hydrological considerations are especially significant in terms of: (1) solute and nutrient sources; (2) controls relative to the distribution of water flows among precipitation–groundwater–runoff; (3) influences of lake size on water residence times; and (4) the influence of catchment size relative to lake volume on biogeochemical responses. The dependence of water bodies on riparian and catchment attributes links lake and stream responses tightly to heterogeneity and changes in the surrounding landscape, whether these changes are induced vegetational transformations from climate change or altered land and water use by humans in the catchments. The altitudinal position of lakes and streams in the local landscape and hydrological flow system introduces heterogeneous responses among adjacent streams and lakes. Responses differ among seasons, not only because climate change does not occur uniformly over the year, but also because the array of sensitive ecological processes differs among seasons. Likewise, neither lake, stream, or wetland provide homogeneous entities of response to climate change. A vast array of interacting factors contributes to the responses of aquatic ecosystems to climate change, and surprises should be expected.

RESEARCH NEEDS

Five broad research needs have been identified.

1. *Long-term research* and monitoring should be maintained and expanded at key locations. Often, responses to climate are complex and unpredictable from first principles (Schindler, 1997).

2. *Models* of aquatic system behaviour should be improved and tested against long-term data and manipulative field experiments.

3. *Climate models should be improved* to include outputs of *wind and clouds* and at temporal and spatial scales more suitable for *subregional analyses*.

4. The heterogeneity of potential responses should be recognized and a *predictive understanding of this heterogeneity* should be developed.

5. A better understanding of the temperature responses of aquatic organisms and communities is needed, especially for winter.

ACKNOWLEDGEMENTS

Co-authors have contributed different sections and provided comments on the entire manuscript. Linda Mortsch and Frank Quinn are acknowledged for sections on climate, climate trends and future climate scenarios; Ray Assel for materials on Great Lakes Ice; Peter Dillon, Hayla Evans and Roland Hall for information on palaeoclimates and terrestrial ecosystems; Carl Bowser for his emphasis on the importance of hydrological processes and for helping to coordinate the effort; Everett Fee and David Schindler for information from ELA and north-western Ontario and biogeochemical and DOC responses; Everett Fee for the phytoplankton information; John Eaton for his contributions on the biological responses; Katherine Webster for contributions to biogeochemistry, general editing and figure development; John Magnuson for contributions on fish, interacting stresses, physical limnology, and general synthesis; Bill Feeney for drafting figures; and Alice Justice for assistance with production. We thank the American Society of Limnology and Oceanography and the North American Benthological Society for organizing the symposium from which our paper evolved and the US Environmental Protection Agency and the US Geological Survey for their sponsorship.

REFERENCES

- Adams, M. S., Meinke, T. W., and Kratz, T. K. 1990. 'Primary productivity in three northern Wisconsin lakes', *Verh. Internat. Verein. Limnol.*, **24**, 432–437.
- Allen, M. M. and Stanier, R. Y. 1968. 'Selective isolation of blue-green algae from water and soil', *J. Gen. Microbiol.*, **51**, 203–209.
- Anderson, J. C. 1987. 'On the use of lake ice conditions to monitor climatic change', *Canadian Climate Centre Report No. 87-8*. AES, Downsview, p. 53.
- Anderson, T. W. 1989. 'Vegetation changes over 12 000 years: changes in eastern Ontario and adjacent areas gives evidence of global change', *GEOS (Energy, Mines and Resources Canada)*, **18**, 39–47.
- Anderson, M. P. and Cheng, X. 1993. 'Long and short term transience in a groundwater/lake system in Wisconsin, USA', *J. Hydrol.*, **145**, 1–18.
- Anderson, T. W. and Lewis, C. F. M. 1992. 'Climatic influences of deglacial drainage changes in southern Canada at 10 to 8 ka suggested by pollen evidence', *Geogr. Phys. Quat.*, **46**, 255–272.
- Anderson, W., Robertson, D. M., and Magnuson, J. J. 1996. 'Evidence of recent warming and El Niño variations in ice breakup of Wisconsin lakes', *Limnol. Oceanogr.*, **41**, 815–821.
- Arnell, N., Bates, B., Lang, H., Magnuson, J. J., and Mulholland, P. 1996. 'Hydrology and freshwater ecology', in Watson, R. T., Zinyowera, M. C., and Moss, R. H. (Eds), *Climate Change 1995: Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analyses*, Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York. 880 pp.
- Assel, R. A. 1986. 'Fall and winter thermal structure of Lake Superior', *J. Great Lakes Res.*, **12**, 251–262.
- Assel, R. A. 1990. 'An ice-cover climatology for Lake Erie and Lake Superior for the winter seasons 1897–98 to 1982–83', *Int. J. Climatol.*, **10**, 731–748.
- Assel, R. A. 1991. 'Implications of CO₂ global warming on Great Lakes ice cover', *Climate Change* **18**, 377–395.
- Assel, R. A. and Robertson, D. M. 1995. 'Changes in winter air temperatures near Lake Michigan during 1851–1993, as determined from regional lake-ice records', *Limnol. Oceanogr.* **40**, 165–176.
- Assel, R. A., Quinn, F. H., Leshkevich, G. A., and Bolsenga, S. J. 1983. 'Great Lakes ice atlas', *NOAA Atlas No. 4*. Great Lakes Environmental Research Lab., Ann Arbor, MI.
- Assel, R. A., Snider, C. R., and Lawrence, R. 1985. 'Comparison of 1983 Great Lakes winter weather and ice conditions with previous years', *Monthly Weather Rev.*, **113**, 291–303.
- Assel, R. A., Robertson, D. M., Hoff, M. H. and Selgeby, J. H. 1995. 'Climatic-change implications from long-term (1823–1994) ice records for the Laurentian Great Lakes', *Ann. Glaciol.*, **21**, 383–386.
- Assel, R. A., Janowiak, J. E., Young, S. and Boyce, D. 1996. 'Winter 1994 weather and ice conditions for the Laurentian Great Lakes', *Bull. Am. Meteorol. Soc.*, **77**, 71–88.
- Atmospheric Environment Service, 1982a. *Canadian Climate Normals 1951–80, Temperature and Precipitation — Quebec*. Supply and Services Canada, Ottawa.
- Atmospheric Environment Service, 1982b. *Canadian Climate Normals 1951–80, Temperature and Precipitation — Atlantic Provinces*. Supply and Services Canada, Ottawa.
- Atmospheric Environment Service, 1982c. *Canadian Climate Normals 1951–80, Temperature and Precipitation — Prairie Provinces*. Supply and Services Canada, Ottawa.
- Atmospheric Environment Service, 1982d. *Canadian Climate Normals 1951–80, Temperature and Precipitation — Ontario*. Supply and Services Canada, Ottawa.
- Atmospheric Environment Service, 1982e. *Canadian Climate Normals 1951–80, Degree Days*, Volume 4. Supply and Services Canada, Ottawa.
- Atmospheric Environment Service, 1982f. *Canadian Climate Normals 1951–80, Frost*, Volume 6. Supply and Services Canada, Ottawa.
- Atmospheric Environment Service, 1994. 'Modelling the global climate system', *Climate Change Digest, CCD 94-01*. Supply and Services Canada, Ottawa. p. 20.

