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## Decadal regulation of phytoplankton abundance and water clarity in a large continental reservoir by climatic, hydrologic and trophic processes

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### ABSTRACT

Large continental reservoirs are impacted by multiple stressors including climate change, watershed development, food-web alteration, water extraction, hydroelectric-power generation, and industrial aquaculture. Such complexity makes it difficult to identify the hierarchical relationships among regulatory processes, forecast effects of environmental change, or develop adaptive management strategies. Here we present a regression-based analysis of 19 years of limnological change in a representative main-stem reservoir within central North America to suggest that phytoplankton abundance and water clarity are regulated by hierarchical but independent mechanisms. The Qu'Appelle arm of Lake Diefenbaker, Canada, was monitored during summers (May–August) of 1995–2013 to evaluate the unique and interactive effects of continental climate systems, regional meteorology, river hydrology and limnological characteristics on phytoplankton abundance and water clarity. Regression models explained 48–52% of historical variation despite the absence of pronounced temporal patterns in monthly or summer phytoplankton abundance and water clarity. Phytoplankton abundance (mainly diatoms, flagellates) was correlated positively with soluble reactive phosphorus concentrations and inversely with the density of large herbivores, factors which were themselves correlated to variation in chemical conditions (oxygen, dissolved inorganic carbon) and dissolved organic carbon content, respectively. In contrast, water clarity varied directly as a function of climate systems (producing warm, dry winters) and inversely with river flow. We conclude that anticipated climate change (warmer, less runoff) will improve water clarity in lacustrine regions of large prairie reservoirs on decadal scales by reducing inorganic turbidity, while nutrient fluxes associated with economic development may independently regulate algal abundance.

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### Introduction

As with natural lakes, water quality in large continental reservoirs is impacted by climate change (Chen et al., 2007; Marce et al., 2010; Sukenik et al., 2012), watershed development (Hall et al., 1999a; Jackson et al., 2001; Leigh et al., 2010) and food-web alteration (Post et al., 2002), all of which interact and vary in intensity through time. In addition, reservoirs may be managed for water extraction (Baldwin et al., 2008; Joeckel and Diffendal, 2004), hydroelectric power generation (Soumis et al., 2004) and industrial aquaculture (Figueredo and Giani, 2005; Guo and Li, 2002), while ontogenetic changes in internal nutrient supply can cause a decadal-scale upsurge in algal production (Hall et al., 1999a; Thornton et al., 1990). Such complex interactions between multiple stressors makes it difficult to identify the hierarchical relationships among regulatory processes, forecast effects of environmental change, or develop adaptive management strategies to balance economic and environmental issues (Crossman et al., 2013; Marce et al., 2010).

Climate variability and directional warming are expected to have pronounced effects on water resources in the northern Great Plains (Barrow, 2009). Present-day climate variability arises from the interaction of three major climate systems and three air masses (Arctic, Pacific, Gulf of Mexico) that supply moisture into the continental interior (Bonsal and Shabbar, 2008; Bryson and Hare, 1974). Variation in the North Atlantic Oscillation during winter (NAO<sub>w</sub>) appears to regulate cyclonic activity over the Prairies early each year (Hurrell, 1995; Wang et al., 2006) and is associated with changes in timing of ice melt, algal production and development of the clear water phase during spring (Dröscher et al., 2009; Weyhenmeyer et al., 1999). Similarly, the Pacific Decadal Oscillation (PDO) (Mantua et al., 1997) and El Niño–Southern Oscillation (ENSO) (Trenberth and Hurrell, 1994) regulate influx of Pacific precipitation to the Prairies and runoff from western mountains (Shabbar et al., 2011; St. Jacques et al., 2010) and can interact to produce exceptionally warm, dry conditions in winter and spring (Mantua et al., 1997; McCabe et al., 2004) and which, in turn, alter plankton phenology (McGowan et al., 2005b; Winder and Schindler, 2004). Finally, general circulation models predict that the mean annual temperature of the Canadian Prairies will increase ~4 °C by 2050 (Barrow, 2009; Lapp et al., 2012), leading to higher hydrological variability and intensification of

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both droughts (Lapp et al., 2013; van der Kamp et al., 2008) and pluvial periods (Winter and Rosenberry, 1998). These events will further lead to more variable water chemistry (Pham et al., 2009; Starks et al., 2014), altered regional hydrology (Pomeroy et al., 2007; Schindler and Donahue, 2006) and changes in heat budgets that regulate planktonic production (Johnk et al., 2008; Paerl and Otten, 2013; Winder and Sommer, 2012), community composition (Cantin et al., 2011; Huisman et al., 2004; Magnuson et al., 1997), and outbreaks of potentially-toxic cyanobacteria (Donald et al., 2011; Sukenik et al., 2012).

