

Lakes as sentinels and integrators for the effects of climate change on watersheds, airsheds, and landscapes

D. W. Schindler*

Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada

Abstract

Lakes provide unique sentinels and integrators of events in their catchments and airsheds and in the total landscapes in which they are embedded. A variety of physical, chemical, and biological properties of lakes are amenable to simple, precise, and inexpensive long-term monitoring. Changes to watersheds caused by climate warming can in turn affect the properties of lakes to which they drain. Examples include changes to nutrient inputs, the balance between base cations and strong acid anions, carbon cycles, and mercury, in some cases associated with insect outbreaks and forest fires caused by warmer weather. Paleolimnology also allows integration and interpretation of changes in lakes and catchments for millennia. Such studies indicate that much drier conditions occurred in the past in central and western Canada, causing the closing of lake basins, increased salinity, eutrophication, and even the disappearance of some lakes, as forested catchments were invaded by grasslands. Such historical perspectives indicate that large areas of western Canada may be adversely affected by climate warming.

Understanding the relationships between lakes, their catchments, and their airsheds is of critical importance to predicting the quantity and quality of freshwater under the predicted climate change. Often, important effects of climate warming on lakes will be via effects on other human stressors, such as chemicals or invasive species or stresses to catchments. Lakes also have properties that allow us to use them as sentinels of stress in the terrestrial and wetland ecosystems that are found in their catchments. Here I present a number of examples of how these complex relationships can lead to surprising results and potentially serious errors in projection of the freshwater quantity and quality for future needs.

Why lakes are superior sentinels and integrators for whole landscapes

Lakes collect clues to biological and geochemical events and human perturbations in terrestrial and wetland parts of the catchment, as well as in lacustrine environments. We rely on the waters of lakes for drinking water and recreation, and in some areas lakes supply a significant source of food. Therefore, it is essential that we pay close attention to activities in the catchment that can have detrimental effects on water quality and aquatic communities. Airborne pathways for contaminants to lakes and their catchments are becoming more important as we increasingly pollute the atmosphere. Airsheds are also major vectors for carrying terrestrial prefossilized materials to lakes. Pollen, seeds, leaves, etc., that are added to the sedimentary record are important to paleoecologists who wish to deduce the state of catchments or landscapes in the distant past. Transfer of chemicals from catchments to lakes can also occur via airborne pathways. In short, to keep lakes healthy and in good condition, we must be good

stewards of both airsheds and catchments. Most lakes retain water long enough to allow integrated “signals” in the form of prefossilized materials, chemical residues, etc., to be deposited in lake muds. If sediments can be dated and fossils interpreted correctly, they are useful as both sentinels and integrators of the effects of changing climate on entire landscapes. Some examples are given below.

Several features of lakes make them excellent sites to monitor for the health of catchments and airsheds. Thanks to wind-driven water circulation, lakes have much less horizontal heterogeneity than uplands or wetlands, so that results from a few sampling points are usually representative of an entire water body.

With the exception of great lakes, lakes are also relatively easy to monitor. There are few other ecosystems where representative sampling of all trophic levels and many other ecosystem properties can be done with simple equipment.

Analytical methods for most characteristics of lakes are also very precise. Changes in water chemistry can be detected at the parts per billion, sometimes even parts per trillion, levels. Analyses are not costly. Excellent keys allow most planktonic, benthic, and fish species to be identified, and many of the key species are readily recognizable by nonspecialists.

Also, a lake keeps a library of fossils in the sediments, which allows us to analyze historical events before modern monitoring methods were developed. But caution is necessary in reading this library, because it is an incomplete representation of the ecosystem, as a result of poor preservation of many fossils and chemical signatures. Only a small percentage of aquatic organisms leave fossils, so reading the record accurately can be compared to reading a manuscript where 80% or more of the words have been randomly deleted. Like early scriptures, there can often be more than one interpretation, and some interpretations can be erroneous. The science of paleolimnology has developed

* Email address: d.schindler@ualberta.ca

considerably in recent years, and the use of multiple proxies increases the reliability of conclusions (Smol 2008).

Together, these features make lakes superior as sentinels and integrators of landscape change to any other ecosystem type on earth.

Sentinels of water quantity: lake levels and stream flows

There is some confusion over the abundance of water on the landscape and how much of it we can use if we wish to sustain the health of aquatic ecosystems. In order to sustain our “water capital” for future generations, we cannot use more than the annual “interest,” as represented by the annual runoff of water from continents to the sea, in a given year. Annual runoff from the continents is the balance between precipitation on continental landscapes minus evapotranspiration from vegetated catchments and evaporation from water surfaces. Lake levels and stream flows are therefore among the most important sentinel properties of sustainable water that we should measure, because without them we can have no idea when we begin to use more than ecosystems can supply on a long-term basis. For lakes, it is important to know the rate of outflow, because the water renewal time is an important indicator of the retention of nutrients, sulfate, and other chemicals (Schindler et al. 1978; Kelly et al. 1987). For example, most eutrophication models are based on water renewal concepts (Dillon and Rigler 1974; Vollenweider 1976; Schindler et al. 1978). Lake levels and outflows are, however, subject to considerable short-term variability, which must be properly analyzed in order to detect long-term trends. Fortunately, modern computers and time-series software make this an easy task.

Some Canadian examples—Canada provides excellent examples of how important detailed knowledge of lake levels and river flows can be, and how the lack of such knowledge can lead to huge problems. The country contains over three million lakes, including several great lakes. Canadians are always assured by the media and politicians that we have plenty of water. There is much talk of shipping water to the United States and even sending tankers of water to countries where water is scarce. Dealing in “virtual water,” via the harvesting of grain, meat, fish, hydropower, and oil for use in other countries, is a staple of the Canadian economy (Schendel et al. 2007). Canada is the world’s second largest exporter of virtual water, with 95 Gm³ yr⁻¹ used to produce the above-mentioned commodities, with little thought given to water conservation.

A closer look reveals a huge fallacy in the assumption of Canadian water abundance. Much of western Canada is subhumid to semiarid. Precipitation is low in the prairies and in the north. Fortunately, evaporation and evapotranspiration are also low, which is why lakes generally remain intact where they are not exploited by humans. Many Canadian lakes have water renewal times on the order of hundreds of years, and for a large part of the western prairies and the north, annual runoff is less than 100 mm yr⁻¹ (Hydrological Atlas of Canada 1993).

Table 1. Renewable water resources for five countries with large water supplies.

	Supply (km ³ yr ⁻¹)	% world supply
Brazil	5418	12.4
Russian Federation	4313	10.0
Canada	2850	6.5
United States	2818	6.4
People’s Republic of China	2812	6.4

Modified from Sprague (2007).

We also often hear that the United States and China are short of water. Yet the runoff per unit area of Canada, the United States, and China are nearly identical (Sprague 2007, Table 1). The subhumid to semiarid western prairies that are the source of much of Canadian agriculture have runoff that is much below the Canadian average. Much of the water that Canada has occurs in the far north, where agriculture and industry do not occur. In short, if Canada is to have adequate water for future population and economic growth, it has no water to spare. With climate warming facing the planet, it is important for Canada to develop conservation strategies to protect freshwaters supplies.