- Bartlein, P. J. and Webb, III, T. 1985. 'Mean July temperature at 6000 yr BP in eastern North America: regression equations for estimates from fossil-pollen data', *Syllogeus*, **55**, 301–342.
- Bayley, S. E., Behr, R. S., and Kelly, C. A. 1986. 'Retention and release of sulfur from a freshwater wetland', *Water Air Soil Pollut.*, **31**, 101–114.
- Bayley, S. E., Schindler, D. W., Parker, B. R., Stainton, M. P., and Beaty, K. G. 1992a. 'Effects of forest fire and drought on acidity of a base-poor boreal forest stream: similarities between climatic warming and acidic precipitation', *Biogeochemistry*, **17**, 191–204.
- Bayley, S. E., Schindler, D. W., Beaty, K. G., Parker, B. R., and Stainton, M. P. 1992b. 'Effects of multiple fires on nutrient yields from streams draining boreal forest and fen watersheds: nitrogen and phosphorus', *Can. J. Fish. Aquat. Sci.*, **49**, 584–596.
- Bazzaz, F. A. 1990. 'The response of natural ecosystems to the rising global CO₂ levels', *Annu. Rev. Ecol. Syst.*, **21**, 167–196.
- Blumberg, A. F. and DiToro, D. M. 1990. 'Effects of climate warming on dissolved oxygen concentrations in Lake Erie', *Trans. Am. Fish. Soc.*, **119**, 210–223.
- Bodaly, R. A., Rudd, J. W. M., Fudge, R. J. P., and Kelly, C. A. 1993. 'Mercury concentrations in fish related to size of remote Canadian Shield Lakes', *Can. J. Fish. Aquat. Sci.*, **50**, 980–987.
- Boer, G. J., McFarlane, N. A., and Lazare, M. 1992. 'Greenhouse gas-induced climate change simulated with the CCC second-generation general circulation model', *J. Climate*, October 1992, 1045–1077.
- Bolsenga, S. J. and Norton, D. C. 1993. 'Great Lakes air temperature trends for land stations, 1901–1987', *J. Great Lakes Res.*, **19**, 379–388.
- Brown, R. W. and Taylor, W. W. 1993. 'Factors affecting the recruitment of Lake Whitefish in two areas of northern Lake Michigan', *J. Great Lakes Res.*, **19**, 418–428.
- Bunce, J. A. 1994. 'Responses of respiration to increasing atmospheric carbon dioxide concentrations', *Physiol. Plantarum*, **90**, 427–430.
- Calkin, P. E. and Feenstra, B. H. 1985. 'Evolution of the Erie Basin Great Lakes', in Karrow, P. F. and Calkin, P. E. Eds, *Quaternary Evolution of the Great Lakes. Geol. Assoc. Can., Spec. Pap.*, **30**, 149–170.
- Campbell, I. D. and McAndrews, J. H. 1991. 'Cluster analysis of late Holocene pollen trends in Ontario', *Can. J. Bot.*, **69**, 1719–1730.
- Campbell, I. D. and McAndrews, J. H., 1993. 'Forest disequilibrium caused by Little Ice Age cooling', *Nature*, **366**, 336–338.
- Canale, R. P. and Vogel, A. H. 1974. 'Effects of temperature on phytoplankton growth', *J. Env. Eng. Div., Am. Soc. Civil Eng.*, **100**, 231–241.
- Carpenter, S. R., Fisher, S. G., Grimm, N. B. and Kitchell, J. F. 1992. 'Global change and freshwater ecosystems', *Annu. Rev. Ecol. Syst.*, **23**, 119–139.
- Changnon, S. A., Jr., Leffler, S. and Shealy, R. 1989. 'Impacts of extremes in Lake Michigan levels along Illinois shoreline: low levels. Report prepared for U.S. Environment Protection Agency, Washington, D.C.' in Smith, J. B. and Tirpak, D. A. (Eds). *The Potential Effects of Global Climate Change on the United States*. Hemisphere Publishing Corp., New York. pp. 3–1 to 3–48.
- Chen, C. Y. and Folt, C. L. 1996. 'Consequences of fall warming for zooplankton overwintering success', *Limnol. Oceanogr.*, **41**, 1077–1086.
- Christie, G. C. and Regier, H. A. 1988. 'Measures of optimal thermal habitat and their relationship to yields of four commercial fish species', *Can. J. Fish. Aquat. Sci.*, **45**, 301–314.
- Connell, D. W. and Miller, G. J. 1984. *Chemistry and Ecotoxicology of Pollution*. John Wiley and Sons, Inc., New York. 444 pp.
- Countant, C. C. 1981. 'Foreseeable effects of CO₂-induced climate change: freshwater concerns', *Environ. Conserv.*, **8**, 285–297.
- Crissman, R. D. 1989. 'Impacts on electricity generation in New York State', in *Report of the First U.S.–Canada Symposium on Impacts of Climate Change on the Great Lakes Basin* US National Climate Program Office and Canadian Climate Centre. pp. 109–118.
- Croley, T. E., II. 1990. 'Laurentian Great Lakes double-CO₂ climate change hydrological impacts', *Climat. Change*, **17**, 27–47.
- Croley, T. E., II. 1993. 'CCC GCM 2 × CO₂ hydrological impacts on the Great Lakes, in *Climate, Climate Change, Water Level Forecasting and Frequency Analysis*, Supporting documents, Vol. 1, Water Supply Scenarios. Task Group 2, Working Committee 3, IJC, Levels Reference Study, Phase II.
- Croley, T. E., II and Hartmann, H. C. 1985. 'Resolving Thiesson polygons', *J. Hydrol.*, **76**, 363–379.
- Croley, T. E., II and Hunter, T. S. 1994. 'Great Lakes monthly hydrologic data', *NOAA Technical Memorandum ERL GLERL-83*, p. 83.
- Croley, T. E., II, Quinn, F. H., Kunkel, K., and Changnon, S. J. 1994. 'Potential Great Lakes hydrology and lake level impacts resulting from global warming', *GLERL Report No. 931*. Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan, p. 6.
- Croley, T. E., II, Quinn, F. H., Kunkel, K. and Changnon, S. J. 1995. 'Potential Great Lakes hydrology and lake level impacts resulting from global warming', in *Preprint Vol: Sixth Conference on Global Change Studies*. American Meteorological Society, Boston, Massachusetts. pp. 67–72.
- Cronan, C. S. 1990. 'Patterns of organic acid transport from forested watersheds to aquatic ecosystems', in Perdue, E. M. and Gjessing, E. T. (Eds), *Organic Acids in Aquatic Ecosystems*. John Wiley & Sons Ltd., New York. pp. 245–260.
- Davison, I. R. 1991. 'Environmental effects on algal photosynthesis: temperature', *J. Phycol.*, **27**, 2–8.
- DeNoyelles, F. Jr., Reinke, D., Knoechel, R., Treanor, D., and Altenhofen, C. 1980. 'Continuous culturing of natural phytoplankton communities in the Experimental Lakes Area: effects of enclosure, in situ incubation, light, phosphorus and cadmium', *Can. J. Fish. Aquat. Sci.*, **37**, 424–433.
- DeStasio, B. T., Hill, D. K., Kleinhans, J. M., Nibbelink, N. P., and Magnuson, J. J. 1996. 'Potential effects of global climate change on small north temperate lakes: physics, fishes and plankton', *Limnol. Oceanogr.*, **41**, 1136–1149.
- Devito, K. J. and Dillon, P. J. 1993a. 'The importance of runoff and winter anoxia to the P and N dynamics of a beaver pond', *Can. J. Fish. Aquat. Sci.*, **50**, 2222–2234.
- Devito, K. J. and Dillon, P. J. 1993b. 'The influence of hydrologic conditions and peat oxia on the phosphorus and nitrogen dynamics of a conifer swamp', *Wat. Resour. Res.*, **29**, 2675–2685.
- Dillon, P. J. and LaZerte, B. D. 1992. 'Response of the Plastic Lake catchment, Ontario to reduced sulfur deposition', *Environ. Pollut.*, **77**, 211–217.

