Implications of climate warming for Boreal Shield lakes: a review and synthesis

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Abstract: Climate change is a reality. A warming climate will have large effects on lakes of the Boreal Shield. Our ability to forecast these effects, however, is hampered by a very incomplete understanding of the actual interactions between weather and many aspects of lake ecosystems. Climate change will affect lakes in very complex ways. Changing weather conditions will have direct effects on thermal habitats; however, there will also be very important indirect effects on lake ecosystems through influences on watershed processes that affect the thermal and chemical characteristics of lakes. Altered habitat conditions will affect the resident biota in both positive and negative ways and may favour range expansions of some native and non-native species. Our understanding of the altered biological interactions that will structure lake communities in a warmer climate is still limited, making the prediction of biological outcomes very difficult. Modelling efforts, experiments and empirical analyses of relationships between important attributes of lakes, lake communities, and weather conditions in the past are beginning to further our ability to predict likely future effects. Much more work is needed in all these research areas to further our understanding of the probable effects of climate change on Boreal Shield lakes. Because of the potential interactions of climate with other large-scale environmental stressors such as UV-B irradiance, exotic species invasions, base cation depletion, and acidification, future studies need to consider multiple stressor effects.

Key words: climate, lakes, temperature, transparency, zooplankton, phytoplankton, fish.

Résumé : Le changement climatique est une réalité. Un réchauffement climatique aura des effets importants sur les lacs du Bouclier boréal. Notre capacité à prédire ces effets est cependant ralentie par une compréhension très incomplète des interactions actuelles entre le temps qu'il fait et plusieurs aspects des écosystèmes lacustres. Le changement climatique affectera les lacs de façon très complexe. Les conditions météorologiques changeantes auront des effets directs sur les habitats thermiques; cependant, il y aura également des effets indirects sur les écosystèmes lacustres via leurs influences sur les processus dans les bassins versants, lesquels affectent les caractéristiques thermales et chimiques des lacs. Une altération des conditions des habitats affectera le biote local de façon positive et négative et pourrait favoriser l'expansion de l'aire d'espèces indigènes et non-indigènes. Notre compréhension de l'altération des interactions biologiques qui vont structurer les communautés lacustres, sous un climat plus chaud, est encore limitée, ce qui rend la prédiction des issues biologiques très difficile. Les efforts de modélisation, les expériences et les analyses empiriques des relations entre des caractéristiques importantes des lacs, les communautés lacustres et les conditions météorologiques du passé commencent à améliorer notre capacité à prédire des effets futurs possibles. Il faut redoubler d'effort dans tous ces domaines de recherche pour pousser notre compréhension des effets probables du changement climatique sur les lacs du Bouclier boréal. À cause d'interactions possibles du climat avec d'autres stress environnementaux majeurs, comme l'irradiance UV-B, l'invasion par des espèces adventices, l'épuisement des cations par l'acidification, les études à venir doivent prendre en considération les effets de stress multiples.

Mots-clés : climat, lacs, température, transparence, zooplancton, phytoplancton, poisson.

[Traduit par la Rédaction]

Introduction

Climate change is expected to have profound effects on Boreal Shield lakes (Schindler et al. 1990, 1996*a*; Schindler 1998). However, the true nature and magnitude of the changes to aquatic ecosystems that will result from a warming climate are still very poorly understood. A warmer climate will affect lake thermal structure in complex ways. Warmer air temperatures do not necessarily create warmer aquatic habitats. Surface mixed-layer (epilimnion) temperatures in lakes are generally expected to warm (De Stasio et al. 1996; Stefan et al. 1998); however, the amount of coldwater habitat in many Boreal Shield lakes may actually increase with warmer weather (De Stasio et al. 1996; Snucins and Gunn 2000; Keller et al. 2005). The biological changes resulting from changed thermal habitats are expected to be very complex, involving direct and indirect effects, and species interactions at various levels of aquatic food webs (De Stasio et al. 1996; Moore et al. 1996; Schindler 2001).

While our knowledge of the potential effects of climate change on aquatic ecosystems is still limited, it is advancing. This paper seeks to contribute to that advancement of knowledge by providing a summary of the potential responses of aquatic systems to future climate change, based

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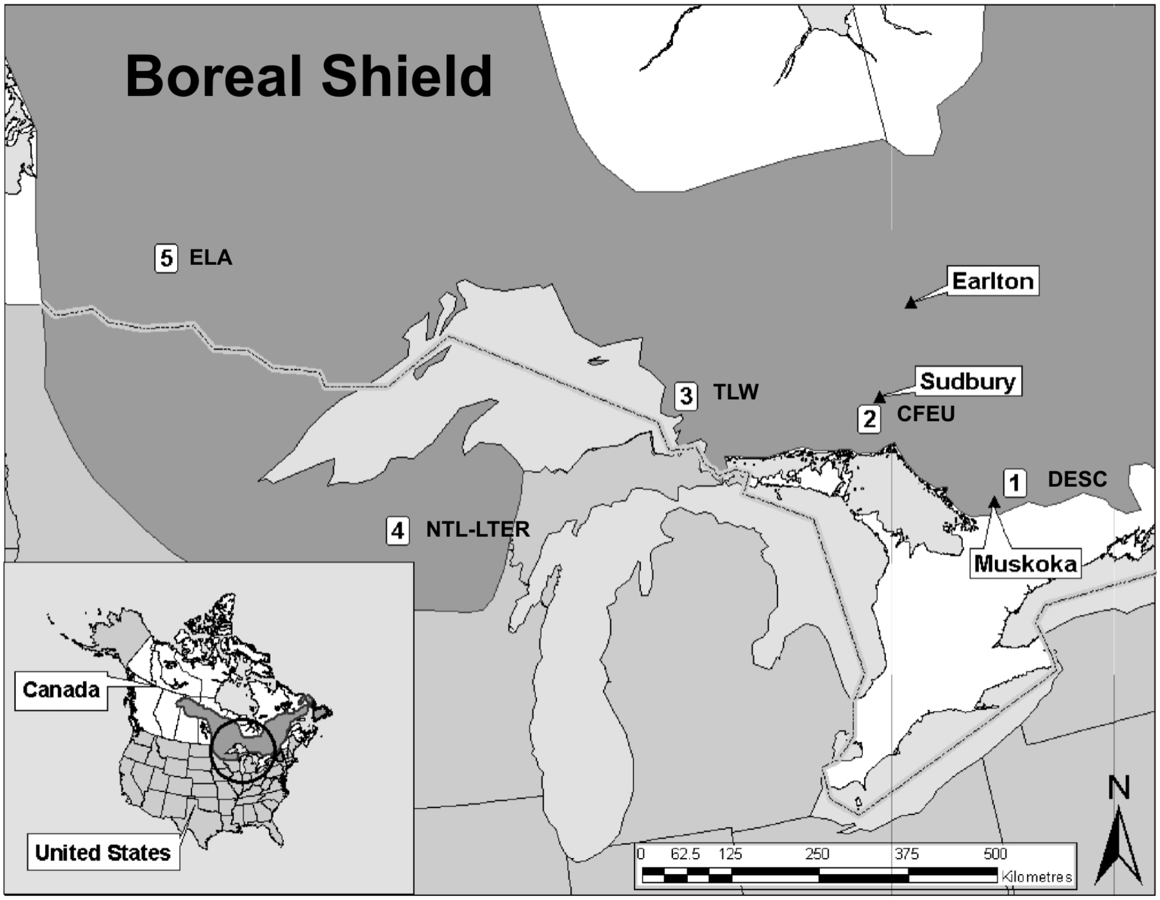
Fig. 1. The Boreal Shield Ecozone (shaded in dark grey). Locations of weather stations (Sudbury, Earlton, Muskoka) referred to in this paper, and locations of long-term aquatic research and monitoring sites on the central Boreal Shield are indicated: 1, DESC (Dorset Environmental Science Centre); 2, CFEU (Cooperative Freshwater Ecology Unit) http://www.livingwithlakes.ca; 3, TLW(Turkey Lakes Watershed) http://www.tlws.ca; 4, NTL-LTER (North Temperate Lakes- Long Term Ecological Research Site) http://lterquery.limnology.wisc.edu; 5, ELA (Experimental Lakes Area) http://www.umanitoba.ca/institutes/fisheries.