Lessons on water quantity from the past—Paleoecological studies show that even small but prolonged changes in climate can have some rather sobering effects on the water balance in lakes. The North American continent was a much drier place from 4000 to 8000 yr ago. Temperatures were very similar to temperatures in the latter years of the 20th and early years of the 21st century. The differences from recent climate were very small compared to those that are predicted to result from increased greenhouse gas emissions.

Lake Winnipeg is a great (Lake Erie-sized, 24,400 km²) lake on the eastern edge of the Interior Plains. The climate near the lake is currently subhumid. Much of the inflow enters via the Winnipeg River, which drains a forested basin containing thousands of lakes to the east and southeast of the lake. A flight over the area gives the impression that water is very plentiful. In fact, 6.5% of the surface area of Manitoba is covered by water (Statistics Canada 2005). The lake also receives the Saskatchewan River, which drains a huge, subhumid to semiarid basin to the west, originating at the continental divide in the Rocky Mountains of Alberta. In the early years of the 20th century, the Saskatchewan River’s input of water to Lake Winnipeg was greater than that of the Winnipeg River, but several large dams and hundreds of small ones, for hydroelectric power and irrigation, coupled with recent warming, decreasing snowpacks, and periods of drought, have changed the balance. Our recent analyses show that May–August flows from the Saskatchewan River into Lake Winnipeg are about 20% of the values recorded in the early years of the 20th century.

Several paleoecological studies have shown how slight changes in the balance between precipitation and evapotranspiration can dramatically change conditions in lakes. Dry conditions in the early to middle Holocene have been

explained by changes in atmospheric circulation. Drier air masses from the west appear to have blocked maritime-tropical air masses from the south more effectively than they do today (Lewis et al. 2001). During this period, the prairies expanded into areas that are now forested, reaching as far east as southern parts of the Great Lakes basin.

Lewis et al. (2001) reviewed the status of Lake Winnipeg in the Holocene. They found evidence that the south basin of the lake was desiccated and the north basin much reduced in size. During this period, grasslands surrounded the south basin and much of the north basin of the lake. Lewis et al. (2001) deduced likely climatic conditions at that time by comparing pollen remains in lake sediments from that period to those of contemporary plant communities. The climate near the south basin of Lake Winnipeg in the middle Holocene was similar to that of Medicine Hat, Alberta, in the 20th century. The latter area has been termed the "Empire of Dust" for the unsuccessful attempts by Europeans to turn its semiarid terrain into productive agricultural land in the early 20th century (Jones 2002). The climate of the middle-north basin was deduced to be similar to that of present day Saskatoon, at the prairie-forest boundary, a region where average precipitation is generally limiting to growth of terrestrial plants, and where many lakes are closed basins or have long water renewal times. Lewis et al. (2001) calculated that the south basin of the lake had a climate where precipitation minus potential evapotranspiration ($p - ep$) was 480–490 mm less than at present. For the north basin $p - ep$ was 170–360 mm less than it is today. These conditions appear to have lasted for about 3500 yr, from 7500 yr to 4000 yr B.P. Of course, when the basins of the lake were without outflow, salinity would have increased very rapidly. Eventually, glacial rebound and a more humid climate connected the two basins of the lake.

Lake Manitoba, a great lake by most standards at 4624 km², was almost totally desiccated in the same period (Teller and Last 1982). There were few wetlands in the southern prairies during that period, and ¹⁴C analyses of basal peat in contemporary wetlands indicate that many were formed only 3000 to 4000 yr ago (Zoltai and Vitt 1990). Studies of fossils in lake sediments (Fritz et al. 2000; Laird et al. 2003) show that long and severe droughts also characterized the western prairies in most centuries before the 20th. Clearly, the western prairies were a very dry place in most centuries before the 20th, at temperatures much cooler than those that are expected to occur in the next several hundred years, due to the expected increases and long atmospheric lives of major greenhouse gases.

Conditions were little better farther to the east. It had been widely assumed that lakes of eastern Canada flowed to the sea since glaciers melted, because contemporary climates are quite humid. More recent work indicates that this is untrue. In the Experimental Lakes Area (ELA), Laird and Cumming (2008) discovered that in the mid-Holocene, lake levels were several meters below current levels, well below levels that would allow lakes to drain. This area is within the Winnipeg River drainage, which empties into Lake Winnipeg, so that is not surprising given the lake levels as described above. In more recent studies,

Croley and Lewis (2006) and Lewis et al. (in press) deduced that even the St. Lawrence Great Lakes were closed basins in the middle Holocene. The level of Lake Huron was tens of meters below the current outflow. Water loss by evaporation would have rendered the lakes much more saline than they are today. Bands of ferrous sulfide in the lake sediments deposited at that time indicate that anoxia was more common than it is today. These observations fit well with the climate models of McCormick (1990), who projected that a twofold increase in CO₂ would cause a reduction in large-scale mixing and a loss of dissolved oxygen in bottom waters. Of course, increased anoxia and reducing conditions in many lakes would aggravate the return of phosphorus from lake sediments, enhancing eutrophication. The decline and loss of water renewal would also be expected to enhance eutrophication by causing increased nutrient retention, as discussed later.

All of the lake conditions described above occurred under climate conditions only slightly cooler but drier than at present. Evaporation would have been lower than in the 20th century, and certainly much lower than at the temperatures predicted by current greenhouse models. Unless there are huge increases in precipitation (not predicted by current models), the water balance of midcontinental lakes will be adversely affected by the future warmer climates. Longer open water seasons and warmer water temperatures will occur due to warming induced by greenhouse gases. Long-term trends in lake levels and stream flows are therefore very important integrators of variation in water balances and sentinels of impending water scarcity.

Taken together, physical studies indicate a bleak future for Canadian freshwater supplies and the organisms, societies, and industries that depend on them, with a rapidly warming climate. Earlier snow melts, earlier ice-out in spring, and dwindling glacial flows will change the seasonality of flows and disrupt usual biological patterns (Hari et al. 2006; Winder et al. 2009). We have already seen changes. In the western prairies, average annual temperatures have increased by 2–3°C in the past 40 yr. Annual river flows have declined (Rood et al. 2005), most dramatically in summer (Schindler and Donahue 2006; Rood et al. 2008). There is less snow, and spring melt is occurring earlier (Schindler and Donahue 2006). Lake levels in most closed basins have declined (Van der Kamp et al. 2008). Other lakes became nearly closed basins in the latter years of the 20th century. For example, outflow from Lake Wabamun, a popular recreational site west of Edmonton, ceased in 1993 and did not resume until 2006. Salinity in the lake increased by 20% during the period, partly the result of evaporation, but partly the result of salts from a water treatment plant that was built to artificially restore lake levels by using water from the North Saskatchewan River (Schindler et al. 2004).

Climate warming will cause changes to lake levels and flow regimes that will translate to huge financial losses to hydroelectric generation, irrigated agriculture, fisheries, and other industries (Bruce and Tin 2006). The effects on society could be expensive, perhaps catastrophic. Clearly, measurements of lake levels and stream flows are sentinels for many important events that reach well beyond the

bodies of water themselves. They should be among the highest priority sentinel measurements that we make.