- Drake, B. G. 1992. 'The impact of rising CO₂ on ecosystem production', *Water Air Soil Pollut.*, **64**, 25–44.
- Dredge, L. A., Mott, R. J., and Grant, D. R. 1992. 'Quaternary stratigraphy, paleoecology, and glacial geology, Iles de la Madeleine, Quebec', *Can. J. Earth Sci.*, **29**, 1981–1996.
- Eaton, J. G. and Scheller, R. M. 1996. 'Effects of climate warming on fish thermal habitat in streams of the United States', *Limnol. Oceanogr.*, **41**, 1109–1115.
- Edwards, T. W. D. and Fritz, P. 1988. 'Stable-isotope paleoclimate records for southern Ontario, Canada: comparison of results from marl and wood', *Can. J. Earth Sci.*, **25**, 1397–1406.
- Engstrom, D. R. and Hansen, B. C. S. 1985. 'Postglacial vegetation change and soil development in southeastern Labrador as inferred from pollen and chemical stratigraphy', *Can. J. Bot.*, **63**, 543–561.
- Eppley, R. W. 1972. 'Temperature and phytoplankton growth in the sea', *Fish. Bull.*, **70**, 1063–1085.
- Everett, J. T., Troadec, J.-P., Regier, H. A., Krovnnin, A., Okemwa, E., and Lluch Belda, D. 1996. 'Fisheries', in *The Intergovernmental Panel on Climate Change Working Group 2, Report on Impact Assessment and Adaptation Strategies*. Geneva, Switzerland. Chapter 8.
- Fee, E. J. 1976. 'The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area, northwestern Ontario: implications for primary production estimates', *Limnol. Oceanogr.*, **21**, 767–783.
- Fee, E. J., Hecky, R. E., and Welch, H. E. 1987. 'Phytoplankton photosynthesis parameters in central Canadian lakes', *J. Plankton Res.*, **9**, 305–316.
- Fee, E. J., Shearer, J. A., DeBruyn, E. R., and Schindler, E. U. 1992. 'Effects of lake size on phytoplankton photosynthesis', *Can. J. Fish. Aquat. Sci.*, **49**, 2445–2459.
- Fee, E. J., Hecky, R. E., Regehr, G. W., Hendzel, L. L., and Wilkinson, P. 1994. 'Effects of lake-size on nutrient availability in the mixed-layer during summer stratification', *Can. J. Fish. Aquat. Sci.*, **51**, 2756–2768.
- Fee, E. J., Hecky, R. E., Kasian, S. E., and Cruikshank, 1996. 'Effects of lake size, water clarity, and climatic variability on mixing depths in Canadian Shield Lakes', *Limnol. Oceanogr.*, **41**, 912–920.
- Freeberg, M. H., Taylor, W. W., and Brown, R. W. 1990. 'Effect of egg and larval survival on the year-class strength of lake whitefish I Grand Traverse Bay, Lake Michigan', *Trans. Am. Fish. Soc.*, **119**, 92–100.
- Fry, F. E. J. 1947. 'Effects of the environment on animal activity', *Publ. Ontario Fish. Res. Lab.*, **68**, 1–62.
- Fry, F. E. J. 1971. 'The effect of environmental factors on the physiology of fish', in Hoar, W. S. and Randall, D. J. (Eds), *Fish Physiology: Environmental Factors*. Academic Press, New York. pp. 1–98.
- Giberson, D. J., Rosenberg, D. M., and Wiens, A. P. 1991. 'Changes in abundance of burrowing mayflies in Southern Indian Lake: lessons for environmental monitoring', *Ambio*, **20**, 139–142.
- Grimm, E. C. and Jacobson, G. L., Jr. 1992. 'Fossil-pollen evidence for abrupt climate changes during the past 18000 years in eastern North America', *Climate Dynam.*, **6**, 179–184.
- Guildford, S. J., Hendzel, L. L., Kling, H. J., Fee, E. J., Robinson, G. G. C., Hecky, R. E., and Kasian, S. E. M. 1994. 'Effects of lake size on phytoplankton nutrient deficiency status', *Can. J. Fish. Aquat. Sci.*, **51**, 2769–2783.
- Gullett, D., Skinner, W., and Vincent, L. 1992. 'Development of an historical Canadian climate database for temperature and other climate elements', *Climatol. Bull.*, **26**, 125–131.
- Hairston, N. G. 1996. 'Zooplankton egg banks as biotic reservoirs in changing environments', *Limnol. Oceanogr.*, **41**, 1087–1092.
- Hall, R. I. 1993. 'Paleolimnological analysis of lake-watershed interactions and long term lake trophic status', *PhD Thesis*, Biology Dept., Queen's University, Kingston, Ontario, Canada. p. 323.
- Hansen, J., Fung, I., Lacis, A., Rind, D., Ruedel, G., Lebedeff, S., Ruedy, R., and Stone, P. 1988. 'Global climate changes as forecast by the Goddard Institute for Space Studies three-dimensional model', *J. Geophys. Res.*, **93**, 9341–9364.
- Hartmann, H. C. 1990. 'Climate change impacts on Laurentian Great Lakes levels', *Climate Change*, **17**, 49–67.
- Headrick, M. R. and Carline, R. F. 1993. 'Restricted summer habitat and growth of northern pike in two southern Ohio impoundments', *Trans. Am. Fish. Soc.*, **122**, 228–236.
- Healey, F. P. and Hendzel, L. L. 1980. 'Physiological indicators of nutrient deficiency in lake phytoplankton', *Can. J. Fish. Aquat. Sci.*, **37**, 442–453.
- Heath, S., Bennett, W. A., Kennedy, J., and Beiting, T. L. 1994. 'Heat and cold tolerance of the fathead minnow, *Pimephales promelas*, exposed to the synthetic pyrethroid cyfluthrin', *Can. J. Fish. Aquat. Sci.*, **51**, 437–440.
- Hecky, R. E. and Hesslein, R. H. 1996. 'Contributions of benthic algae to lake food webs as revealed by stable isotope analysis', *J. North Am. Benthol. Soc.*, **14**, 582–598.
- Hecky, R. E. and Kilham, P. 1988. 'Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment', *Limnol. Oceanogr.*, **33**, 796–822.
- Hemond, H. F. 1990. 'Wetlands as the source of dissolved organic carbon to surface waters', in Perdue, E. M. and Gjessing, E. T. (Eds), *Organic Acids in Aquatic Ecosystems*. John Wiley & Sons, New York. pp. 301–313.
- Hill, D. K. and Magnuson, J. J. 1990. 'Potential effects of global climate warming on the growth and prey consumption of Great Lakes fish', *Trans. Am. Fish. Soc.*, **119**, 265–275.
- Hokanson, K. E. F. 1977. 'Temperature requirements of some percids and adaptations to the seasonal temperature cycle', *J. Fish. Res. Bd. Can.*, **34**, 1524–1550.
- Holmes, J. A. 1990. 'Sea lamprey as an early responder to climate change in the Great lakes Basin', *Trans. Am. Fish. Soc.*, **119**, 292–300.
- Hondzo, M. and Stefan, H. G. 1991. 'Three case studies of lake temperature and stratification response to warmer climate', *Wat. Resour. Res.*, **27**, 1837–1846.
- Hondzo, M. and Stefan, H. G. 1993. 'Regional water temperature characteristics of lakes subjected to climate change', *Climatic Change*, **24**, 187–211.
- Houghton, J. J., Meiro Filho, L. G., Callander, B. A., Harris, N., Kattenberg, A., and Maskell, K. (Eds) 1996. *Climate Change 1995: The Science of Climate Change*, Contribution of Working Group I to the Second Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York. 584 pp.