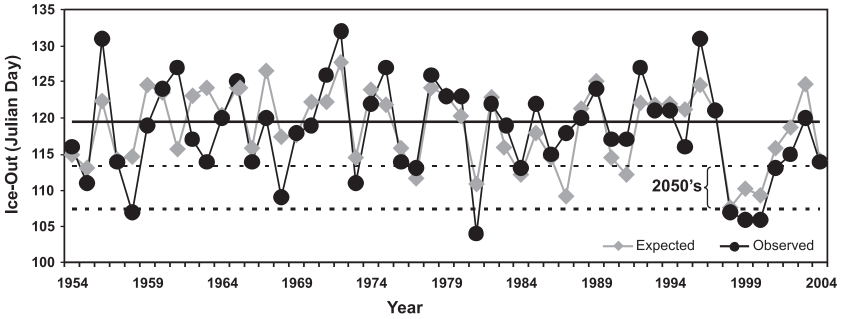


on the literature and drawing on examples of lake responses to observed weather variations over the last several decades. Determining the direct and indirect linkages between weather and aquatic habitats based on existing observations is important to developing our ability to make realistic forecasts of the future effects of climate change.

This paper largely examines findings for lakes in the central portion of the Boreal Shield Ecozone, particularly in northern and south-central Ontario, Canada. These lakes have been the focus of intensive study over many decades through a number of long-term research and monitoring programs (Fig. 1). However, much of the information provided, which draws on the international literature, is broadly applicable across the Boreal Shield (Fig. 1), Canada's largest ecozone, containing 22% of Canada's freshwater surface area and supporting many resource-based industries that make a huge contribution to the Canadian economy (Urquizo et al. 2000). The Boreal Shield is the area where the hard, weathering-resistant geology of the Precambrian Shield is overlain by northern mixed wood forests, predominantly conifers. Hardwood forests occur along the southern edge of the ecozone. Surface waters are very dilute, with high sensitivity to environmental stressors such as acidification, shoreline development, and climate change. Summaries of ecological conditions and threats to ecosystems in the Boreal Shield Ecozone are provided in Urquizo et al. (2000) and Gunn et al. (2004).

An overview of past and current climatic conditions of the Precambrian Shield region that contains the Boreal Shield, and forecasts for future conditions, are provided in Magnuson et al. (1997). Briefly, much of this area is now generally warmer and wetter than it has been since the end of the last glaciation, and warming trends are forecasted to continue (Magnuson et al. 1997). However, estimated changes in temperature and precipitation over the last 6000 years vary widely in magnitude and direction between different areas of the Boreal Shield (Hengeveld et al. 2005). More recently (1948–2003) the dominant trends across the Boreal Shield have been increases in temperature and precipitation (Hengeveld et al. 2005). Future changes in temperature and precipitation are expected to vary widely in different areas of the Boreal Shield, and predictions from different climate models vary greatly. For example, projections for 2050 from 30 different climate models show wide variation in summer temperature and precipitation (1.4 to 4.3 °C and –16 to +24%, respectively) for northeastern Ontario (Hengeveld 2004). While reasonable forecasts of future temperatures can be made, model predictions of changes in local

Fig. 2. Ice-off dates observed for Ramsey Lake in Sudbury, Ontario and predicted from an empirical model using mean February to April Sudbury air temperatures (Gao and Stefan 1999; $-3.05 \times T_{F,M,A} + 0.002$ lake area (km^2) + 104.3). The figure is modified from Keller et al. (2006*a*). Predictions of ice-off dates from temperatures forecasted for the 2050's (range from four GCM runs, see text) are indicated by the dashed horizontal lines, and the solid horizontal line indicates ice-off predicted by the 1961–1990 baseline temperature.



precipitation patterns are less reliable because of an inability to account for important factors such as changes in storm tracks (Hengeveld et al. 2005).

Many of the examples shown in this paper are drawn from studies conducted in the Sudbury region of northeastern Ontario. For many decades this area near the geographical centre of the Boreal Shield (Fig. 1) has been the focus of intensive research and monitoring programs investigating the effects of various anthropogenic stressors on lakes. In particular, through studies of the natural recovery of lakes after sulphur emission reductions and through neutralization experiments, Sudbury area studies are providing the opportunity to understand how aquatic ecosystems recover after reductions in acid deposition (Keller et al. 2007) and how these recovery processes are affected by interactions with other stressors such as climate change (Keller et al. 2005). Recovery from acidification is expected to become much more widespread across acid-affected areas of the Boreal Shield as a result of acid deposition reductions (Government of Canada 2005). Sudbury studies combined with results from a number of other long-term research and monitoring sites on the central Boreal Shield (Fig. 1) provide an important opportunity to begin to understand the potential effects of climate change within a realistic, multiple stressor context. It is clear that the effects of the major stressors that will affect Boreal Shield lakes in the future, including climate change, will be closely linked.

Overview of habitat changes related to a warming climate

Ice phenology

Longer ice-free seasons will result from climate warming because of later freezing and earlier ice breakup. Widespread trends toward longer ice free seasons have been observed over the last 150 years across the Northern Hemisphere (Magnuson et al. 2000) and more regionally in southern Ontario (Futter 2003).