Water quality: effects of climate warming on lake chemistry via lake-catchment interactions

Landscape carbon sources and lakes: a pivotal relationship—The transparency of many oligotrophic lakes appears to be a precarious balance between supplies of chromophoric dissolved organic matter (CDOM; typically measured as its dissolved organic carbon content, DOC) from catchments and in situ destruction by photobleaching, microbial and photodegradation, flocculation, and other processes (Dillon and Molot 1997a; Schindler and Curtis 1997). A survey of recent works indicates that we do not understand all facets of this balance and that it is sensitive to regional climates and interactions with other human effects on lakes.

CDOM acts as an important “sunscreen,” limiting the penetration of ultraviolet (UV) and visible wavelengths of solar radiation (Scully and Lean 1994). It thus controls both the depth of the euphotic zone in lakes where particulate matter is low and the depth to which harmful effects of UV can reach. In general, we have found that the supply of CDOM to lakes is in direct proportion to runoff volume (Schindler et al. 1992), although some studies have found the opposite (reviewed by Tranvik et al. 2009). Lakes receiving less CDOM become clearer, with deeper thermoclines as inflow to and outflow from lakes dwindles (Schindler et al. 1996a,b; Gunn et al. 2001). The resulting longer residence time simply allows CDOM to be more effectively degraded in situ, as evidenced by a declining ratio of DOC in outflow to that in inflow (D. W. Schindler et al. 1997). This is the result of increased photobleaching of chromophoric compounds and photodegradation of DOC in situ (Dillon and Molot 1997a). Decreased input of CDOM under drought conditions is also a factor affecting lake clarity (D. W. Schindler et al. 1997). As catchments become drier, wetlands and wet soils become less connected with streams as water levels in aquifers decline. As a result, there is less inflow of new CDOM. With increased residence times of both water and CDOM, the amount and condition of DOC is increasingly determined by in situ processes. Lakes that have been closed basins for some time have very high concentrations of very well bleached but highly refractory DOC (Curtis and Adams 1995; Arts et al. 2000). Hence, the usual assumption that lakes with high DOC are well protected from damaging UV radiation is not valid in lakes that have been closed basins for long periods. In order to correctly predict what the effects of climate warming will be, we need to better understand the delicate balance between qualitative and quantitative aspects of DOC input and outflow, and the time constants for photobleaching, microbial degradation, and flocculation processes.

Another factor that affects the CDOM input to lakes is the proportion of wetlands in the catchment (Dillon and Molot 1997b; Creed et al. 2003). Wetlands generally dry out as climate warms. In addition, human destruction of wetlands is pervasive. Most settled landscapes in Canada have had 70% or more of their wetlands drained or filled

(Natural Resources Canada 2004). In short, climate warming and wetland destruction together are reducing the ability of catchments to produce the sunscreen that protects aquatic organisms from UV radiation.

Recently Creed et al. (2008) have shown that DOC loading to headwater lakes of the Precambrian Shield can be predicted from simple digital terrain analysis models. Elevation alone was able to explain 63% of the variance in measured DOC. When simple regional climatic indicators were added (growing degree days, runoff coefficients), the variance explained increased to 89%. The database included sites with a wide variety of temperature and precipitation conditions. Thus, very simple models may allow prediction of the vulnerability of lakes to UV under a warming climate. It will be important to develop such models for a wide variety of areas.

The combination of increased surface temperatures, which will increase the stability of thermal stratification, and clearer water resulting from removal and bleaching of CDOM will greatly change the UV exposure of organisms. Recently, it has been shown that transient thermoclines play an important role in UV exposure of planktonic organisms, by trapping them in near-surface light for unpredictable periods that can last up to several hours (Xenopoulos and Schindler 2001; Xenopoulos et al. in press). The rate of change in water density increases rapidly with increasing temperature.

Recent studies have predicted that water temperatures in northern North America could increase as much as 6°C (Poff et al. 2002). A lake that has had surface temperatures of 20–22°C in the 20th century might increase to 26–28°C. The latter temperatures are well above the lethal temperatures for lake trout, whitefish, and many other cold stenotherms. Such a warming would also increase the density gradient through the thermocline by about 30%. The frequency and duration of transient thermocline should also increase unless there are offsetting increases in wind velocity.

The effect of climate on the relationship between DOC, stratification, and UV exposure complicates other interactions between lakes and their catchments. In catchments that contain forests and wetlands, several changes to chemical yields have been documented as a result of climate warming and the resulting forest fires. These include changes to nutrient inputs and the resulting productivity of lakes (Schindler et al. 1996a).

Another pathway that requires more exploration is the increasing acute toxicity of some polycyclic aromatic hydrocarbons (PAHs) under exposure to UV radiation (Bowling et al. 1983). For many years the biochemical mechanisms producing the toxicity were not understood, but recent work indicates that increased production of reactive oxygen species and lipid peroxidation occurs in fish (Choi and Oris 2000).

Another important function of lakes in the carbon cycles of landscapes is as repositories (sinks) and exchangers for terrestrial carbon, including dissolved inorganic and particulate forms as well and as DOC. Cole et al. (2007) calculate that as global averages, lakes receive 1.9 Pg C yr⁻¹ from terrestrial systems, burying 0.2 Pg in sediments, releasing 0.8 Pg to the atmosphere, and sending 0.9 Pg to

the oceans via rivers. While these numbers are quite rough, they indicate that lakes play a major role in global carbon budgets. For the boreal forest, lakes have been ignored in carbon budgets, although they make up 10–15% of the surface area of most boreal landscapes. Most studies have calculated that the boreal forest is either a small source or a small sink of CO₂ (Goodale et al. 2002). If lakes were properly accounted for, most boreal landscapes would probably be net sources, because much of the CO₂ emitted from their surfaces originates from terrestrial vegetation that is decomposing in the lake. For example, average losses of DOC to lakes from terrestrial catchments at ELA are 4–9 g C m⁻² yr⁻¹. Dillon and Molot (1997b) gave similar rates, 1–9 g C m⁻² yr⁻¹. Studies at both sites indicate that on average, 50–80% of the entering DOC is either sedimented or released to the atmosphere (Dillon and Molot 1997a; Schindler and Curtis 1997). Beaver ponds may be even more important, releasing up to 200 g C m² y⁻¹, as both CO₂ and methane (Roulet et al. 1997).

The fluxes of carbon to and from lakes probably differ greatly between lakes and regions. It will be important to understand these differences and how they will change under the combination of climate warming and other human insults. For example, both eutrophication (Schindler et al. 1975) and changes to food webs caused by removal of piscivorous predators (D. E. Schindler et al. 1997) can reverse the direction of carbon exchange with the atmosphere, effectively making lakes sinks rather than sources of carbon. Both insults are widespread problems (Post et al. 2002; Schindler and Vallentyne 2008). Conversely, reservoir construction can vastly increase the loss of carbon to the atmosphere, both as CO₂ and as methane (Kelly et al. 1997; St. Louis et al. 2000; International Rivers Network 2006; Kemenes et al. 2007). Despite several papers on the topic, hydroelectric power is still regarded as greenhouse gas-free power by most politicians and regulators. Clearly, not only climate change but also its interaction with other aspects of global change will have important bearing on how lakes affect global carbon cycles.

