The effects of a warm spring on phytoplankton and zooplankton population dynamics in small eutrophic lakes in the Canadian prairies: Implications of a changing climate

Presented by

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A Thesis submitted to the Faculty of Graduate Studies of the

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Abstract

Climate projections predict warming trends for the Canadian prairies. This study investigated effects of warmer spring temperatures on phytoplankton-zooplankton populations in small eutrophic lakes. A two-year study of three eutrophic lakes with contrasting spring weather conditions, i.e., 2005 – a 'normal' spring and 2006 – a warm spring (+2°C), demonstrated that warmer water temperatures were associated with increased total phytoplankton and relative cyanobacteria biomass and a shift in zooplankton dominance from daphniids to rotifers. Zooplankton hatching experiments and computer simulations tested the hypothesis that a warm spring differently affected daphniid and rotifer emergence from resting eggs. Experimental conditions mimicking an earlier spring (shorter photoperiod) resulted in fewer daphniid but not rotifer hatchlings, and computer simulations indicated that these changes in hatching success could be responsible for shifts from daphniid- to rotifer-dominated systems. Overall, a warm spring negatively affected daphniid populations, indirectly by increasing cyanobacteria prevalence and directly by decreasing hatching success.

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Water resources in the Canadian prairies

Water bodies in the Canadian prairies are facing a number of environmental threats that often act in synergy. Particularly over the past century, growing urban populations and intensifying rural land-use have caused increasing concern for our lakes and rivers. In the western provinces, from Manitoba to Alberta, lakes and rivers in the prairies have been subjected to multiple stressors from anthropogenic sources. Nutrient inputs, particularly those from sewage, livestock operations, and fertilizer applications, have led to significant eutrophication of prairie water-bodies (Quinlan et al. 2002). In years with droughts, common in the prairies, irrigation practices compromise water quantity and in-stream flow needs for many fishes. Contaminants, such as mercury, enter food webs and motivate fisheries officials to recommend consumption guidelines. Non-native species introductions, such as Common Carp (*Cyprinus carpio*) a hundred years ago (Stewart and Watkinson 2004), have caused restructuring of many food webs. Physical aspects of lakes and rivers have been altered, usually motivated by political and/or economic reasons. In some cases, water-bodies previously disconnected for hundreds of years have been merged, e.g., Devils Lake linkage to the Sheyenne River in North Dakota, USA (Aronow 1957).

Climate change has recently become an important public issue. A growing consensus among scientists suggests that climate change is linked to human activities. The International Panel on Climate Change report (IPCC 2007) states that increasing greenhouse gas concentrations over the last 50 years from anthropogenic sources have very likely caused warming global temperatures. In fact, some scientists have suggested that climate change, acting directly, but also synergistically with other human stresses, has led to "[a]n impending water crisis in Canada's western prairie provinces" (Schindler and Donahue 2006). The purpose of this introduction is to discuss the implications of climate change on, primarily, Canadian prairie water-bodies. A comprehensive review of climate change effects for lakes is well beyond the scope of this paper and has been the subject of many reviews (Schindler et al. 1990; De Stasio et al. 1996; Magnuson et al. 1997; Schindler 1997, 2001; Blenckner 2005; Mooij et al. 2005). Instead, important aspects of climate warming and variability on Canadian prairie lakes are presented. In conclusion, the overall goals and scope of the research project are highlighted within the context of its potential contribution to furthering our understanding of climate change impacts on plankton dynamics in prairie water-bodies.

Climate warming and variability in the Canadian prairies

In the Canadian prairies, current and future climate change has serious consequences for air temperature, water availability and inter-annual weather predictability. Historical datasets from across the Canadian prairies over the past 80 to 114 years show that air temperatures have increased by 1 to 4°C, with the greatest changes observed since 1970 (Schindler and Donahue 2006). Over the same period of time, a 14 to 24% reduction in precipitation has been accentuated by increasing evaporative losses. As a result, drought frequency and severity have increased in some parts of the prairies (Tebaldi et al. 2006), sometimes causing economic strain approaching that experienced during the mid-1930s. In addition, in some parts of the prairies, summer river flows are currently 20 to 84% lower than they were during the early 1900s (Schindler and Donahue 2006). Cumulatively, rising air temperatures and intensified agricultural practices have caused decreasing water flows owing to shrinking glaciers in the Canadian Rockies, increased evaporative losses, and greater irrigation demands (Hoppe 2003). In many prairie rivers, dependence on glacier water is substantial. For instance, the Saskatchewan River system receives 87% of its volume from the spring glacier melt in the Rockies (Schindler 2001).