- Hynes, H. B. N. 1975. 'The stream and its valley', *Int. Verein. Theor. Ang. Limnol., Verhand.*, **19**, 1–15.
- Johnson, T. B. and Evans, D. O. 1990. 'Size dependent winter mortality of young-of-the-year white perch: climate warming and the invasion of the Laurentian Great Lakes', *Trans. Am. Fish. Soc.*, **119**, 779–785.
- Jones, B. R., Hokanson, K. E. F., and McCormick, J. H. 1972. 'Winter temperature requirements for maturation and spawning of yellow perch, *Perca flavescens* (Mitchell)', in Marois, M. (Ed.), *Proceedings, World Conference Towards a Plan of Action for Mankind*, Vol. 3, Biological Balance and Thermal Modifications. Pergamon Press, New York. pp. 189–192.
- Kasian, S. E. M., Findlay, D. L., Regehr, G., Beaty, K. G., Cruikshank, D. R., Shearer, J. A., in press. Natural variability of phytoplankton composition over decadal time scales in the Experimental Lakes Area. *Can. J. Fish. Aquat. Sci.*
- Kasischke, E. S., Christensen, N. L., Jr., and Stocks, B. J. 1995. 'Fire, global warming, and the carbon balance of boreal forests', *Ecol. Appl.*, **5**, 437–451.
- Keith, V. F., DeAvila, C., and Willis, R. M. 1989. 'Effect of climatic change on shipping within Lake Superior and Lake Erie', in *The Potential Effects of Global Climate Change on the United States*. US Environmental Protection Agency, Washington, D.C. App. H, Infrastructure.
- Krabbenhoft, D. P. and Webster, K. E. 1995. 'Transient hydrogeological controls on the chemistry of a seepage lake', *Wat. Resour. Res.*, **31**, 2295–2305.
- Kratz, T. K., Webster, K. E., Bowser, C. J., Magnuson, J. J., and Benson, B. J. 1997. The influence of landscape position on northern Wisconsin lakes. *Freshwat. Biol.*, **37**, 209–217.
- Kunkel, K. E., Mortsch, L. D., and Lewis, P. 1993. 'The climate of the Great Lakes — St. Lawrence Basin', in Lee, D. H. (Ed.), *Climate, Climate Change, Water Level Forecasting and Frequency Analysis*, Final Report of Task Group 2 Working Committee 3 for the IJC Levels Reference Study, Phase II, Vol. 1. pp. 5–14.
- Lazerte, B. D. 1993. 'The impact of drought and acidification on the chemical exports from a minerotrophic conifer swamp', *Biogeochemistry*, **18**, 153–175.
- Leino, R. L. and McCormick, J. H. 1993. 'Responses of juvenile largemouth bass to different pH and aluminum levels at overwintering temperatures: effects on gill morphology, electrolyte balance, scale calcium, liver glycogen, and depot fat', *Can. J. Zool.*, **71**, 531–543.
- Lenihan, J. M. and Neilson, R. P. 1994. 'A rule-based vegetation formation model for Canada', *J. Biogeogr.*, **20**, 615–628.
- Lewis, C. F. M. and Anderson, T. W. 1989. 'Oscillations of levels and cool phases of the Laurentian Great Lakes caused by inflows from glacial lakes Agassiz and Barlow-Ojibway', *J. Paleolimnol.*, **2**, 99–146.
- Lewis, C. F. M. and Anderson, T. W. 1992. 'Stable isotope (O and C) and pollen trends in eastern Lake Erie, evidence for a locally induced climate reversal of Younger Dryas age in the Great Lakes basin', *Climate Dynam.*, **6**, 241–250.
- Lin, P. 1995. 'Adaptations to temperature in fish: salmonids, centrarchids and percids', *PhD Thesis*, University of Toronto, Canada. p. 170.
- Liu, K. B. 1990. 'Holocene paleoecology of the boreal forest and Great Lakes — St. Lawrence forest in Northern Ontario', *Ecol. Monogr.*, **60**, 179–212.
- Lodge, D. M. 1993. 'Species invasions and deletions: community effects and responses to climate and habitat change', in Kareiva, P. M., Kingsolver, J. G., and Huey, R. B. (Eds), *Biotic Interactions and Global Change*, Sinauer Associates Inc., Sunderland, MA, pp. 367–387.
- Magnuson, J. J. 1976. 'Managing with exotics — a game of chance'. *Trans. Am. Fish. Soc.*, **105**, 1–9.
- Magnuson, J. J. and DeStasio, B. T. 1996. Thermal niche of fishes and global warming', in Wood, C. M. and McDonald, D. G. (Eds), *Global Warming — Implications for Freshwater and Marine Fish*, SEB Seminar Series. Cambridge University Press, Cambridge. pp. 377–408.
- Magnuson, J. J., Crowder, L. B., and Medvick, P. A. 1979. 'Temperature as an ecological resource', *Am. Zool.*, **19**, 331–343.
- Magnuson, J. J., Regier, D. K., Holmes, H. A., Meisner, J. D., and Shuter, B. J. 1989. 'Potential responses of Great Lakes fishes and their habitat to global climate warming', in Smith, J. B. and Tirpak, D. A. (Eds), *The Potential Effects of Global Climate Change on the United States*. Environmental Protection Agency, EPA-230-05-89-055, Washington, D.C. App. E, Aquatic Resources.
- Magnuson, J. J., Meisner, J. D., and Hill, D. K. 1990. 'Potential changes in the thermal habitat of Great Lakes fish after global climate warming', *Trans. Am. Fish. Soc.*, **119**, 254–264.
- Manabe, S. and Stouffer, R. J. 1980. 'Sensitivity of a global climate model to an increase of CO₂ concentration in the atmosphere', *J. Geophys. Res.*, **85**, 5529–5554.
- Mandrak, N. E. 1989. 'Potential invasion of the Great Lakes by fish species associated with climate warming', *J. Great Lakes Res.*, **15**, 306–316.
- Maykut, G. A. and Untersteiner, N. 1971. 'Some results from a time dependent thermodynamic model of sea ice', *J. Geophys. Res.*, **76**, 1550–1575.
- McAndrews, J. H. and Campbell, I. D. 1993. 'The mean July temperature in Eastern Canada from Bartlein and Webb's (1985) pollen transfer functions: comments and illustrations', in Tekla, A. (Ed.), *Proxy Climate Data and Models of the Six Thousand Years Before Present Time Interval: The Canadian Perspective*, Canadian Global Climate Change Program Incidental Report Series No. IR93-3. The Royal Society of Canada. pp. 22–25.
- McCormick, M. J. 1990. 'Potential changes in thermal structure and cycle of Lake Michigan due to global warming', *Trans. Am. Fish. Soc.*, **119**, 183–195.
- McFadden, J. D. 1965. 'The interrelationship of lake ice and climate in central Canada', *Technical Report Number 20*. Department of Meteorology, University of Wisconsin–Madison. 115 pp.
- McFarlane, N. A. 1991. 'The Canadian Climate Centre second-generation global circulation model', in Sanderson, M. (Ed.), *Proceedings, Symposium on Climate Scenarios*. University of Waterloo, Waterloo. pp. 3–15.
- McFarlane, N. A., Boer, G. J., Blanchet, J.-P., and Lazare, M. 1992. 'The Canadian Climate Centre second generation general circulation model and its equilibrium climate', *J. Climate*, **5**, 1013.
- McIver, D. L. and Isaac, J. L. 1989. *Bioclimatic profiles for Canada, 1951–80*. Canadian Climate Centre, Environment Canada.