Comparison of observed ice-out dates for Ramsey Lake in Sudbury, northeastern Ontario, with ice-out dates predicted from an empirical model using February through April air temperatures (Gao and Stefan 1999) indicated generally good agreement ($r = 0.75$; Fig. 2). Much of the unexplained variation likely results from other factors such as solar radiation, snow depth and wind that are not considered in the model and for which lake-specific data are not commonly available. This suggests that this simple model and those for other aspects of ice phenology developed by Gao and Stefan (1999) from data on Minnesota lakes and verified with data from lakes in Wisconsin, Maine, and Ontario, are broadly applicable to Boreal Shield lakes, including those in northern Ontario.

As an example, two of these models are applied to Ramsey Lake (792 ha, 8.4 m mean depth), using forecasts of future temperatures for northeastern Ontario.

$$\begin{aligned}\text{Ice off date (Julian day)} &= -3.05 \times \text{TEMP}_{\text{FMA}} \\ &\quad + 0.002 \times \text{lake area (km}^2) + 104.3\end{aligned}$$

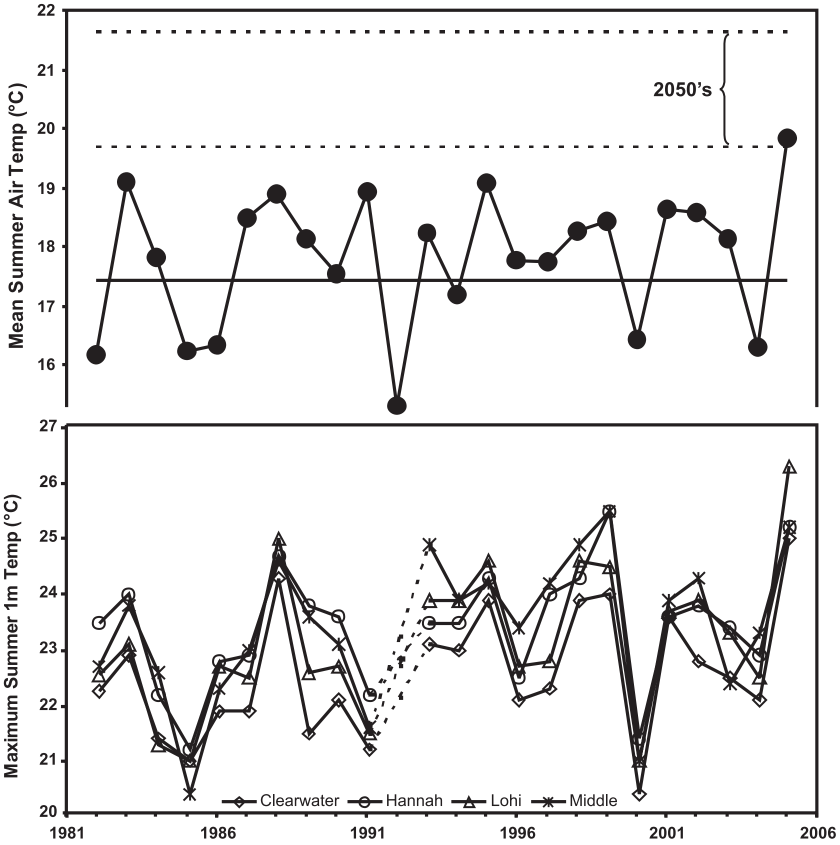
$$\begin{aligned}&\text{Ice on date (Julian day)} \\ &\quad = 1.414 \times \text{mean depth (m)} + 0.003 \\ &\quad \times \text{lake area (km}^2) + 3.666 \times \text{TEMP}_{\text{O,N,D}} + 325.2\end{aligned}$$

Forecasts of future changes in climate from different global circulation models (GCMs) and scenarios vary substantially. Using monthly temperatures predicted from two GCMs, each run under two different scenarios (CGCM2 A21, CGCM2 B21; http://www.cccma.bc.ec.gc.ca/models/cgcm3.shtml: HadCM3 A1F1, HadCM3 B11; http://www.cses.washington.edu/cig/fpt/climatemodels.shtml), ice-off dates were predicted to be, on average, 5.3 (4.5–5.8), 8.6 (6.1–12.0), and 15.4 (10.5–22.9) days earlier, respectively, in the 2020's, 2050's and 2080's in comparison to the 1961 to 1990 baseline. Ice-on was predicted to occur 4.2 (2.2–7.3), 8.0 (3.6–14.1), and 13.7 (5.3–24.3) days later, in the 2020's, 2050's and 2080's, respectively.

Taken together, these estimates predict substantial increases in the length of the ice-free period for this example lake; on average 9.5, 16.6, and 29.1 days in the 2020's, 2050's and 2080's, respectively. This analysis indicates that substantial increases in ice-free period duration are expected for lakes on the Boreal Shield.

Since ice phenology is also affected by lake size and depth, small, shallow lakes will usually freeze slightly earlier and thaw slightly earlier than larger, deeper lakes (Stewart and Haugen 1990; Gao and Stefan 1999). However, over the range of morphometry common in most Shield lakes this effect will be minimal. In Ontario, for example,

Fig. 3. Long-term patterns in maximum summer (June–August) surface water temperature in four Sudbury, Ontario, lakes and mean summer air temperature at Sudbury. Forecasts of mean summer air temperatures for the 2050's (range from four GCM runs, see text) are indicated by the dashed horizontal lines, and the solid horizontal line indicates the mean summer air temperature during the 1961–1990 baseline period.



over 95% of the ~227 000 lakes are under 100 ha in size (Cox 1978). Over the range of 0 to 100 ha, the above models predict morphometry-related variations in ice-free period duration of only ~2 days. Effects of morphometry will be more pronounced in larger, deeper lakes, primarily because of later freezing. For example, lakes of 500 ha area and ~13 m mean depth will freeze ~10 days later than lakes of 10 ha area and ~6 m mean depth according to the above equation for ice-on date.