Recent advances in computer modeling and more comprehensive datasets have enabled scientists to forecast climate changes with a greater level of certainty. Regional climate models (RCMs), downscaled from third generation global circulation models (GCMs), predict transient changes in climate as greenhouse gas concentrations increase. In any given study, several RCMs are employed and predictions are assessed in conjunction with their agreement with historical patterns of change. On average, in the Canadian prairies, RCMs for 2040-60 predict an increase of 2.5 to 5.6°C in air temperature and an increase of 3 to 36% in precipitation (Shepherd and McGinn 2003). Seasonal timing of increased precipitation, however, is critical for meeting our water needs. Generally, annual precipitation will increase in Alberta while southern parts of Saskatchewan and Manitoba could experience decreasing summer precipitation (Shepherd and McGinn 2003). For the eastern Prairie Provinces, this could have important ramifications, as water needs are likely to be greatest during summer months. Increased temperatures would also affect evaporative losses. For example, at the Experimental Lakes Area, Ontario, an increase from 14 to 16°C resulted in a 30% increase in evaporation rates (Schindler 2001). Across the prairies, this could result in a net loss in the water balance.

Climate change is consistent with warming temperatures but also increasing inter-annual variability. Recently, new advances have been made to characterize future occurrences of extreme events (IPCC 2007). For some parts of the Canadian prairies, indicators of climate extremes such as heat waves, dry days, warm nights, and precipitation intensity are expected to increase in magnitude (Tebaldi et al. 2006). Also, analysis of historical data suggests that increased inter-annual variability in precipitation events has already occurred as a result of climate change (Shepherd and McGinn 2003; Wulder et al. 2007). From 1978-2002, snow cover across central Canada became increasingly variable, particularly in the Canadian prairies (Wulder et al. 2007). In the prairies, changes in winter precipitation would have direct implications for soil water recharge but also the magnitude of spring runoff to water bodies. Furthermore, inter-annual fluctuations in climate will likely have important implications for aquatic ecosystems. This is especially pertinent in lakes where changes in weather phenomena have a strong effect on plankton dynamics (George and Hewitt 2006).

Prairie lakes face physical and chemical changes

Climate change will have several implications for physical and chemical aspects of lakes across the prairies. Lakes with small volumes and shallow morphologies, typical of many Canadian prairie lakes, are particularly sensitive to climate change. In these water-bodies, water temperature closely correlates with ambient air temperature given their high surface area to volume ratios (Carpenter et al. 1992). As a result, smaller heat capacities of small shallow lakes compared to deep lakes leads to their weaker abilities to dampen environmental changes (Adrian et al. 1999).

The effects of climate change on lakes in the Canadian prairies will depend on seasonal timing of warming. For example, weather conditions in spring have strong effects on physical aspects of small lakes. In these small water bodies, a warming trend in spring is typically correlated with earlier melting of ice and snow. Since the mid-1960s, ice-off and peak spring runoff has advanced by 2 and 2.5 days, respectively, per 1°C increase in March air temperatures in small Minnesota lakes (USA) (Johnson and Stefan 2006). This tight coupling of ambient weather conditions with physical aspects in small lakes will also have important consequences for aquatic organisms. For example, in European lakes, an earlier clear-water phase in shallow lakes was correlated with warming April temperatures but not winter temperatures as was found for deep lakes (Gerten and Adrian 2000).

For lakes in the prairies, symptoms of climate change will likely resemble those of eutrophication (Mooij et al. 2005). Increased evaporation and decreased summer water flows could lead to lower water levels and longer retention times in lakes even with increased precipitation. As a result, under these conditions, nutrient concentrations will increase and chemical ions will have longer to react, thus enhancing phytoplankton productivity (Schindler 2001). In shallow eutrophic lakes this could lead to decreased water transparency (Mooij et al. 2005).

In small lakes, climate change could also lead to greater internal nutrient loading. In shallow polymictic lakes, an earlier ice-off and a longer open-water season may intensify internal loading by increasing the time of sediment resuspension (Niemistö and Horppila 2007). In contrast, lakes that are deep enough to stratify could experience earlier and shallower thermocline development with climate warming (De Stasio et al. 1996) decreasing nutrient fluxes from the sediments. Moreover, increased nutrient availability could also occur as a result of temperature-dependent microbial activity in the sediments. This was shown in a mesocosm experiment where warmer water temperatures produced increased phosphorus concentrations (Mckee et al. 2003) suggesting that climate change could further compound cultural eutrophication problems in the Canadian prairies.

Biological changes within the Canadian prairie lakes

Predicting biological responses to climate change is difficult and few generalities can be made. In an investigation across ecosystems, Parmesan (2006) found that over half of the species investigated have shown changes in distributions and/or phenologies. For example, in north temperate lakes, environmental fluctuations are important seasonal indicators for many organisms. In these lakes, a warming spring has led to advancing phytoplankton and, in some cases, zooplankton phenologies (Gerten and Adrian 2000). In Canadian prairie lakes, abundance of phytoplankton should generally increase as a result of positive physiological responses to temperature and increased nutrient availability (as discussed above). Recently, climate change researchers have begun combining regional climate models with ecological simulation models. One such model developed to investigate climate change in shallow eutrophic lakes in the UK suggested that climate change might not increase annual phytoplankton biomass (Elliott et al. 2005). These models, however predicted increased spring phytoplankton biomass, largely as a result of greater cyanobacteria productivity. Several other studies also suggest that cyanobacteria may become more important at warmer water temperatures (Robarts and Zohary 1987).