The role of methane in the exchange of carbon between catchments, lakes, and the atmosphere requires further investigation. In addition to its importance in reservoirs as mentioned above, recent studies show that it is released from the thaw lakes that occur as permafrost melts (Walter et al. 2006), accounting for up to 14% of ecosystem carbon balance (Christian et al. 2008). Direct emission of methane to the atmosphere via ebullition from epilimnion sediments has recently been found to be a surprisingly important carbon pathway (Bastviken et al. 2008). While the carbon pathways leading to methane production have not been well studied, presumably a good part of methane emitted to the atmosphere from lakes can also be traced to organic matter produced in the terrestrial catchments of lakes.

Lake acidity—Climate affects the balance between base cations and strong acid anions: The pH and alkalinity of lakes are largely a balance between geochemical and biological processes that produce and consume base cations and strong acid anions, in the airsheds and catchments, as well as within lakes. In addition, changes in particular

biologically important ions such as ammonium, nitrate, and bicarbonate can be important.

The responses and interactions of catchments and lakes at ELA during a 20-yr period of warming and drying show how complicated the response to climate warming can be. Boreal forested catchments usually retain the strong acid anions sulfate and nitrate. The former is sequestered by reduction to sulfide and sedimentation with ferrous iron in anoxic wetlands and wet soils. The latter is consumed by growing vegetation or perhaps denitrified, although there are few rates available (Menyailo and Krasnoshchekov 2004). Under climate warming and drought, much of the sequestered sulfur is reoxidized, resulting in acid pulses in streams during subsequent flow events (Bayley et al. 1992a; Lazerte 1993; Eimers et al. 2007). In contrast, base cation yields appear to diminish under drought conditions. Weathering and stream transport are both reduced in dry catchments. As a result of these two processes, to maintain charge balance streams become more acidic (Schindler et al. 1996a; Parker et al. in press). Similar reactions to drought have been observed at the Dorset catchments in eastern Ontario (Lazerte 1993; Eimers et al. 2007), and I assume that they are widespread in lakes and catchments.

In contrast to their catchments, ELA lakes have sediments that are sources of base cations to overlying water, due to mineralization in sediments (Anderson and Schiff 1987). Lakes also sequester the strong acid anions sulfate and nitrate. The former is microbially reduced to sulfide under anoxic conditions in lake sediments, followed by sedimentation as FeS, if sufficient iron is present (Rudd et al. 1986). As in the catchments, most nitrate is consumed by vegetation, because denitrification is very low (Chan and Campbell 1980). In most circumstances, alkalinity-generating processes in lakes outstrip alkalinity-consuming processes in catchments (Schindler et al. 1996a). Under drought conditions, it is possible for streams to become more acidic while the lakes to which they drain become more alkaline (Schindler 1997).

Recent studies show that calcium concentrations in some soft-water lakes are low enough to limit the distribution of some invertebrates, such as crustacean zooplankton (Jeziorski and Yan 2006). Calcium concentrations in some regions are declining enough to cause losses of some crustaceans (Jeziorski et al. 2008) and probably mollusks. The reasons appear to be complex interactions between airsheds, catchments, and lakes. In many areas, base cations in soils have become depleted from decades of acidic deposition. Entering hydrogen ions simply exchange for exchangeable base cations, which are lost in proportion to the runoff of strong acid anions (Neary and Dillon 1988; Likens et al. 1998; Gbondo-Tugbawa and Driscoll 2003).

Clear-cutting can also exacerbate losses of calcium and other base cations (Watmough et al. 2004). Parker et al. (in press) show that there has been a long-term decline in calcium and other base cations in precipitation at ELA, an area with neither logging or high acidic deposition. It is hypothesized that increased use of low tillage agricultural practices in the nearby Lake Agassiz basin of Minnesota and Manitoba may be responsible for the decline. In short, it is clear that concentrations of base cations, as well as the balance between

base cations and strong acid anions, are sensitive to climate change. The results can be important for the nutrient regimes of biota, and are therefore important sentinels to measure.

Effects of climate on nutrient balances—As mentioned early in the paper, the productivity and trophic state of lakes is a balance between nutrient supplies and water renewal, which cause washout of nutrients. In natural headwater lakes, precipitation on lake surfaces and runoff from terrestrial catchments both contribute phosphorus and nitrogen to lakes (Parker et al. in press). Under drought, inputs of nutrients decline, but in-lake retention increases. The response of the lake is determined by the balance between these two processes. The above-mentioned 20-yr period of warming and drought at ELA caused Lake 239 to slowly become more oligotrophic because the input of phosphorus declined as a result of increased periods when input streams did not flow. Retention of nutrients also increased, but not enough to fully compensate for lost inputs. As a result of declining phosphorus, phytoplankton standing crop also declined (Schindler et al. 1996a).

In contrast, point sources of nutrients directly to lakes, such as sewage outfalls, do not vary with runoff conditions. In this case, decreasing water renewal rates can cause higher nutrient concentrations in receiving lakes, as a result of increased nutrient retention. The result is that lakes become more eutrophic. Warmer conditions may also exacerbate many of the symptoms of eutrophication, such as increased cyanobacterial blooms and increased hypolimnetic oxygen depletion caused by longer periods of stratification (Schindler 2001).

Eutrophication is widespread in inhabited regions of the Earth, and in general climate warming will exacerbate the eutrophication problem (Schindler and Vallentyne 2008). The most important sentinels will be phosphorus and nitrogen concentrations and the measures of water renewal discussed above.

Forest fires add unpredictability to the effects of climate change on lake—Climate warming is predicted to cause a considerable increase in the incidence of forest fire in western and northern North America (Amiro et al. 2002; Flannigan et al. 2005). These estimates may be very conservative, because they were made before the recent widespread devastation of western forests caused by mountain pine beetle and spruce beetle had occurred. The beetle increase has been attributed to the increasing frequency of warm winter temperatures, which have allowed better survival of beetle larvae. The resulting expanses of dead trees have already converted forests from net sinks to net sources of carbon (Kurz et al. 2008). They provide increased fuel loads over vast areas, and severe forest fires are almost certain to follow within a few years, further increasing their strength as sources.

Forest fires in the catchments of lakes and streams vastly change the relationships between lakes and catchments. Physical effects of fire on small lakes include increased wind stress, which can deepen thermoclines, increase turbidity, and increase the height of surface waves (Parker et al. in press). The increased wind velocity at the surface

would be expected to enhance gas exchange in lakes. The effects appear to diminish in importance for lakes with surface areas over 5 km², where protection by shoreline vegetation is less important (Fee et al. 1996).

Forest fires also increase the export of nitrogen and phosphorus to lakes (Wright 1976). The effects are short lived. At ELA, exports of nutrients had declined after 3 yr as forests regenerated (Bayley et al. 1992b).