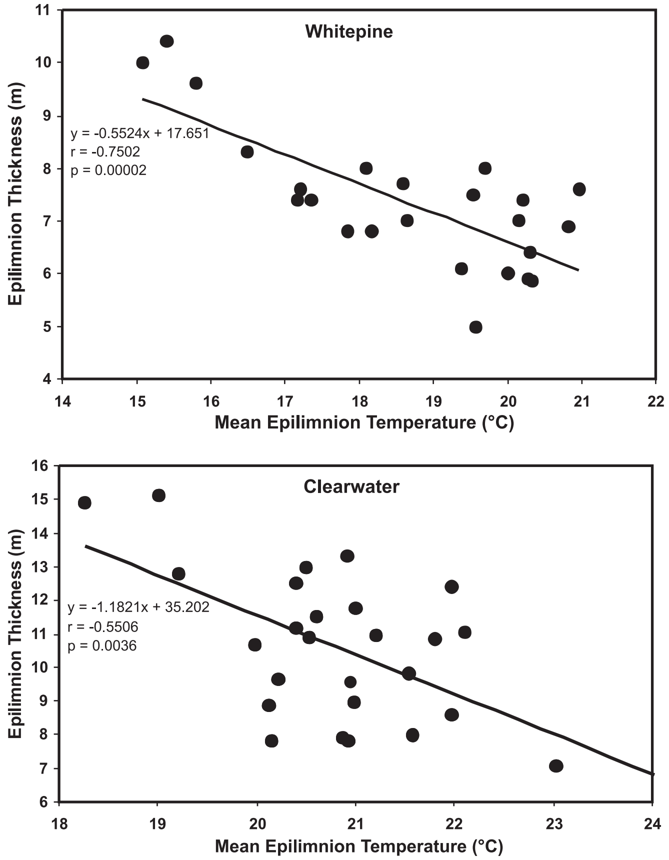
Lake thermal structure

Hot summer temperatures do result in elevated surface water temperatures (Fig. 3); however, temporal patterns in surface mixed-layer water temperatures are often not well-predicted from air temperatures alone (De Stasio et al. 1996; Gao and Stefan 1999; Snucins and Gunn 2000). Since heating is predominantly a radiative process in lakes (Wetzel 1975), variations in solar radiation as well as air temperature are important. For the lakes shown in Fig. 3, summer (June through August) air temperatures only explained between 36 and 40% of the long-term variation in maximum summer surface temperatures ($r = 0.60$ to 0.63; $p < 0.05$; $n = 23$). The depth to which heat is distributed by mixing greatly influences surface and mixed-layer temperatures. There is generally a negative correlation between epilimnion thickness and epilimnion temperature in northeastern Ontario lakes (Fig. 4).

Lake temperatures will be affected by a warmer climate in various ways. Thermal structure is affected directly by weather but is also greatly influenced by watershed processes that affect lake clarity, which are also affected by weather. Responses to changes in weather will be very different in clear and coloured lakes (Snucins and Gunn 2000). Warmer aquatic habitats will not necessarily result from warmer air temperatures. Surface mixed-layer (epilimnion) temperatures are generally expected to warm; however, warmer weather may actually increase the amount of late-season coldwater habitat in many Boreal Shield lakes (De Stasio et al. 1996; Snucins and Gunn 2000; Keller et al. 2005). This pattern is likely to be widespread in lakes with the moderate to high (over ~3 mg/L) dissolved organic carbon (DOC) concentrations typical of Boreal Shield lakes (Snucins and Gunn 2000; Keller et al. 2005).

Longer periods of thermal stratification are expected to result from climate warming (Robertson and Ragotzkie 1990; De Stasio et al. 1996) extending periods of thermal habitat separation for some biota, and providing a greater possibility for late-season dissolved oxygen depletion in bottom waters. Warmer weather may increase thermal gradients below the epilimnion (Stefan et al. 1998; Snucins and Gunn 2000) and increased weather variability may affect the occurrence of secondary thermal gradients near the lake surface (Xenopoulos and Schindler 2001), with possible consequences for lake biota.

Fig. 4. Relationships between epilimnion thickness and mean epilimnion temperature during late-summer in Whitepine (89 km N of Sudbury) and Clearwater (12 km S of Sudbury) lakes.



Linkages between weather, lake transparency and thermal structure

Meteorological conditions strongly drive patterns in the thermal structure of moderate to large-size lakes (Robertson and Ragotzkie 1990; Fee et al. 1996; King et al. 1997, 1999*a*). Wind is a major factor determining the depth of mixing in larger lakes, with longer fetch permitting effective mixing by wind energy. Wind can sometimes be an important factor affecting thermal structure in smaller lakes when changes in wind speed are very large, as in the case of Clearwater Lake (76.5 ha) near Sudbury (Tanentzap 2006; Tanentzap et al.[1]). However, various studies have demonstrated that variations in attributes of the thermal structure of the relatively small (<500 ha) lakes that dominate the Boreal Shield landscape are usually best explained by variations in lake transparency, not directly by variations in weather, including wind and air temperature (Fee et al. 1996).

In nutrient rich lakes, phytoplankton have a great effect on lake transparency. However, in typical unproductive Boreal Shield lakes DOC is usually the main determinant of lake transparency and therefore it mainly determines important aspects of lake thermal structure including thermocline depth (Pérez-Fuentetaja et al. 1999), epilimnion thickness (Cahill et al. 2005; Keller et al. 2006*b*), and the depth of the 10 °C isocline, a simple measure of the amount of coldwater habitat (Dillon et al. 2003; Keller et al. 2005). The major effects of climate change on lake thermal structure in small Boreal Shield lakes will therefore likely be an indirect effect of changes in weather on DOC concentrations.

The effects of weather on DOC will be varied and complicated. Weather-related influences may operate on very different time scales, and long and short-term influences may compete. Shifts in vegetation types (Pienitz and Vincent 2000), changes in wetland size (Molot and Dillon 1997), and changes in the rates of basic processes of organic matter breakdown controlling DOC production (Freeman et al. 2001) are factors that may result in long-term, gradual change. Shorter-term factors such as severe droughts can have dramatic effects by reducing the supply of DOC to lakes from their watersheds (Schindler et al. 1990) and by increasing the retention time of lakes allowing greater removal of DOC by various processes, including sedimentation and photo-oxidation (Curtis and Schindler 1997; Molot and Dillon 1997).

The relative importance of different climatic factors, such as temperature and precipitation, in affecting DOC concentrations is still very unclear (e.g., Tranvik and Jansson 2002; Evans et al. 2002), and other factors such as acid deposition history may also have substantial effects (Evans et al. 2006). Some recent evidence suggests that warmer air temperatures may result in increased DOC (Freeman et al. 2001; Keller et al.[2]). Possible mechanisms include increased production or enhanced breakdown of organic matter.

Figure 5 shows the increases in DOC concentrations observed in 24 near-neutral northeastern Ontario lakes between 1981 and 2003–2005 as air temperatures generally increased. Increased DOC concentrations have also been observed in other lakes in northeastern Ontario near Sudbury, and in south-central Ontario near Dorset (Somers 2006; Keller et al.[2]) during the general warming trends (1.5, 1.1, and 1.1 °C, respectively, at the Earlton, Sudbury and Muskoka weather stations; Fig. 1) observed over the last three decades (1970–2003). If a warming climate increases future DOC concentrations, thinner surface mixed layers and increased coldwater habitat would generally be expected (Keller et al. 2005, 2006*b*).