Blenckner (2005) stressed the importance of including landscape features such as geographical position, catchment characteristics and lake morphometry when assessing climate-induced change in lakes. For example, in Lake 239 at the Experimental Lakes Area, NW Ontario, effects of catchment disturbance (a forest fire) and a warming trend likely combined to cause greater phytoplankton abundance (Schindler et al. 1990). In

Lake 239, forest fires and declining runoff led to decreased inputs of allochthonous dissolved organic carbon (DOC), deepening the photic zone and allowing greater algal productivity. Landscape features typical of many Canadian prairie lakes, such as nutrient-rich soils and shallow morphometry, suggest that phytoplankton will likely bloom earlier, increase in total biomass, and shift composition towards greater proportions of cyanobacteria with climate change.

Climate change will potentially affect zooplankton in several ways. In some cases, zooplankton, such as *Daphnia* and rotifers, have shown advancement of their spring phenologies with spring warming (Gerten and Adrian 2000). In contrast, other studies have shown that spring population development of *Daphnia* has remained relatively static in time over the years despite an earlier diatom bloom (George and Taylor 1995; Winder and Schindler 2004). In some systems, increasing phytoplankton biomass could lead to greater zooplankton biomass in situations where food quality is maintained (Straile 2000). However, under conditions of increased nutrient concentrations and water temperatures, cyanobacteria can become an important component of plankton biomass. In fact, several authors have observed that increasing relative cyanobacteria biomass has led to shifts towards smaller daphniid species, e.g., from *D. galeata* to *D. cucullata* (Adrian and Deneke 1996; DeMott et al. 2001).

When assessing impacts of climate change on biological systems, timing of change needs further consideration. In the Canadian prairies, many zooplankton survive long harsh winters (>4 months) by entering diapause. For zooplankton, warming could cause changes in this life-history trait. For example, in a small temperate lake, a fall warming caused *Epischura lacustris* resting eggs to hatch prematurely and *Daphnia* *catawba* to switch from sexual to asexual reproduction (Chen and Folt 1996). Overall, this could potentially decrease fall production of over-wintering resting eggs and lead to important reductions in recruitment for spring populations.

Warmer summer water temperatures could also impact zooplankton populations and their interactions with phytoplankton. In mesocosm experiments, increasing water temperatures from 18 to 25°C resulted in *Daphnia* population instability and on several occasions, extinctions (Beisner et al. 1997). *Daphnia*-algal interactions were directly affected as differential temperature-dependent responses in *Daphnia* and algal growth rates produced longer time-lags between trophic levels, but also indirectly by increasing proportions of cyanobacteria. In summary, responses of zooplankton populations to climate change will likely vary depending on species-level characteristics, changes in zooplankton-algal interactions, but also timing of warming and its effects on zooplankton life-histories.

Implications of climate change for fish will likely result from both direct and indirect effects of warming. Changes that occur at lower trophic levels could have important ramifications especially for young-of-year fish in early summer. In Lake Washington, USA, juvenile sockeye salmon (*Oncorhynchus nerka*) switch to feeding on *Daphnia* in spring. However, recent climate variability has caused negative changes in daphniid over-wintering and spring populations, thus forcing juvenile salmon to rely on less profitable prey (Hampton et al. 2006). Similar changes in predator-prey interactions could threaten many economically important recreational and commercial fisheries found in the Canadian prairies, e.g., Walleye in Lake Winnipeg.

Climate change has also allowed range expansion of aquatic organisms. In the Laurentian Great Lakes, recent invasions of non-native species from the Ponto-Caspian regions by ballast water discharge from container ships may have been facilitated by a warming climate (Schindler 2001). Schindler (2001) argues that warm-water Eurasian species, such as zebra mussels (*Dreissena polymorpha*) and large predatory cladocerans (*Bythotrephes longimanus*), could out-compete native cold-water species with climate change. In the Canadian prairies, potential human and/or natural dispersal of these species could have important repercussions for fisheries such as in Lake Winnipeg.

Warming could also have direct implications for native fish distributions. Fish species with narrow temperature tolerances are most at risk. Opposite effects will likely be seen for cold and warm stenothermic fishes. Model simulations predict that Brook Trout (*Salvelinus fontinalis*), a cold-water species, could lose nearly 50% of their range by the year 2050 (Chu et al. 2005). Moreover, other fishes predicted to benefit from warmer temperatures, e.g., Walleye (*Sander vitreus*) and Smallmouth Bass (*Micropterus dolomieu*) (Chu et al. 2005) may not experience range expansion if intensified land-use practices, eutrophication, and contaminant concentrations continue to degrade suitable fish habitat.

Biological variability: Can we predict change?

Overall, responses of biological systems to climate change could be variable and complex. In the boreal forest, current observations of climate change responses such as forest fires, insect infestations, treeline expansion and forest composition show agreement with predicted scenarios (Soja et al. 2007). In many cases, Soja et al. (2007) also show that changes have occurred more quickly than anticipated suggesting rapid non-linear