Under most conditions, mercury deposited from the atmosphere is retained in wetlands and wet soils of catchments, where it is bound to reduced sulfur in organic matter (Grigal 2003). This binding can be disrupted by fire. A forest fire in the catchment of Moab Lake, in Jasper National Park, Alberta, in 2000 caused increased runoff of both mercury and nutrients to the lake. The nutrient input caused an increase in productivity that caused high recruitment of juvenile rainbow trout in the years following the fire. Adult fishes of several species switched from feeding on invertebrates to feeding on young rainbow trout. Most species increased in trophic position as indicated by ¹⁵N. As a result, biomagnification increased, causing an increase in the mercury content of several fish species. Increases in some were enough to require consumption advisories to be put into place (Kelly et al. 2006). Turetsky et al. (2006) calculated that increased incidence of fire in northern boreal forested regions could result in a 15-fold increase in mercury emissions to the atmosphere, so there are also broad regional implications for the mercury content of fishes.

Organochlorine (OC) contaminants are also sequestered in terrestrial catchments (Davidson et al. 2003). In contrast to mercury, organochlorine concentrations in aquatic organisms from Moab Lake decreased after fire (Demers et al. 2007). We hypothesize that the difference from mercury is because the fire destroyed the OC compounds, so that there was no increased input of the compounds. Fish growth increased as the result of high nutrient inputs, so that growth dilution caused the decline in concentration of the OCs. It follows that growth dilution probably also decreased mercury concentrations in Moab Lake fish, i.e., they might have increased even more if mercury inputs had increased but nutrient inputs had not.

Fish as sentinels and integrators—Much of the focus in this workshop has been on chemical, microbial, and planktonic sentinels and integrators of the effects of climate warming. I propose that fish are possibly the best organisms in lakes at both functions. Other higher members of the food chain also show some promise.

Fish respond to climate warming in several ways in northern lakes. As ice-out occurs earlier, the date of spring spawning tends to move earlier as well. Fall spawning also occurs later. For example, the average onset of lake trout spawning at ELA is now 10–15 days later than it was in the mid-1970s (K. H. Mills pers. comm.). On the other hand, the lethal temperatures of some species of coldwater fishes are likely to be exceeded in many northern lakes. In larger lakes that contain both cold stenotherms and warm-water species, we can expect that the latter will slowly replace the former as waters warm.

Fish are also sensitive integrators and sentinels of the effects of a wide variety of persistent contaminants that biomagnify, bioaccumulate, and cause adverse effects, such as organochlorine pesticides, mercury, polychlorinated biphenyls (PCBs), and, more recently polybrominated and polyfluorinated chemicals (Kidd et al. 1995a,b; Blais et al. 2006; Kelly et al. 2006). They can concentrate contaminants that are undetectable or nearly so in water by thousands or even millions of times (Kidd et al. 1995a,b; CACAR 2003). Often, the first effect of these chemicals is the appearance of lip papillomas, skin lesions, or other symptoms in fish or aquatic birds (Gilbertson et al. 1976). Physiological indicators, such as mixed function oxidase enzymes, are also elevated before population-level effects are detectable (Arinç et al. 2000). Fish can therefore serve as sensitive indicators of low-level contaminant problems.

Contaminant problems can be linked to climate. For example, glaciers are repositories for semivolatile contaminants, which generally are released at warm temperatures and condense on ice and snow at cooler temperatures. They can thus move gradually to higher latitudes and altitudes (Wania and Mackay 1993; Blais et al. 1998). Glacial surfaces collected large amounts of toxic chemicals in the 1960s and 1970s, before many of them were banned. While more recent strata have lower levels of contamination of these earlier chemicals (dichloro-diphenyl-trichloroethane (DDT), toxaphene, PCBs, etc.), they contain increasing concentrations of chemicals that have expanding use (for example, hexachlorocyclohexane, hexachlorobenzene). Warmer climates allow such contaminants to be in vapor form longer each year and to travel both to higher latitudes and higher altitudes. Also, melting of glaciers is allowing the high levels of contaminants in older strata to be liberated now, increasing contaminant export to lakes and their biota (Donald et al. 1999; Blais et al. 2001).

Fortunately, scientists discovered some time ago that these contaminants were high enough in fish to potentially harm fish-eating birds and mammals (Muir et al. 1988). As a result, action has been taken to control many contaminants. Recent studies show that levels of most contaminants are decreasing in northern fishes (CACAR 2003). In brief, science and policy both responded to the harmful effects of contaminants to keep species from becoming extinct and humans and other top carnivores from being extensively harmed. I believe that this is one of environmental science's success stories.

Amphipods have also been shown to react to water temperature in an integrating fashion. In Alberta, *Gammarus lacustris* has a 1-yr life cycle in lowland and montane areas, a 2-yr life cycle at subalpine elevations, and a 3-yr life cycle in high alpine lakes. Changes in life cycles occur in full-year steps, because growth is only possible in the ice-free season, which lasts about 4 months. Two warm years in succession in alpine lakes allow animals to complete their life cycle in 2 yr instead of the usual 3 (Wilhelm and Schindler 2000). The result is greater abundance of amphipods, which are an important food source for fish, and the top predator in fishless alpine lakes. It is still not clear whether the plasticity of this response is under genetic or environmental control.

In summary, well-designed monitoring programs to use lakes as sentinels and integrators of the effects of climate must be broad in focus. Many of the effects on aquatic biota will be the cumulative effects of warming on both lakes and their catchments, or on the cumulative effects of warming and other stresses imposed by humans. Some of the most sensitive and useful sentinel characteristics of lakes are also simple and inexpensive to monitor. They include physical, chemical, and biological measurements. Sentinel characteristics that signal complex interactions may be more difficult to design, and it will be necessary to devote considerable research to discovering them. As climate warms and an increasing variety of human insults are applied both directly to lakes and to their catchments, it will be important to develop comprehensive lake-based monitoring programs that provide early warning of important changes in both lakes and catchments.

Acknowledgments

C.F.M. Lewis, Melissa Moos, Brian Parker, and Marguerite Xenopoulos kindly supplied prepublication copies of their recent papers that were useful in preparing the manuscript. Margaret Foxcroft assisted in the final manuscript assembly. Reviews by William Lewis and an anonymous reviewer helped to improve the final manuscript. Attendance at the Lake Tahoe conference and manuscript preparation were supported by a Discovery Grant to the author from the Natural Sciences and Engineering Research Council of Canada.

References

- AMIRO, B. D., M. D. FLANNIGAN, B. J. STOCKS, AND B. M. WOTTON. 2002. Perspectives on carbon emissions from Canadian forest fires. *For. Chronicle* **78**: 388–390.
- ANDERSON, R. F., AND S. L. SCHIFF. 1987. Alkalinity generation and the fate of sulfur in lake sediments. *Can. J. Fish. Aquat. Sci.* **44**: 188–193.
- ARINÇ, E., A. SEN, AND A. BOZCAARMUTLU. 2000. Cytochrome P4501A and associated mixed-function oxidase induction in fish as a biomarker for toxic carcinogenic pollutants in the aquatic environment. *Pure Appl. Chem.* **72**: 985–994.
- ARTS, M. T., R. D. ROBARTS, F. KASAI, M. J. WAISER, V. P. TUMBER, A. J. PLANTE, H. RAI, AND H. J. DE LANGE. 2000. The attenuation of ultraviolet radiation in high dissolved organic carbon waters of wetlands and lakes on the northern Great Plains. *Limnol. Oceanogr.* **45**: 292–299.
- BASTVIKEN, D., J. J. COLE, M. L. PACE, AND M. C. VAN DE BOGERT. 2008. Fates of methane from different lake habitats: Connecting whole-lake budgets and CH₄ emissions. *J. Geophys. Res.* **113**: G02024, doi: 10.1029/2007JG000608.
- BAYLEY, S. E., D. W. SCHINDLER, K. G. BEATY, B. R. PARKER, AND M. P. STANTON. 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.
- , B. R. PARKER, M. P. STANTON, AND K. G. BEATY. 1992a. Effect 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.
- BLAIS, J. M., S. CHARPENTIER, F. PICK, L. E. KIMPE, A. ST AMAND, AND C. REGNAULT-ROGER. 2006. Mercury, polybrominated diphenyl ether, organochlorine pesticide, and polychlorinated