Responses of lakes will, however, vary widely between different regions of the Boreal Shield, since specific regional weather conditions will also vary greatly. Comparisons of past long-term lake records from different regions illustrate this variability. In contrast to the general increases in DOC concentrations observed in northeastern and south-central Ontario in recent decades, DOC concentrations in northwestern Ontario lakes at the Experimental Lakes Area declined greatly during a warming period (1.6 °C), with very severe

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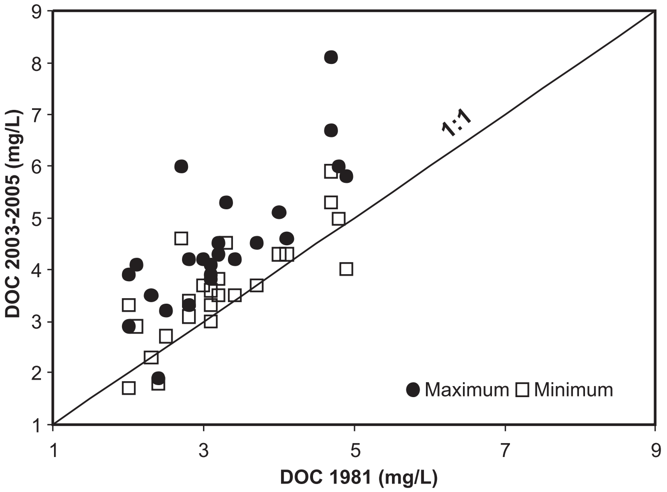
[1] Tanentzap, A.J., Yan, N.D., Keller, W., Girard, R., Heneberry, J., Gunn, J.M., Hamilton, D.P., and Taylor, P.A. Cooling lakes while the world warms: the effects of forest re-growth and increased dissolved organic matter on the thermal regime of a temperate urban lake. Limnol. Oceanogr. Submitted for review.

[2] Keller, W., Paterson, A., Somers, K., Dillon, P., Heneberry, J., and Ford, A. Relationships between dissolved organic carbon concentrations, weather, and acidification in small Boreal Shield lakes. Can. J. Fish. Aquat. Sci. Submitted for review.

Fig. 5. Relationships between DOC concentrations in 24 non-acidic northeastern Ontario lakes in surveys (single mid summer samples) conducted in 1981 and 2003–2005. Open and closed symbols indicate relationship of 1981 values with minimum and maximum values, respectively, observed during 2003 to 2005. The lakes are located 37 to 133 km from Sudbury.



intermittent droughts (1970–1990: Schindler et al. 1996*a*, 1997). Such regional variability underscores the need for regional scale forecasts of climate change to permit realistic predictions of effects on lakes.

While some modeling results predict increased runoff on much of the Boreal Shield with a doubling of atmospheric CO_2 (Clair et al. 1998), it has generally been suggested that reduced DOC export will result from a warmer, drier, climate because of reduced runoff (Fee et al. 1996; Schindler et al. 1996*a*; Snucins and Gunn 2000). Such a hydrological effect, however, could be offset by enhanced organic matter production and decomposition in watersheds under warmer temperatures and with greater variability in moisture conditions over long time periods. Consistently wet conditions inhibit decomposition of organic matter and promote accumulation as peat. During dry periods, oxidation of upper peat layers can produce labile DOC that is flushed to lakes under subsequent wet conditions (Dillon and Molot 1997; Freeman et al. 2001). Future weather variability, not simply changes in average conditions, may be very important in determining lake DOC concentrations and the resulting lake thermal structure.

Weather events and stressor interactions

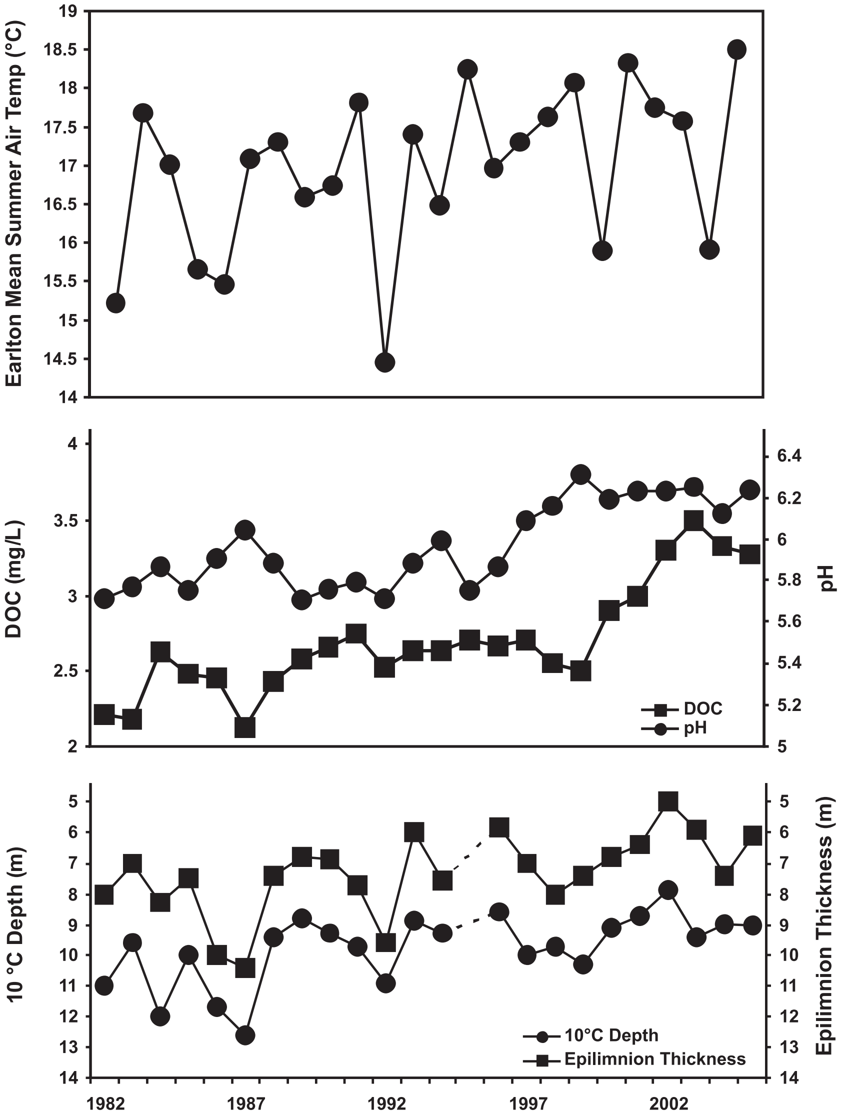
If the timing and magnitude of runoff events change substantially in the future, effects on lake chemistry can be expected. For example, summer storms can be a major source of DOC loadings to lakes (Hinton et al. 1997) while heavy spring runoff may reduce DOC concentrations because of dilution effects (Hudson et al. 2003). Hydrology is closely coupled to the loadings of chemical constituents to Boreal Shield lakes (Schindler et al. 1976; Webster et al. 1996, 2000; Aherne et al. 2004; Dillon and Molot 2005). If changes in patterns of hydrological events change the timing and magnitude of nutrient and major ion exports to lakes, substantial effects on aquatic habitats, and aquatic communities are likely.