Large reservoirs in continental interiors are often found in fertile catchments subject to extensive anthropogenic influence including agriculture (nutrients, erosion, pesticides, drainage), urbanization (microbes, pharmaceuticals, metals, nutrients), and hydrologic modifications (Bolgrien et al., 2009; Fernandez et al., 2014; Hall et al., 1999a). For example, ancestral European settlement of the Canadian Prairies since 1880 has transformed the grasslands due to mechanized cultivation (since 1920), fertilization (since the 1940s) and localized urban development (Bunting et al., 2011; Hall et al., 1999b; Leavitt et al., 2006). Over 70% of surface cover has been converted to grain and livestock farming while permanent surface water cover has declined over 50% to 5–8% of land area (Bunting et al., 2011; Hall et al., 1999b). Elevated fluxes of nutrients and suspended solids have increased algal productivity, reduced water clarity, and intensified blooms of cyanobacteria in natural lakes (Leavitt et al., 2006; Orihel et al., 2012) although less is known of the responses of regional reservoirs (McGowan et al., 2005a; North et al., 2014). Large-scale elimination of wetlands by farming has changed runoff of snow and rain (Pomeroy et al., 2007; van der Kamp et al., 2008), an important control on the fluxes of nutrients and other solutes to aquatic ecosystems in the grasslands (Pham et al., 2008; Starks et al., 2014). Similarly, reservoirs in continental interiors are often subject to regulated but extensive (>5 m) variation in lake water-level reflecting the highly seasonal nature of local snowmelt (March–April) (Akinremi et al., 1999; Fang and Pomeroy, 2007), the importance of snowmelt from the Rocky Mountains to the hydrological budgets of main-stem reservoirs (June) (Saskatchewan Water Security Agency, SWSA, 2012), and the use of large reservoirs for industrial, urban, and agricultural applications (Hall et al., 1999a).

Complex, hierarchical, and temporally-variable interactions between multiple stressors complicate development of a mechanistic understanding of how humans and climate interact to regulate water quality and ecosystem structure in reservoirs (Crossman et al., 2013; Hart and Calhoun, 2010). To address this issue, we analyzed a 19-year time series from a large lacustrine embayment (Qu'Appelle arm) of the Lake Diefenbaker reservoir to quantify how environmental variability associated with climatic regimes, regional meteorology, hydrologic variability and intrinsic limnological properties related to human activity (nutrient content, food-web structure, etc.) influences phytoplankton abundance and water clarity in continental reservoirs. Such long-term ecological research (LTER) is of particular use in developing robust predictive models for changes in biological, chemical, and physical properties of aquatic ecosystems, and allowing scientists and managers to develop management strategies to adapt to future environmental change (Adrian et al., 2009; Chen et al., 2007). The empirical models developed here serve as an important first step to identifying targets for potential future management action both in this region and in similar sub-humid ecozones around the world (e.g., southern South America, central Asia, central China, Australia).

## Methods

### Site description

Lake Diefenbaker is a 220-km long reservoir located ~554 m above sea level (a.s.l.) on the South Saskatchewan River, Canada, and which serves as headwater to Qu'Appelle River drainage basin (Hall et al.,

1999a; Hecker et al., 2012). The reservoir's catchment which lies mainly within Alberta, Saskatchewan, and upstate Montana was originally mixed-grass Prairie, but it is presently under predominantly (~65%) agricultural land use (cereal crops, pasture, livestock) (Hall et al., 1999a). The reservoir lies within a broad glacial outwash valley formed by the meltwaters of the Wisconsin ice sheet (Christiansen, 1960) and is underlain by cretaceous marine sedimentary bedrock (Bearpaw formation) with a thick overburden of glacial till and predominantly dark-brown chernozemic soils (Acton et al., 1998). There are no major urban centers in the immediate vicinity of Lake Diefenbaker, although Calgary (pop. 990,000), Red Deer (pop. 97,100) and Medicine Hat (pop. 61,200) lie 200–400 km upstream in the upper catchment within Alberta while smaller Swift Current, Saskatchewan (pop. 15,500) is located ~50 km south of the reservoir.