- McLain, A. S., Magnuson, J. J., and Hill, D. K. 1994. 'Latitudinal and longitudinal differences in thermal habitat for fishes influenced by climate warming: expectations from simulations', *Verh. Int. Verein. Limnol.*, **25**, 2080–2085.
- Meisner, J. D. 1990. 'Potential loss of thermal habitat for Brook Trout, due to climatic warming, in two southern Ontario streams', *Trans. Am. Fish. Soc.*, **119**, 282–291.
- Meisner, J. D., Goodier, J. L., Regier, H. A., Shuter, B. J., and Cristie, W. J. 1987. 'Lab assessment of climate warming on Great Lakes basin fishes', *J. Great Lakes Res.*, **13**, 340–352.
- Meisner, J. D., Rosenfeld, J. S., and Regier, H. A. 1988. 'The role of groundwater in the impact of climate warming on stream salmonines', *Fisheries*, **13**, 2–8.
- Mekis, E. and Hogg, W. D. 1997. 'Rehabilitation and analysis of Canadian daily precipitation time series', *J. Climate*, in press.
- Melo, O. T. 1989. 'Electric supply and demand in Ontario', in *Report of the First U.S.-Canada Symposium on Impacts of Climate Change on the Great Lakes Basin*, Sept. 27–29, 1988. Oak Brook, Illinois. pp. 134–143.
- Metcalfe, J. R., Ishida, S., and Goodison, B. E. 1994. 'A corrected precipitation archive for the Northwest Territories', *Environment Canada–Mackenzie Basin River Study, Interim Report #2*. 110–117.
- Meyer, J. L. and Pulliam, W. M. 1992. 'Modification of terrestrial-aquatic interactions by a changing climate', in Firth, P. and Fisher, S. G. (Eds), *Global Climate Change and Freshwater Ecosystems*. Springer-Verlag, New York. pp. 177–191.
- Mierle, B. and Ingram, R. 1991. 'The role of humic substances in the mobilization of mercury from watersheds', *Water Air Soil Pollut.*, **56**, 349–357.
- Minns, C. K. and Moore, J. E. 1995. 'Factors limiting the distributions of Ontario's freshwater fishes: the role of climate and other variables, and the potential impacts of climate change', in Beamish, R. J. (Ed.), *Climate Change and Northern Fish Populations. Can. Spec. Publ. Fish. Aquat. Sci.*, **121**, 137–160.
- Minns, C. K., Randall, R. G., Chadwick, E. M. P., Moore, J. E., and Green, R. 1995. 'Potential impact of climate change on the habitat and population dynamics of juvenile Atlantic salmon (*Salmon salar*) in eastern Canada', in Beamish, R. J. (Ed.), *Climate Change and Northern Fish Populations. Can. Spec. Publ. Fish. Aquat. Sci.*, **121**, 699–708.
- Moore, M. V., Folt, C. L., and Stemberger, R. S. 1995. 'Consequences of elevated temperatures for zooplankton assemblages in temperate lakes', *Arch. Hydrobiol.*, **268**, 1–31.
- Moore, M. V., Pace, M. L., Mather, J. R., Murdoch, P. S., Howarth, R. W., Folt, C. L., Chen, C. Y., Hemond, H. F., Flebbe, P. A., and Driscoll, C. T. 1997. Potential effects of climate change on freshwater ecosystems of the New England/Mid Atlantic region', *Hydrol. Process.*, **11**, 925–947.
- Mortsch, L. D. (Ed.) (1990) *Eastern Canadian Boreal and Sub-Arctic Wetlands: A Resource Document*. Atmospheric Environment Service, Environment Canada, Climatological Studies No. 42. 169 pp.
- Mortsch, L. D. and Quinn, F. H. 1996. 'Climate change scenarios for the Great Lakes Basin ecosystem studies', *Limnol. Oceanogr.*, **41**, 903–911.
- Mott, R. J., Grant, D. R., Stea, R. R., and Occhietti, S. 1986. 'A late glacial climatic oscillation in Atlantic Canada — an Allerod/Younger Dryas equivalent', *Nature*, **323**, 247–250.
- Overpeck, J. T., Rind, D., and Goldberg, R. 1990. 'Climate-induced changes in forest disturbance and vegetation', *Nature*, **343**, 51–53.
- Parkinson, C. L. and Washington, W. M. 1979. 'A large-scale numerical model of sea ice', *J. Geophys. Res.*, **84**, 311–337.
- Pereira, D. L., Anderson, C. S., Radomski, P. J., Sak, T., and Stevens, A. 1995a. 'Potential to index climate with growth and recruitment of temperate fish', in Beamish, R. J. (Ed.), *Climate Change and Northern Fish Populations. Can. Spec. Publ. Fish. Aquat. Sci.*, **121**, 709–717.
- Pereira, D. L., Bingham, C., Spangler, G. R., Cohen, Y., Conner, D. J., and Cunningham, P. K. 1995b. 'Growth and recruitment of freshwater drum (*Aplodinotus grunniens*) as related to long-term temperature patterns', in Beamish, R. J. (Ed.), *Climate Change and Northern Fish Populations. Can. Spec. Publ. Fish. Aquat. Sci.*, **121**, 617–629.
- Peters, R. L. 1990. 'Effects of global warming on forests', *Forest Ecol. Manage.*, **35**, 13–33.
- Phillips, D. W. 1990. *The Climates of Canada*. Supply and Services Canada. Environment Canada 176 pp.
- Phillips, D. W. and McCulloch, J. A. W. 1972. *The Climate of the Great Lakes Basin* Climatological Studies No. 20. Atmospheric Environment Service, Downsview. p. 40.
- Pickering, Q. H. 1968. 'Some effects of dissolved oxygen concentrations upon the toxicity of zinc to the bluegill, *Lepomis macrochirus* RAF', *Water Res.*, **2**, 187–194.
- Poff, J. L. 1992. 'Regional hydrologic response to climate change: an ecological perspective', in Firth, P. and Fisher, S. G. (Eds), *Global Climate Change and Freshwater Ecosystems*. Springer-Verlag, New York. pp. 88–115.
- Post, W. M., Pastor, J., King, A. W., and Emanuel, W. R. 1992. 'Aspects of the interaction between vegetation and soil under global change', *Water Air Soil Pollut.*, **64**, 345–363.
- Quinn, F. H. 1981. 'Secular changes in annual and seasonal Great Lakes precipitation, 1854–1979, and their implications for Great Lakes water resource studies', *Wat. Resour. Res.*, **17**, 1619–1624.
- Quinn, F. H. and Norton, D. C. 1982. 'Great Lakes precipitation by months, 1900–1980', *NOAA Data Report ERL GLERL-20*. p. 29.
- Rastetter, E. B., McKane, R. B., Shaver, G. R., and Melillo, J. M. 1992. 'Changes in C storage by terrestrial ecosystems: how C–N interactions restrict responses to CO₂ and temperature', *Water Air Soil Pollut.*, **64**, 327–344.
- Regier, H. A., Holmes, J. A., and Pauly, D. 1990a. 'Influence of temperature changes on aquatic ecosystems: an interpretation of empirical data', *Trans. Am. Fish. Soc.*, **119**, 374–389.
- Regier, H. A., Magnuson, J. J., and Coutant, C. C. (Convenors), 1990b. 'Symposium on effects of climate change on fish, Proceedings', *Trans. Am. Fish. Soc.*, **119**, 173–389.
- Regier, H. A., Lin, P., Ing, K. K., and Wichert, G. A. 1996. 'Likely responses to climate change of fish associations in the Laurentian Great Lakes: concepts, methods and findings', *Boreal Env. Res.*, **1**, 1–15.
- Reinert, R. E., Stone, L. J., and Willford, W. A., 1974. 'Effect of temperature on accumulation of methylmercuric chloride and p,p' DDT by rainbow trout (*Salmo gairdneri*)', *J. Fish. Res. Bd Can.*, **31**, 1649–1652.