Droughts can have very dramatic impacts on many characteristics of aquatic ecosystems. Decreased water renewal because of reduced precipitation and increased evaporation can increase lakewater concentrations of many chemical constituents (Schindler et al. 1990). As indicated above, very severe and prolonged drought can lead to reduced DOC concentrations because of reduced inputs via runoff and greater in-lake removal of DOC (Schindler et al. 1990; Schindler et al. 1996*b*; Schindler et al. 1997; Curtis and Schindler 1997). Droughts can also result in oxidation of reduced sulphur stored in saturated areas of lake catchments from years of elevated atmospheric deposition. Such drought-related effects have been widely observed in Ontario (Keller et al. 1992*a*; Kelso et al. 1992; Dillon et al. 1997). Wetlands are particularly important sites for sulphur storage within lake catchments (Dillon and LaZerte 1992; Dillon et al. 1997; Aherne et al. 2004). Remobilization of stored acidity when wet conditions resume can cause lake re-acidification and many related physical and chemical changes including metal and sulphur mobilization, increased clarity, changes in thermal structure, and increased UV-B penetration (Yan et al. 1996). Such effects, with major impacts on lake biota, including phytoplankton and zooplankton (Arnott et al. 2001), were observed in Sudbury area lakes following the 2 year drought of 1986–87 (Keller et al. 1992*a*; Yan et al. 1996). Weather-induced acid generation and metal release may also be a large concern for artificial waste management systems that rely on maintaining saturated conditions, such as mine tailings covers, wetland treatment systems, and tailings impoundments, if climate change results in drier conditions or greater variability in moisture regimes.

While drought-induced re-acidification events may set back the recovery of acidified lakes, there is some evidence that in the long-term, a warming climate may actually enhance lake recovery. Studies on alpine lakes in Europe have documented decreases in lake acidity and increases in base cation concentrations accompanying trends of increasing air temperatures (Sommaruga-Wograth et al. 1997; Rogora et al. 2003). These changes appear to reflect increased weathering rates. Since depletion of base cations, particularly calcium, is an important concern for lakes and forests in some areas of northern Ontario (Keller et al. 2001; Watmough and Dillon 2003, 2004), enhancement of weathering rates to help restore available base cation pools may be a benefit from a warming climate, in the context of recovery from acidification. In turn, recovery from acidification may affect the thermal responses of lakes to climate change. The increases in DOC concentrations that accompany decreased lake acidity (Dixit et al. 2001; Keller et al. 2003) and their potential effects on lake thermal structure need to be considered in forecasts of future lake conditions in acidified regions (Keller et al. 2005; Tanentzap et al.[1]).

Whitepine Lake, a small, deep, oligotrophic lake near Sudbury, Ontario, that is recovering from acidification, provides an example of long-term changes in interacting patterns of summer air temperature, pH, DOC, and thermal characteristics (Fig. 6). As might be predicted, this lake has undergone significant changes in thermal structure including

Fig. 6. Patterns in mean summer air temperature, DOC concentrations and pH, and late-summer 10 °C degree depth and epilimnion thickness, in Whitepine Lake, 89 km N of Sudbury (figure based on Keller et al. 2005, with additional data).



trends toward a shallower epilimnion and increased cold-water habitat as pH, DOC concentrations, and air temperatures generally increased over the last two decades (Fig. 6; Keller et al. 2005).

Biological effects

Temporal and spatial dynamics

Earlier ice breakup may increase the exposure of organisms to UV radiation during long spring days, and cold spring temperatures may increase the susceptibility of some biota to damage (Williamson et al. 2002). Zooplankton species that migrate to surface waters seeking warmer temperatures may be especially vulnerable to high UV levels (Persaud and Williamson 2005). Earlier ice breakup may also interrupt the temporal synchrony of biological cycles such as spring peaks in phytoplankton and zooplankton populations (Winder and Schindler 2004). Earlier or stronger warming and development of thermal stratification may change typical separations, overlaps and interactions between aquatic biota (King et al. 1999*b*; Mehner 2000; Jansen and Hesslein 2004; George and Hewitt 2006; Wagner and Benndorf 2007). Later freezing will also contribute to increased length of ice-free seasons. Longer ice-free seasons will increase the opportunities for temporal niche differentiation between species (Hampton 2005). Changes in niche overlap and their ecological effects are expected to vary greatly depending on the particular thermal and biological characteristics of specific lakes (De Stasio et al. 1996; Moore et al. 1996). Both temporal and spatial disconnects in zooplankton dynamics have been observed and related to climatic factors in Lake Washington (Hampton 2005; Romare et al. 2005).

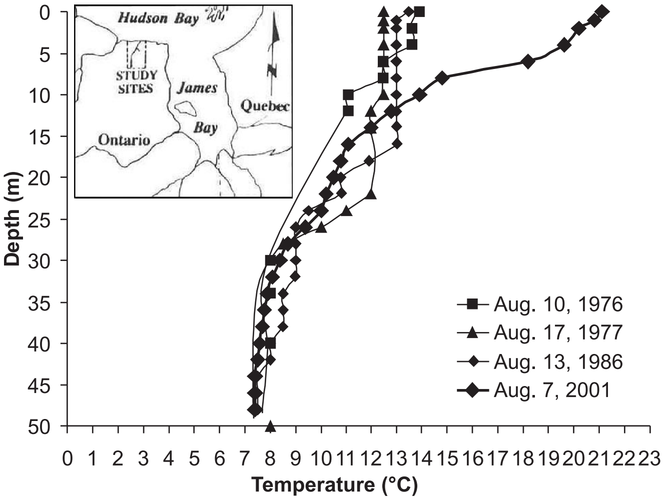
The most extreme effects of thermal changes are likely to occur in clear lakes of shallow depth where suitable thermal habitats for some species may completely disappear or refuges from predation may be greatly reduced or eliminated. Fortunately, such lakes, which may also be the most sensitive to other stressors like UV-B irradiance, appear to be relatively uncommon on the Boreal Shield (Molot et al. 2004). It is difficult to estimate possible responses of biota to the complete warming of clear shallow lakes. Water temperatures of 25 °C or greater could occur from climate warming (De Stasio et al. 1996). Such temperatures probably approach the thermal limits of some zooplankton taxa and cold stenotherms respond negatively to temperatures >20 °C (Moore et al. 1996). Substantial thermal effects may occur well before upper thermal limits are reached among both zooplankton and fish populations (e.g., Chen and Folt 2002; Gunn 2002). On the other hand, the availability of even small thermal refuges for fish may modify population responses to thermal stress (Gunn 2002).