Regional climate is classified as sub-humid continental, exhibits a moisture deficit of 30–60 cm/year, and is characterized by short warm summers (mean 19 °C in July), cold winters (mean –16 °C in January), and low mean annual temperatures (~1 °C) with high seasonal variability. Most regional runoff occurs in spring during a brief snowmelt period in late March or early April (Pham et al., 2009; Pomeroy et al., 2007) although monthly inflows to Lake Diefenbaker are highest in June and early July when melt-waters arrive from the Rocky Mountains (Akinremi et al., 1999; Fang and Pomeroy, 2007; SWSA, 2012). Reservoir hydrology varies widely among years with a four-fold difference between minimum and maximum annual inflows since 1995 and a >6-m seasonal variation in lake level (Hall et al., 1999a; Quiñones-Rivera et al., in this issue).

Lake Diefenbaker is a large (area = 394 km<sup>2</sup>, deep ( $Z_{\max}$  ~62 m) basin with a relatively short residence time (~1.3 years) characteristic of large riverine reservoirs in central North America (Bolgrien et al., 2009; Hall et al., 1999a). Surface waters in the Qu'Appelle arm (area ~50 km<sup>2</sup>;  $Z_{\max}$  ~23 m) are cool and well oxygenated (Dröscher et al., 2009; Sadeghian et al., in this issue) with low nutrient content and phytoplankton abundance relative to other regional lakes (Leavitt et al., 2006; Patoine et al., 2006). In general, the embayment warms slowly and is polymictic although in some years limited thermal stratification is observed during late-July or August (Dröscher et al., 2009; Hudson and Vandergucht, in this issue). Phytoplankton are characteristic of well-mixed mesotrophic lakes with abundant diatoms in spring giving way to later-summer assemblages of flagellates and occasional cyanobacteria (Hecker et al., 2012; McGowan et al., 2005b; Patoine et al., 2006). The zooplankton community is composed mainly of cyclopoid (*Diatocyclops thomasi*) and calanoid (*Leptodiaptomus siciloides*) copepods, but also includes large (*Daphnia pulex*, *Daphnia galeata mendotae*, *Diaphanosoma birgei*, *Holopedium gibberum*) and small (*Bosmina longirostris*, *Daphnia retrocurva*) cladocerans at lower densities (Patoine et al., 2006). Fish assemblages include 25 native and stocked species, such as walleye (*Sander vitreus*), northern pike (*Esox lucius*), rainbow trout (*Oncorhynchus mykiss*), lake char (*Salvelinus namaycush*), yellow perch (*Perca flavescens*), cisco (*Coregonus artedii*), bigmouth buffalo (*Ictiobus cyprinellus*), and white sucker (*Catostomus commersonii*) (for full list, see SWSA, 2012).

Paleolimnological analyses demonstrate that the downstream lacustrine portions of Lake Diefenbaker have experienced three intervals of contrasting water quality since valley inundation in 1967 (Hall et al., 1999a; Lucas et al., in this issue; Tse et al., in this issue). First, lake production increased ca. 1968–1975 when diatoms were characteristic of eutrophic conditions (*Stephanodiscus niagarae*, *Stephanodiscus parvus*) and colonial and N<sub>2</sub>-fixing cyanobacteria were present. Second, reservoir production declined ca. 1975–1986, as mesotrophic diatoms (*Tabellaria flocculosa* str. Illp, *Fragilaria crotonensis*, *Aulacoseira ambigua*) replaced eutrophic species (Hall et al., 1999a; Lucas et al., in this issue). Finally, the trophic status of Lake Diefenbaker increased again after ca. 1986, with elevated abundance of productive diatoms (*A. ambigua*), chlorophytes and colonial cyanobacteria (Hall et al., 1999a; Tse et al., in this issue). During this latter transition, water-column chlorophyll

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