- Reycraft, J. and Skinner, W., 1993. 'Canadian lake ice conditions: an indicator of climate variability', *Climatic Persp.*, **15**, 9–15.
- Rizzo, B. W. and Wilken, E. 1992. 'Assessing the sensitivity of Canada's ecosystems to climatic change', *Climatic Change*, **21**, 37–55.
- Robertson, D. M., Ragotzkie, R. A., and Magnuson, J. J. 1992. 'Lake ice records used to detect historical and future climate changes', *Climatic Change*, **21**, 407–427.
- Rosenberg, N. J., Kimball, B. A., Martin, P., and Cooper, C. F. 1990. 'From Climate and CO₂ enrichment to evapotranspiration', in Waggoner, P. E. (Ed.), *Climate Change and U.S. Water Resources*. Wiley, New York. pp. 151–175.
- Rowe, J. S. 1977. *Forest Regions of Canada*. Department of Fisheries and the Environment, Canadian Forestry Service, Publication 1300. p.172.
- St Louis, V. L., Rudd, J. W. M., Kelley, C. A., Beaty, K. G., Bloom, N. S., and Flett, R. J. 1994. 'Importance of wetlands as sources of methyl mercury to boreal forest ecosystems', *Can. J. Fish. Aquat. Sci.*, **51**, 1065–1076.
- Schindler, D. W. 1977. 'Evolution of phosphorus limitation in lakes: natural mechanisms compensate for deficiencies of nitrogen and carbon in eutrophied lakes', *Science*, **195**, 260–262.
- Schindler, D. W. 1997. 'Widespread effects of climatic warming on freshwater ecosystems', *Hydrol. Process.*, **11**, 1043–1067.
- Schindler, D. W. and Fee, E. J. 1973. 'Diurnal variation of dissolved inorganic carbon and its use in estimating primary production and CO₂ invasion in Lake 227', *J. Fish. Res. Bd Can.*, **30**, 1501–1510.
- Schindler, D. W., Frost, V. E., and Schmidt, R. V. 1973. 'Production of epilithiphyton in two lakes of the Experimental Lakes Area, northwestern Ontario', *J. Fish. Res. Bd Can.*, **30**, 1511–1524.
- Schindler, D. W., Beaty, K. G., Fee, E. J., Cruikshank, D. R., DeBruyn, E. R., Findlay, D. L., Linsey, G. A., Shearer, J. A., Stainton, M. P., and Turner, M. A. 1990. 'Effects of climatic warming on lakes of the central boreal forest', *Science*, **250**, 967–970.
- Schindler, D. W., Bayley, S. E., Parker, B. R., Beaty, K. G., Cruikshank, D. R., Fee, E. J., Schindler, E. U., and Stainton, M. P. 1996a. 'The effects of climatic warming on the properties of boreal lakes and streams at the Experimental Lakes Area, northwestern Ontario', *Limnol. Oceanogr.*, **41**, 1004–1017.
- Schindler, D. W., Curtis, P. J., Parker, B. R., and Stainton, M. P. 1996b. 'Consequences of climate warming and lake acidification for UV-B penetration in North American boreal lakes', *Nature*, **379**, 705–708.
- Schlesinger, M. and Zhao, Z. 1988. 'Seasonal climate changes induced by doubled CO₂ as simulated by the OSU atmospheric GCM/mixed-layer ocean model', *Climate Research Institute Report*. Oregon State University, Corvallis.
- Scully, N. M. and Lean, D. R. S. 1994. 'The attenuation of ultraviolet radiation in temperate lakes', *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **43**, 135–144.
- Sedell, J. R. and Dahm, C. N. 1990. 'Spatial and temporal scales of dissolved organic carbon in streams and rivers', in Perdue, E. M. and Gjessing, E. T. (Eds), *Organic Acids in Aquatic Ecosystems*. John Wiley & Sons, New York. pp. 261–279.
- Shearer, J. A., Fee, E. J., DeBruyn, E. R., and DeClercq, D. R. 1987. 'Phytoplankton primary production and light attenuation response to the experimental acidification of a small Canadian Shield lake', *Can. J. Fish. Aquat. Sci.*, **44** (Suppl. 1), 83–90.
- Shuter, B. J. and Post, J. R. 1990. 'Climate, population viability, and the zoogeography of temperature fishes', *Trans. Am. Fish. Soc.*, **119**, 314–336.
- 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.
- Sinokrot, B. A. and Stefan, H. G. 1993. 'Stream temperature dynamics: measurements and modeling', *Wat. Resour. Res.*, **29**, 2299–2312.
- Sinokrot, B. A., Stefan, H. G., McCormick, J. H., and Eaton, J. G. 1995. 'Modeling of climate change effects on stream temperatures and fish habitats below dams and near groundwater inputs', *Climatic Change*, **30**, 181–200.
- Skinner, W. R. and Gullett, D. W. 1993. 'Trends of daily maximum and minimum temperature in Canada during the past century', *Climatol. Bull.*, **27**, 63–77.
- Slivitsky, M. and Mathier, L. 1993. 'Climate changes during the 20th century on the Laurentian Great Lakes and their impacts on hydrologic regime', in Duckstein, L. and Parent, E. (Eds), NATO Advanced Studies Institute Series, Series E-Vol. 275, Kluwer, pp. 235–251.
- Smayda, T. J. 1980. 'Phytoplankton species succession', in Morris, I. (Ed.), *The Physiological Ecology of Phytoplankton*. University of California Press, Berkeley. pp.493–570.
- Smith, J. B. 1991. 'The potential impacts of climate change on the Great Lakes', *Bull. Am. Meteorol. Soc.*, **72**, 21–28.
- Smith, V. H. 1991. 'Competition between consumers', *Limnol. Oceanogr.*, **23**, 707–712.
- Smol, J. P. 1982. 'Postglacial changes in fossil algal assemblages from three Canadian lakes', *PhD Thesis*, Queen's University, Kingston, Ontario, Canada. p.151.
- Smol, J. P. and Boucherle, M. M. 1985. 'Postglacial changes in algal and cladoceran assemblages in Little Round Lake, Ontario', *Arch. Hydrobiol.*, **103**, 25–49.
- Sreenivasa, M. R. and Duthie, H. C. 1973. 'The postglacial diatom history of Sunfish Lake, southwestern Ontario', *Can. J. Bot.*, **51**, 1599–1609.
- Stefan, H. G. and Fang, X. 1994. 'Model simulations of dissolved oxygen characteristics of Minnesota lakes: past and future', *Environ. Manage.*, **18**, 73–92.
- Stefan, H. G. and Fang, X. 1995. 'A methodology to estimate year-round effects of climate change on water temperature, ice and dissolved oxygen characteristics of temperate zone lakes with application to Minnesota', *Project Report 377*. St. Anthony Falls Lab, Univ. of Minnesota, Minneapolis.
- Stefan, H. G. and Preud'homme, E. B. 1993. 'Stream temperature estimation from air temperature', *Wat. Res. Bull.*, **29**, 27–45.
- Stefan, H. G. and Sinokrot, B. A. 1993. 'Projected global climate change impact on water temperatures in five north central U.S. streams', *Climatic Change*, **24**, 353–381.
- Stefan, H. G., Hondzo, M., and Fang, X. 1993a. 'Lake water quality modeling for projected future climate scenarios', *J. Environ. Qual.*, **22**, 417–431.