- biphenyl concentrations in fish from lakes along an elevation transect in the French Pyrénées. *Ecotoxic. Environ. Saf.* **63**: 91–99.
- , D. W. SCHINDLER, D. C. G. MUIR, D. B. DONALD, AND B. ROSENBERG. 1998. Accumulation of persistent organochlorine compounds in mountains of western Canada. *Nature* **395**: 585–588.
- , AND OTHERS. 2001. Fluxes of semi-volatile organochlorines in Bow Lake, a remote high altitude, glacier-fed sub-alpine lake in the Canadian Rocky Mountains. *Limnol. Oceanogr.* **46**: 2019–2031.
- BOWLING, J. W., G. J. LEVERSEE, P. F. LANDRUM, AND J. P. GIESY. 1983. Acute mortality of anthracene-contaminated fish to sunlight. *Aquat. Toxicol.* **3**: 79–90.
- BRUCE, J., AND T. TIN. 2006. Implications of a 2°C global temperature rise on Canada's water resources: Athabasca River and oil sands development, Great Lakes and hydropower production. Available online: http://assets.wwf.ca/downloads/wwf_globalwarming_implicationsof2degressioncanadawaterresources.pdf.
- [CACAR] CANADIAN ARCTIC CONTAMINANTS ASSESSMENT REPORT II. 2003. Contaminant levels, trends and effects in the Biological Environment. Minister of Indian Affairs and Northern Development Report No. QS-8525-003-EE-A1.
- CHAN, Y. K., AND N. E. R. CAMPBELL. 1980. Denitrification in Lake 227 during summer stratification. *Can. J. Fish. Aquat. Sci.* **37**: 506–512.
- CHOL, J., AND J. T. ORIS. 2000. Evidence of oxidative stress in bluegill sunfish (*Lepomis macrochirus*) liver microsomes simultaneously exposed to solar ultraviolet radiation and anthracene. *Environ. Toxicol. Chem.* **19**: 1795–1799.
- CHRISTIAN, W., L. KUTZBACH, T. SACHS, D. WAGNER, AND E.-M. PFEIFFER. 2008. Methane emission from Siberian arctic polygonal tundra: Eddy covariance measurements and modeling. *Glob. Change Biol.* **14**: 1395–1408.
- COLE, J. J., AND OTHERS. 2007. Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. *Ecosystems* **10**: 171–184.
- CREED, I. F., F. D. BEALL, T. A. CLAIR, P. J. DILLON, AND R. H. HESSLEIN. 2008. Predicting export of dissolved organic carbon from forested catchments in glaciated landscapes with shallow soils. *Glob. Biogeochem. Cycles* **22**: GB4024, doi: 10.1002/2008GB003294.
- , S. E. SANFORD, F. D. BEDALL, L. A. MOLOT, AND P. J. DILLON. 2003. Cryptic wetlands: Integrating hidden wetlands in regression models of export of dissolved organic carbon from forested landscapes. *Hydrol. Process.* **17**: 3629–3648.
- CROLEY II, T. E., AND C. F. M. LEWIS. 2006. Warmer and drier climates that make terminal great lakes. *J. Gt. Lakes Res.* **32**: 852–869.
- CURTIS, P. J., AND H. E. ADAMS. 1995. Dissolved organic matter quantity and quality from freshwater and saltwater lakes in east-central Alberta. *Biogeochemistry* **30**: 59–76.
- DAVIDSON, D. A., A. C. WILKINSON, J. M. BLAIS, L. E. KIMPE, K. M. McDONALD, AND D. W. SCHINDLER. 2003. Orographic cold-trapping of persistent organic pollutants by vegetation in mountains of western Canada. *Environ. Sci. Technol.* **37**: 209–215.
- DEMERS, M. N., E. N. KELLY, J. M. BLAIS, F. R. PICK, V. ST. LOUIS, AND D. W. SCHINDLER. 2007. Organochlorines in trout from lakes over a 1600 meter elevation gradient in the Canadian Rocky Mountains. *Environ. Sci. Technol.* **41**: 2723–2729.
- DILLON, P. J., AND L. A. MOLOT. 1997a. Dissolved organic and inorganic carbon mass balances in central Ontario lakes. *Biogeochemistry* **36**: 29–42.
- , AND ———. 1997b. Effect of landscape form on export of dissolved organic carbon, iron, and phosphorus from forested stream catchments. *Water Resour. Res.* **33**: 2591–2600.
- , AND F. H. RIGLER. 1974. A test of a simple nutrient budget model predicting the phosphorus concentration in lake water. *J. Fish. Res. Board Can.* **31**: 1771–1778.
- DONALD, D. B., AND OTHERS. 1999. Delayed deposition of organochlorine pesticides at a temperate glacier. *Environ. Sci. Technol.* **33**: 1794–1798.
- EIMERS, M. C., S. A. WATMOUGH, J. M. BUTTLE, AND P. J. DILLON. 2007. Drought-induced sulphate release from a wetland in south-central Ontario. *Environ. Monit. Assess.* **127**: 399–407.
- FEE, E. J., R. E. HECKY, S. E. M. KASIAN, AND D. R. CRUIKSHANK. 1996. Effects of lake size, water clarity, and climatic variability on mixing depths in Canadian Shield lakes. *Limnol. Oceanogr.* **41**: 912–920.
- FLANNIGAN, M. D., K. A. LOGAN, B. D. AMIRO, W. R. SKINNER, AND B. J. STOCKS. 2005. Future area burned in Canada. *Clim. Chang.* **72**: 1–16.
- FRITZ, S. C., E. ITO, Z. YU, K. R. LAIRD, AND D. R. ENGSTROM. 2000. Hydrologic variation in the northern Great Plains during the last two millennia. *Quat. Res.* **53**: 175–184.
- GBONDO-TUGBAWA, S. S., AND C. T. DRISCOLL. 2003. Factors controlling long-term changes in soil pools of exchangeable basic cations and stream acid neutralizing capacity in a northern hardwood forest ecosystem. *Biogeochemistry* **63**: 161–185.
- GILBERTSON, M., R. D. MORRIS, AND R. A. HUNTER. 1976. Abnormal chicks and PCB residue levels in eggs of colonial birds on the lower Great Lakes (1971–73). *Auk* **93**: 434–442.
- GOODALE, C. L., AND OTHERS. 2002. Forest carbon sinks in the Northern Hemisphere. *Ecol. Appl.* **12**: 891–899.
- GRIGAL, D. F. 2003. Mercury sequestration in forests and peatlands. A review. *J. Environ. Qual.* **32**: 393–405.
- GUNN, J. M., E. SNUCINS, N. D. YAN, AND M. T. ARTS. 2001. Use of water clarity to monitor the effects of climate change and other stressors on oligotrophic lakes. *Environ. Monit. Assess.* **67**: 69–88.
- HARI, R. E., D. M. LIVINGSTONE, R. SIBER, P. BURKHARD-HOLM, AND H. GÜTTINGER. 2006. Consequences of climatic change for water temperature and brown trout populations in Alpine rivers and streams. *Glob. Change Biol.* **12**: 10–26.
- HYDROLOGICAL ATLAS OF CANADA. 1993. Streamflow [Internet]. Ottawa (ON): Environment Canada [accessed 20 May 2009]. Available from http://www.wsc.ec.gc.ca/hydrology/main_e.cfm?cname=runoff_e.cfm.
- INTERNATIONAL RIVERS NETWORK. 2006. International Rivers Network [Internet]. Berkeley (CA): IRN [accessed 20 May 2009]. Available from <http://www.irn.org>.
- JEZIORSKI, A., AND N. D. YAN. 2006. Species identity and aqueous calcium concentrations as determinants of calcium concentrations of freshwater crustacean zooplankton. *Can. J. Fish. Aquat. Sci.* **63**: 1007–1013.
- , AND OTHERS. 2008. The widespread threat of calcium decline in fresh waters. *Science* **322**: 1374–1377.
- JONES, D. C. 2002. Empire of dust: Settling and abandoning the prairie dry belt. Univ. Calgary Press.
- KELLY, C. A., J. W. M. RUDD, R. H. HESSLEIN, D. W. SCHINDLER, P. J. DILLON, C. T. DRISCOLL, S. A. GHERINI, AND R. E. HECKY. 1987. Prediction of biological acid neutralization in acid-sensitive lakes. *Biogeochemistry* **3**: 129–140.
- , AND OTHERS. 1997. Increases in fluxes of greenhouse gases and methyl mercury following flooding of an experimental reservoir. *Environ. Sci. Technol.* **31**: 1334–1344.