Fish

Longer ice-free seasons, including longer periods of thermal stratification, will likely lead to increased late season dissolved oxygen depletion in lake bottom waters in deeper lakes (De Stasio et al. 1996) with some losses of suitable habitat for cold stenotherms. In small, shallow lakes the occurrence of winterkill may be greatly reduced with shorter periods of ice-cover (Fang and Stefan 1998; Stefan et al. 2001). However, since other factors such as snow cover also affect the occurrence of winterkill, its future extent may be quite variable in different regions with different specific responses to climate change (Danylchuk and Tonn 2003). Overall, longer ice-free seasons likely will generally favour both cold and warmwater fish species by extending the periods or boundaries of suitable thermal habitat conditions (De Stasio et al. 1996; Hostetler and Small 1999). Actual fish population responses to a warming climate will, however, depend on many poorly understood interactions that may involve changes in various components of the habitat (Jones et al. 2006) and altered food web dynamics (Hill and Magnuson 1990; Tonn 1990). Insufficient knowledge of the biological effects and interactions likely to occur is a major hindrance to the development of predictive models of future changes in fisheries due to a warming climate (DeAngelis and Cushman 1990).

The increased surface mixed-layer temperatures resulting from climate warming will likely promote range expansions of warmwater fish species, such as smallmouth bass (*Micropterus dolomieu*) and yellow perch (*Perca flavescens*) (Shuter and Post 1990). Warming of surface waters will benefit some fish species, while others in turn may be affected negatively through species interactions. Invasions by efficient littoral predators such as bass can have large effects on aquatic food webs through predation on littoral prey fish, with negative consequences for native predators such as lake charr (*Salvelinus namaycush*) (Vander Zanden et al. 1999; Lepak et al. 2006). Population assessments in northeastern Ontario lakes have shown a 40% decrease in adult lake charr density in lakes with smallmouth bass present (Selinger et al. 2006). Invasions by perch are not expected to negatively affect lake charr populations because lake charr predation appears to exert an effective control on perch abundance (Gunn and Keller 1990; Gunn et al. 1990).

Fig. 7. Temperature–depth profiles for Hawley Lake in northern Ontario (54° 30′ N, 83° 40′ W), 1976–2001 (figure modified from Gunn and Snucins 2002).



In addition to indirect effects, there will also likely be direct negative effects on some fish species under some circumstances. Dynamic Reservoir Simulation Model (DYRESM) simulations for Wisconsin lakes, based on a doubling of atmospheric CO_2 ($2 \times CO_2$), indicate that maximum surface temperatures could exceed upper lethal limits for fish under certain model scenarios (De Stasio et al. 1996). Such projections may also apply to Ontario.

A striking example of direct damage by elevated temperatures occurred during the warm summer of 2001 at Hawley Lake on the Hudson Bay Lowlands of Ontario (Gunn and Snucins 2002). In the summer of 2001, Hawley Lake showed strong thermal stratification for the first time since intermittent surveys began in 1976, with surface temperatures exceeding 20 °C (Fig. 7). Major die-offs of brook charr (*Salvelinus fontinalis*) and white suckers (*Catostomus commersoni*) were observed in the lower reaches of the Sutton River, a world-class angling river, which drains from Hawley Lake to Hudson Bay.

Another example of direct damage to a fish population by warming water occurred in Gullrock Lake in northern Ontario in the warm years following the 1998 El Niño event. Exposure to bottom temperatures of ~20 °C resulted in the loss of juvenile lake charr stocked in the lake in 1998 (Gunn 2002). Lake charr have a preferred range of 6 to 13 °C (Martin and Olver 1980) and laboratory-derived upper lethal limits of 23.5 to 25.9 °C (Gibson and Fry 1954; Grande and Anderson 1991).

Such cases of direct fish mortality because of elevated temperatures will probably increase as the climate warms and becomes more variable. Cold groundwater discharge areas may be important refuges for coldwater fish species during such heating events (Snucins and Gunn 1995). If a changed climate alters groundwater recharge and discharge patterns, the availability of such key thermal refuge areas may be affected (Meisner 1990). Hot and (or) dry conditions can alter the spatial distribution of fish along stream temperature gradients with dramatic effects in stream reaches influenced by groundwater, affecting fish species interactions and reproductive success (Schlosser et al. 2000).

Plankton

Warmer surface waters may also greatly affect lake plankton. While warming might generally be expected to increase plankton abundance, enclosure experiments suggest that the direct effects of warming may be much smaller than the effects of nutrient concentrations and fish, major drivers of phytoplankton (Moss et al. 2003) and zooplankton (McKee et al. 2002) community dynamics. Experimentally, increased temperature has been shown to destabilize planktonic food webs (Beisner et al. 1997; Strecker et al. 2004). Thus, some of the most important effects of climate change on plankton may be manifested indirectly, through influences on other ecological processes. Phytoplankton abundance and community richness in northwestern Ontario lakes increased during warming and a severe drought, despite reduced nutrient inputs (Findlay et al. 2001). Changes in phytoplankton community composition are expected to occur under a warming climate based on monitoring studies spanning long periods with varying weather conditions (Findlay et al. 2001), from experiments (Strecker et al. 2004) and from model simulations (Elliot et al. 2005).

Different zooplankton species exhibit wide variations in their temperature tolerances and their seasonal phenologies (Chen and Folt 2002). Elevated temperatures (>25 °C) can have a variety of effects on zooplankton communities (Moore et al. 1996). Some model simulations for lakes in northern Wisconsin (De Stasio et al. 1996) and the American Midwest (Hostetler and Small 1999) indicate that surface water temperatures greatly exceeding 25 °C could occur under a 2 × CO_2 scenario. Surface water temperatures >25 °C are uncommon in northern Ontario lakes, but were observed in northeastern Ontario during the extremely hot summer of 2005 (Fig. 3). This may give a preview of future thermal conditions in northern Ontario lakes under a warmer climate.

Elevated temperatures can affect zooplankton directly by influencing survival, growth, development, and reproduction, and indirectly by altering community interactions, phytoplankton food sources, and predation regimes (see detailed review of Moore et al. 1996). Because of the central importance of zooplankton in aquatic food webs, changes in zooplankton communities will have important influences on lake ecosystem dynamics.

Some zooplankton species can survive temperatures over 30 °C, although survivorship and longevity may decrease (Taylor et al. 1993). In contrast, the upper lethal limits for the hypolimnetic crustaceans, *Mysis relicta* and *Senecella calanoides*, are 20.3 and 14.5 °C, respectively (Dadswell 1974). However, upper thermal limits are not known for many of the species important in Boreal Shield lakes and there is also concern about the true relevance of laboratory-derived thermal limits to actual lake populations. Clonal effects on temperature tolerances may limit the general and widespread applicability of laboratory results to natural zooplankton populations (Moore et al. 1996). As well, recent evidence indicates that other factors, such as the low calcium concentrations typical of Boreal Shield lakes, may greatly affect the response of zooplankton to temperature (Ashforth and Yan in press). Determining realistic thermal tolerances for important species in Boreal Shield lakes, to assist in estimation of future climate change effects, remains a research challenge.