- Stefan, H. G., Eaton, J. G., Hondzo, M., Goodno, B. E., Fang, X., Hokanson, K. E. F., and McCormick, J. H. 1993b. 'A methodology to estimate global climate-change impacts on lake waters and fisheries in Minnesota', in Ballentine, J. M. and Stakhiv, E. Z. (Eds), *Proc. First Natl. Conf. on Climate Change and Water Resources Mgt.* US Army Corps Eng., IWR Report 93-R-17. p. II.177–192.
- Stefan, H. G., Hondzo, M., Eaton, J. G., and McCormick, J. H. 1995. 'Predicted effects of global climate on fishes in Minnesota lakes', in Beamish, R. J. (Ed.), *Climate Change and Northern Fish Populations. Can. Spec. Publ. Fish. Aquat. Sci.*, **121**, pp. 57–72.
- Stefan, H. G., Hondzo, M., Fang, X., Eaton, J. G., and McCormick, J. H. 1996. 'Simulated long-term temperature and dissolved oxygen characteristics of lakes in the north-central U.S. and associated fish habitat limits', *Limnol. Oceanogr.*, **41**, 1124–1135.
- Stemberger, R., Herlihy, A. T., Kugler, D. L. and Paulsen, S. G. 1996. 'Climatic forcing on Zooplankton richness in lakes of the northeastern United States', *Limnol. Oceanogr.*, **41**, 1093–1101.
- Sterner, R. W., Hagemeyer, D. D., Smith, W. L., and Smith, R. F. 1993. 'Phytoplankton nutrient limitation and food quality for *Daphnia*', *Limnol. Oceanogr.*, **38**, 857–871.
- Stirling, G. and McQueen, D. J. 1986. 'The influence of changing temperature on the life history of *Daphniopsis ephemeralis*', *J. Plankton Res.*, **8**, 583–595.
- Swackhamer, D. L. and Skoglund, R. S. 1991. 'The role of phytoplankton in the partitioning of hydrophobic organic contaminants in water', in Baker, R. A. (Ed.), *Organic Substances and Sediments in Water.* Lewis Publishers, Chelsea, Michigan. pp. 91–105.
- Taylor, W. W., Smale, M. A., and Freeberg, M. H. 1987. 'Biotic and abiotic determinants of lake whitefish (*Coregonus clupeaformis*) recruitment in northeastern Lake Michigan', *Can. J. Fish. Aquat. Sci.*, **44**, 313–323.
- Teller, J. T. 1985. 'Glacial Lake Agassiz and its influence on the Great Lakes', in Karrow, P. F. and Calkin, P. E. (Eds), *Quaternary Evolution of the Great Lakes.* Geological Association of Canada, Special Paper 30, pp. 1–16.
- Teller, J. T. and Thorleifson, L. H. 1983. 'The Lake Agassiz–Lake Superior connection', in Teller, J. T. and Clayton, L. (Eds), *Glacial Lake Agassiz.* Geological Association of Canada, Special Paper 26, pp. 261–290.
- Terasmae, J. 1961. 'Notes on late Quaternary climatic changes in Canada', *Annales New York Acad. Sci.* **95**, 658–675.
- Tonn, W. M. 1990. 'Climate change and fish communities: a conceptual framework', *Trans. Am. Fish. Soc.*, **119**, 337–352.
- Tonn, W. M., Magnuson, J. J., Rask, M., and Toivonen, J. 1990. 'Intercontinental comparison of small-lake fish assemblages: the balance between local and regional processes', *Am. Nat.*, **136**, 345–375.
- Turner, M. A., Howell, E. T., Robinson, G. G. C., Campbell, P., Hecky, R. E., and Schindler, E. U. 1994. 'Roles of nutrients in controlling growth of epilithon in oligotrophic lakes of low alkalinity', *Can. J. Fish. Aquat. Sci.*, **51**, 2784–2793.
- Twiss, M. R. and Nalewajko, C. 1992. 'Influence of phosphorus nutrition on copper toxicity to three strains of *Scenedesmus acutus* (Chlorophyceae)', *J. Phycol.*, **28**, 291–298.
- Vanderploeg, H. A., Bolsenga, S. J., Fahnenstiel, G. L., Liebig, R. J., and Gardner, W. S. 1992. 'Plankton ecology in an ice-covered bay of Lake Michigan: utilization of a winter phytoplankton bloom by reproducing copepods', *Hydrobiologia*, **243/244**, 175–183.