- KELLY, E. N., D. W. SCHINDLER, V. L. ST. LOUIS, D. B. DONALD, AND K. E. VLADICKA. 2006. Forest fire increases mercury accumulation by fishes via food web restructuring and increased mercury inputs. *Proc. Natl. Acad. Sci. USA* **103**: 19380–19385.
- KEMENES, A., B. R. FORSBERG, AND J. M. MELACK. 2007. Methane release below a tropical hydroelectric dam. *Geophys. Res. Lett.* **34**: L12809, doi: 10.1029/2007GL029479.
- KIDD, K. A., D. W. SCHINDLER, R. H. HESSLEIN, AND D. C. G. MUIR. 1995a. Correlation between stable nitrogen isotope ratios and concentrations of organochlorines in biota from a freshwater food web. *Sci. Total Environ.* **160/161**: 381–390.
- , ———, D. C. G. MUIR, W. L. LOCKHART, AND R. H. HESSLEIN. 1995b. High concentrations of toxaphene in fishes from a subarctic lake. *Science* **269**: 240–242.
- KURZ, W. A., AND OTHERS. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* **452**: 987–990.
- LAIRD, K. R., AND B. F. CUMMING. 2008. Reconstruction of Holocene lake level from diatoms, chrysophytes and organic matter in a drainage lake from the Experimental Lakes Area (northwestern Ontario, Canada). *Quat. Res.* **69**: 292–305.
- , S. R. J. WUNSAM, R. J. OGLESBY, S. C. FRITZ, AND P. R. LEAVITT. 2003. Lake sediments record large-scale shifts in moisture regimes across the northern prairies of North America during the past two millennia. *Proc. Natl. Acad. Sci. USA* **100**: 2483–2488.
- LAZERTE, B. D. 1993. The impact of drought and acidification on the chemical exports from a minerotrophic conifer swamp. *Biogeochemistry* **18**: 153–175.
- LEWIS, C. F. M., AND OTHERS. 2001. Uplift-driven expansion delayed by middle Holocene desiccation in Lake Winnipeg, Manitoba, Canada. *Geology* **29**: 743–746.
- , AND OTHERS. In press. Using geological history of the Laurentian Great Lakes to better understand their future. *Aquat. Ecosys. Health Manag.*
- LIKENS, G. E., K. C. WEATHERS, T. J. BUTLER, AND D. C. BUSO. 1998. Solving the acid rain problem. *Science* **282**: 1991–1992.
- MCCORMICK, M. J. 1990. Potential changes in thermal structure and cycle of Lake Michigan due to global warming. *Trans. Am. Fish. Soc.* **119**: 183–194.
- MENYAILO, O. V., AND Y. N. KRASNOSHCHIKOV. 2004. Denitrification potential and CO₂ emission in the northern forest soils of the Yenisei Meridian. *Biol. Bull.* **30**: 299–303.
- MUIR, D. C. G., R. J. NORSTROM, AND M. SIMON. 1988. Organochlorine contaminants in arctic marine food chains: Accumulation of specific polychlorinated biphenyls and chlordanes-related compounds. *Environ. Sci. Technol.* **22**: 1071–1079.
- NATURAL RESOURCES CANADA. 2004. Wetlands [Internet]. Ottawa: NRC [accessed 20 May 2009]. Available from http://atlas.nrcan.gc.ca/site/english/learningresources/theme_modules/wetlands/index.html.
- NEARY, B., AND P. J. DILLON. 1988. Effects of sulphur deposition on lake water chemistry in Ontario, Canada. *Nature* **333**: 340–343.
- PARKER, B. R., D. W. SCHINDLER, K. BEATY, M. P. STANTON, AND S. KASIAN. In press. Long-term changes in weather, climate, precipitation and stream output at the Experimental Lakes Area. *Can. J. Fish. Aquat. Sci.*
- POFF, N. L., M. M. BRINSON, AND J. W. DAY JR. 2002. Aquatic ecosystems and global climate change [Internet]. Arlington (VA): Pew Center on Global Climate Change [accessed 20 May 2009]. Available from <http://www.pewclimate.org/docUploads/aquatic.pdf>.
- POST, J. R., AND OTHERS. 2002. Canada's recreational fisheries: The invisible collapse? *Fisheries* **27**: 6–17.
- ROOD, S. B., J. PAN, K. M. GILL, C. G. FRANKS, G. M. SAMUELSON, AND A. SHEPHERD. 2008. Declining summer flows of Rocky Mountain rivers: Changing seasonal hydrology and probable impacts on floodplain forests. *J. Hydrol.* **349**: 397–410.
- , G. M. SAMUELSON, J. K. WEBER, AND K. A. WYWROT. 2005. Twentieth-century decline in streamflows from the hydrographic apex of North America. *J. Hydrol.* **306**: 215–233.
- ROULET, N. T., P. M. KRILL, N. T. KOMER, A. DOVE, AND R. A. BOURBONNIERE. 1997. CO₂ and CH₄ flux between a boreal beaver pond and the atmosphere. *J. Geophys. Res.* **102**: 29313–29319.
- RUDD, J. W. M., C. A. KELLY, AND A. FURUTANI. 1986. The role of sulfate reduction in long term accumulation of organic and inorganic sulfur in lake sediments. *Limnol. Oceanogr.* **31**: 1281–1291.
- SCHENDEL, E. K., J. R. MACDONALD, H. SCHREIER, AND L. M. LAVKULICH. 2007. Virtual water: A framework for comparative regional resource assessment. *J. Environ. Assess. Policy Manag.* **9**: 341–355.
- SCHINDLER, D. E., S. R. CARPENTER, J. J. COLE, J. F. KITCHELL, AND M. L. PACE. 1997. Influence of food web structure on carbon exchange between lakes and the atmosphere. *Science* **277**: 248–251.
- SCHINDLER, D. W. 1997. Widespread effects of climatic warming on freshwater ecosystems. *Hydrol. Process.* **11**: 1043–1067.
- . 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. *Can. J. Fish. Aquat. Sci.* **58**: 18–29.
- , S. E. BAYLEY, P. J. CURTIS, B. R. PARKER, M. P. STANTON, AND C. A. KELLY. 1992. Natural and man-caused factors affecting the abundance and cycling of dissolved organic substances in Precambrian Shield lakes. *Hydrobiologia* **229**: 1–21.
- , B. R. PARKER, K. G. BEATY, D. R. CRUIKSHANK, E. J. FEE, E. U. SCHINDLER, AND M. P. STANTON. 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.
- , AND P. J. CURTIS. 1997. The role of DOC in protecting freshwaters subjected to climatic warming and acidification from UV exposure. *Biogeochemistry* **36**: 1–8.
- , S. E. BAYLEY, B. R. PARKER, K. G. BEATY, AND M. P. STANTON. 1997. Climate-induced changes in the dissolved organic carbon budgets of boreal lakes. *Biogeochemistry* **36**: 9–28.
- , B. R. PARKER, AND M. P. STANTON. 1996b. Consequences of climate warming and lake acidification for UV-b penetration in North American boreal lakes. *Nature* **379**: 705–708.
- , AND W. F. DONAHUE. 2006. An impending water crisis in Canada's western prairie provinces. *Proc. Natl. Acad. Sci. USA* **103**: 7210–7216.
- , E. J. FEE, AND T. RUSZCZYNSKI. 1978. Phosphorus input and its consequences for phytoplankton standing crop and production in the Experimental Lakes Area and in similar lakes. *J. Fish. Res. Board Can.* **35**: 190–196.
- , D. LEAN, AND E. J. FEE. 1975. Nutrient cycling in freshwater ecosystems, p 96–105. *In* Productivity of World Ecosystems. Proceedings of a Symposium. August 31–September 1, 1972, Seattle, Washington. National Academy of Sciences.
- , AND J. R. VALLENTYNE. 2008. The algal bowl: Overfertilization of the world's freshwaters and estuaries. Univ. Alberta Press.
- , AND OTHERS. 2004. Lake Wabamun: A review of scientific studies and environmental impacts. Publication No. T769 prepared for the Minister of Alberta Environment.