Warmer temperatures have been observed to correlate with increased zooplankton abundance (Keller et al. 1992*b*) and production (Shuter and Ing 1997) in Ontario lakes and there is evidence of temporal synchrony between some attributes of zooplankton communities within and between different regions of Ontario (Rusak et al. 1999; Arnott et al. 2003) suggesting control by large-scale factors, such as climate. However, there can also be strong heterogeneity in zooplankton and phytoplankton temporal patterns within and across regions, reflecting the importance of local factors in determining the specific responses of communities in individual lakes to broader controls like climate (Arnott et al. 2003). Rusak et al. (2002) demonstrated that lake-specific processes were the major controls on natural variation in north-temperate zooplankton communities during the past two decades, based on a large-scale analysis including lakes from northwestern and south-central Ontario, and northern Wisconsin.

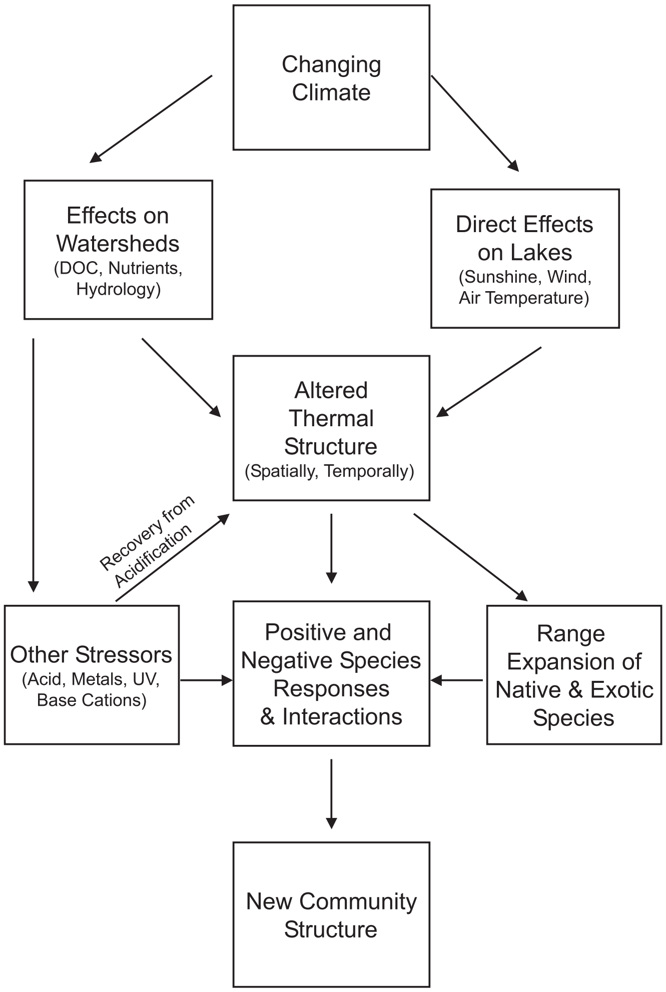
Summary

The implications of climate change for Boreal Shield lakes are large. Scientific understanding of the potential effects of climate change on aquatic ecosystems has advanced substantially since earlier reviews (e.g., Magnuson et al. 1997; Schindler 1998) as reflected by the number (>50) of climate-related papers cited here that were published since 1998. In particular, recent work more strongly emphasizes the importance of the indirect effects of climate, including effects on watershed processes that affect lake clarity, and species interactions, as major potential factors affecting future lake environments. While we are beginning to better understand the possible influences of such factors in the future, under a warming climate, much of the recent work also shows that these are very complex issues that will not be easily or quickly understood. Both long-term gradual changes and changes in the patterns of short-term weather events, and the complex interplay of long and short-term influences need to be considered.

A body of evidence has emerged indicating that weather-related effects on lake transparency will have a large effect on thermal structure in the small lakes that dominate the Boreal Shield landscape (e.g., Pérez-Fuentetaja et al. 1999; Keller et al. 2006*b*). Contrary to earlier expectations of general declines in DOC concentrations and resulting increases in lake transparency with climate warming, recent studies indicate that DOC concentrations may increase under warmer temperatures (e.g., Freeman et al. 2001; Keller et al.[2]). However, observed trends in lake DOC concentrations with respect to past weather variations vary greatly with the specific location and period examined, and are affected by interactions with other stressors such as lake and watershed acidification (e.g., Evans et al. 2006; Keller et al. 2006*b*). There is not yet any agreement on the relative roles of different climatic factors (temperature, precipitation) in determining DOC concentrations. Future effects are expected to vary widely between different lake regions and different lake types within regions.

It is becoming apparent that many of the key future changes in lake communities will result from indirect effects on species interactions resulting from altered habitats. Examples are beginning to emerge of the types and magnitudes of the spatial and temporal species separations and altered

Fig. 8. Simple schematic diagram of possible multiple stressor interactions with climate warming.



species interactions that can result from changes in weather and resulting habitat alterations (e.g., Benndorf et al. 2001; Jansen and Hesslein 2004; Hampton 2005; Romare et al. 2005), but much more study is needed.

Overall, our ability to forecast the nature and extent of likely effects is still very restricted by our limited understanding of the actual direct and indirect interactions between weather, watersheds and lake habitats, and their likely effects on aquatic ecosystems. Our limited knowledge of the altered biological interactions that will accompany the habitat alterations resulting from climate change continues to restrict our ability to make realistic predictions of the future for Boreal Shield lakes.

It is, however, becoming increasingly clear that the effects of climate change on lakes will combine strongly with the effects of other large-scale environmental stressors such as acidification, base cation depletion, UV-B irradiance, and exotic species invasions (Schindler et al. 1996*b*; Yan et al. 1996; Schindler 1998, 2001; Brönmark and Hansson 2002). The effects of these large-scale stressors will be interactive, not independent. Therefore, the additional research required to develop our understanding of the potential effects of climate change on lake ecosytems, such as those on the Boreal Shield, will need to be done within a multiple stressor framework. Some of the major chemical, physical, and biological factors that need to be considered within a multiple stressor context, and potential linkages between them are shown in Fig. 8. A changing climate will change lake thermal structure both directly and indirectly through effects on watershed processes that affect lake clarity and chemistry. Altered thermal and chemical habitat conditions will favour some species and negatively affect others. Positive and negative species interactions, including invasions of new species to altered lake habitats will structure future communities in ways that we cannot yet predict.

Substantial additional work, including both empirical and experimental studies, will be needed to better understand the potential future effects of climate change on Boreal Shield lakes. Given the regional variations in lake responses that are expected to occur, these studies should be paralleled by the development of more refined regional models of future climate and climate variability to permit better predictions of future effects.

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