- Vavrus, S. J., Wynne, R. H., and Foley, J. A. 1996. 'Measuring the sensitivity of southern Wisconsin lake ice to climate variations and lake depth using a numerical model', *Limnol. Oceanogr.*, **41**, 822–831.
- Watras, C. J., Morrison, K. A., and Host, J. S. 1995. 'Concentration of mercury species in relationship to other site-specific factors in the surface waters of northern Wisconsin lakes', *Limnol. Oceanogr.*, **40**, 556–565.
- Webb, J., III, Bartlein, P. J., and Kutzbach, J. E. 1987. 'Climatic change in eastern North America during the past 18,000 years: comparisons of pollen data with model results', in Ruddiman, W. F. and Wright, H. E., Jr. (Eds), *North America and Adjacent Oceans during the Last Deglaciation. Geology of North America*, Vol. K-3. Geological Society of America, Boulder, Colorado. pp. 142–165.
- Webster, K. E. and Brezonik, P. L. 1995. 'Climate confounds detection of chemical trends related to acid deposition in upper midwest lakes in the U.S.A.', *Water Air Pollut.*, **85**, 1575–1580.
- Webster, K. E., Newell, A. D., Baker, L. A., and Brezonik, P. L. 1990. 'Climatically induced rapid acidification of a softwater seepage lake', *Nature*, **347**, 374–376.
- Webster, K. E., Kratz, T. K., Bowser, C. J., Magnuson, J. J., and Rose, W. J. 1996. 'The influence of landscape position on lake chemical responses to drought in northern Wisconsin', *Limnol. Oceanogr.*, **41**, 977–984.
- Wentz, D. A., Rose, W. J., and Webster, K. E. 1995. 'Long-term hydrologic and biogeochemical responses of a softwater seepage lake in north central Wisconsin', *Wat. Resour. Res.* **31**, 199–212.
- Wetzel, R. G. 1992. 'Gradient-dominated ecosystems: sources and regulatory functions of dissolved organic matter in freshwater ecosystems', *Hydrobiology*, **229**, 181–198.
- Wilson, S. E., Walker, I. R., Mott, R. J., and Smol, J. P. 1993. 'Climatic and limnological changes associated with the Younger Dryas in Atlantic Canada', *Climate Dynam.*, **8**, 177–187.
- Wisconsin Department of Natural Resources, 1995. 'Wisconsin's biodiversity as a management issue', *A Report to Department of Natural Resources Managers May 1995*, Madison, Wisconsin. p. 240.
- Wong, S. C. 1979. 'Elevated atmospheric partial pressure of CO₂ and plant growth', *Oecologia*, **44**, 68–74.
- Wood, C. M. and McDonald, D. G. (Eds.) 1996. *Global Warming — Implications for Freshwater and Marine Fish.* SEB Seminar Series, Cambridge University Press, Cambridge.
- Wynne, R. H. and Lillesand, T. M. 1993. 'Monitoring phenological changes in lake ice as a robust indicator of regional climate change using the AVHRR', *Bull. Ecol. Soc. Am., Suppl.*, **74**, 495–496.
- Wynne, R. H., Magnuson, J. J., Clayton, M. K., Lillesand, T. M., and Rodman, D. C. 1996. 'Determinants of temporal coherence in the satellite-derived 1987–1994 ice breakup dates of lakes on the Laurentian Shield', *Limnol. Oceanogr.*, **41**, 832–838.
- Yan, N. D., Keller, W., Scully, N. M., Lean, D. R. S., and Dillon, P. J. 1996. 'Increased UV-B penetration in a lake owing to drought-induced acidification', *Nature*, **381**, 141–143.
- Yu, Z. and McAndrews, J. H. 1994. 'Holocene water levels at Rice Lake, Ontario, Canada: sediment, pollen and plant-macrofossil evidence', *The Holocene*, **4**, 141–152.