- SCULLY, N. M., AND D. R. S. LEAN. 1994. The attenuation of ultraviolet radiation in temperate lakes. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* **43**: 135–144.
- SMOL, J. P. 2008. Pollution of lakes and rivers, 2nd ed. Blackwell.
- SPRAGUE, J. B. 2007. Great wet north? Canada's myth of water abundance, p. 23–35. *In* K. Bakker [ed.], *Eau Canada. The future of Canada's water*. Univ. British Columbia Press.
- ST. LOUIS, V. L., C. A. KELLY, E. DUCHEMIN, J. W. M. RUDD, AND D. M. ROSENBERG. 2000. Reservoir surfaces as sources of greenhouse gases to the atmosphere: A global estimate. *BioScience* **50**: 766–775.
- STATISTICS CANADA. 2005. Average annual runoff [Internet]. Gatineau (QC): Environment Canada [accessed 20 May 2009]. Available from http://www.wsc.ec.gc.ca/hydrology/main_e.cfm?name=runoff_e.cfm.
- TELLER, J. T., AND W. M. LAST. 1982. Pedogenic zones in postglacial sediment of Lake Manitoba, Canada. *Earth Surf. Proc. Land.* **7**: 367–379.
- TRANVIK, L. J., AND OTHERS. 2009. Lakes and reservoirs as regulators of carbon cycling and climate. *Limnol. Oceanogr.* **54**: 2298–2314.
- TURETSKY, M. R., J. W. HARDEN, H. R. FRIEDLI, M. FLANNIGAN, N. PAYNE, J. CROCK, AND L. RADKE. 2006. Wildfires threaten mercury stocks in northern soils. *Geophys. Res. Lett.* **33**: L16403, doi: 10.1029/2005GL025595.
- VAN DER KAMP, G., D. KEIR, AND M. S. EVANS. 2008. Long-term water level changes in closed-basin lakes of the Canadian prairies. *Can. Water Resour. J.* **33**: 23–38.
- VOLLENWEIDER, R. A. 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. *Mem. Ist. Ital. Idrobiol.* **33**: 53–83.
- WALTER, K. M., S. A. ZIMOV, J. P. CHANTON, D. VERBYLA, AND F. S. CHAPIN III. 2006. Methane bubbling from Siberian thaw lakes as a positive feedback to climate warming. *Nature* **443**: 71–75.
- WANIA, F., AND D. MACKAY. 1993. Global fractionation and cold condensation of low volatility organochlorine compounds in polar regions. *Ambio* **22**: 10–18.
- WATMOUGH, S. A., J. AHERNE, AND P. J. DILLON. 2004. Potential impact of forest harvesting on lake chemistry in south-central Ontario at current levels of acid deposition. *Can. J. Fish. Aquat. Sci.* **60**: 1095–1103.
- WILHELM, F. M., AND D. W. SCHINDLER. 2000. Reproductive strategies of *Gammarus lacustris* (Crustacea: Amphipoda) along an elevation gradient. *Funct. Ecol.* **14**: 413–422.
- WINDER, M., D. E. SCHINDLER, T. E. ESSINGTON, AND A. H. LITT. 2009. Disrupted seasonal clockwork in the population dynamics of a freshwater copepod by climate warming. *Limnol. Oceanogr.* **54**: 2493–2505.
- WRIGHT, R. F. 1976. The impact of forest fire on the nutrient influxes to small lakes in northeastern Minnesota. *Ecology* **57**: 649–663.
- XENOPOULOS, M. A., W. J. EDWARDS, D. A. CULVER, AND D. W. SCHINDLER. In press. The real ultraviolet radiation environment experienced by phytoplankton. *Can. J. Fish. Aquat. Sci.*
- , AND D. W. SCHINDLER. 2001. The environmental control of near-surface thermoclines in boreal lakes. *Ecosystems* **4**: 699–707.
- ZOLTAI, S. C., AND D. H. VITT. 1990. Holocene climatic change and the distribution of peatlands in the western interior of Canada. *Quat. Res.* **33**: 231–240.

Editor: Everett Fee

Received: 06 October 2008

Accepted: 19 April 2009

Amended: 12 May 2009