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

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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; Joekel and Diffendal, 2004), hydroelectric power generation (Soumis et al., 2004) and industrial aquaculture (Figueroedo 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 w) 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 (Dröschler 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
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 ecoszones 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; Quiones-Rivera et al., 2015).

Lake Diefenbaker is a large (area = 394 km²), deep (Zmax ~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 km²; Zmax ~23 m) are cool and well oxygenated (Dröscher et al., 2015) 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 polymeric although in some years limited thermal stratification is observed during late-July or August (Dröscher et al., 2009; Hudson and VanderGucht, 2015). 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 cyclopid (Diacyclops 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 artedi), 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., 2015; Tse et al., 2015). First, lake production increased ca. 1968–1975 when diatoms were characteristic of eutrophic conditions (Stephanodiscus niagarae, Stephanodiscus parvus) and colonial and N2-fixing cyanobacteria were present. Second, reservoir production declined ca. 1975–1986, as mesotrophic diatoms (Tabellaria flocculosa str. Ilp, Fragilaria crotonensis, Aulacoseira ambiguus) replaced eutrophic species (Hall et al., 1999a; Lucas et al., 2015). Finally, the trophic status of Lake Diefenbaker increased again after ca. 1986, with elevated abundance of productive diatoms (A. ambiguus), chlorophytes and colonial cyanobacteria (Hall et al., 1999a; Tse et al., 2015). During this latter transition, water-column chlorophyll (Chl a) increased from ~1 μg/L
in 1984 to ~5 μg/L in 1994 (Environment Canada, 1988). Recent publications suggest that modern phytoplankton abundance has remained elevated (McGowan et al., 2005b; Patoine et al., 2006) and that colonial cyanobacteria may be problematic (Hecker et al., 2012), although there has been no comprehensive evaluation of water quality change since the mid-1990s. Whole-basin carbon budgets demonstrate that Lake Diefenbaker has been net heterotrophic (respiration > primary production) during the past 20 years (but see Quiñones-Rivera et al., 2015), although CO2 sequestration has increased since ca. 2003 in this and other basins (Finlay et al., 2009, 2010).

**Climate data**

Time series of climate variables (1995–2010) were assembled from public archives, including the US National Oceanic and Atmospheric Administration (NAO), the Australian National Climate Centre (Southern Oscillation Index, SOI), and the University of Washington Joint Institute for the Study of the Atmosphere and Ocean (PDO). Additionally, we estimated the known synergistic interaction between El Niño phases of ENSO and positive phases of the PDO as the product of their respective indices (Bonsal and Shabbar, 2008; Shabbar and Yu, 2012). The calendar day of year (DOY) of spring ice melt from Lake Diefenbaker was obtained from Vogt et al. (2011).

**Meteorology**

Meteorological measurements (1995–2013) within the catchment were obtained from the Environment Canada National Climate Archives (http://www.climate.weatheroffice.gc.ca/ climateData; April 2014) for the Outlook, Saskatchewan, weather station situated ~28 km north of Lake Diefenbaker (51°29’N, 107°03’W). Mean monthly air temperature (°C), precipitation (mm) and daily wind speed (km/h) were computed for an ice-free (“summer”) period that overlapped with limnological sampling (01 May–31 August). Snow accumulation (mm) was estimated as the sum of monthly precipitation from January–March in each calendar year.

**Hydrology**

Hydrologic data (1995–2010) were collected by the Saskatchewan Water Security Agency (SWSA) and used to assess the monthly or total summer inflow to Lake Diefenbaker (m³/d). Inflow was estimated using standard governmental procedures, based on data from discharge gauges on streams, measurements of lake levels, and estimates of net evaporation (Saskatchewan Water Security Agency, SWSA, 2012 and unpublished).

**Limnological characteristics**

The Qu’Appelle arm of Lake Diefenbaker is one of two large lacustrine embayments in the reservoir and was sampled bi-weekly during summer 1995–2013 using standard protocols as part of a regional long-term ecological monitoring program (QU-LTER) (Finlay et al., 2009; McGowan et al., 2005b; Patoine et al., 2006). Briefly, depth-integrated samples were collected at midday at a standard geo-positioned station (51°01’26.0’N, 106°29.84’W) by pooling casts of a 2-L Van Dorn water bottle deployed at 1-m intervals to 15 m depth. Integrated samples were filtered through a 0.45-μm pore membrane filter and analyzed at the University of Alberta Water Chemistry Laboratory for concentrations of soluble reactive phosphorus (SRP, μg P/L) and total dissolved phosphorus (TDP, μg P/L), as well as dissolved nitrogen (TDN), ammonia (NH₄⁺), and the sum of NO₂⁻ and NO₃⁻ (all μg N/L) (Patoine et al., 2006). Total inorganic (TIC) and dissolved organic carbon (DOC) concentrations (mg C/L) in filtered samples were quantified using a Shimadzu model 5000A (Shimadzu, Kyoto, Japan) total carbon analyzer following Finlay et al. (2009). Water temperature (°C) and oxygen content (mg O₂/L) were computed as average values of depth profiles collected every 1 m using a YSI model 85 meter (YSI, Yellow Springs, Ohio, USA). Surface water pH was measured at 0.5-m depth using a calibrated handheld probe, while water clarity was measured using a 20-cm diameter Secchi disk. Zooplankton densities were estimated bi-weekly, May–August for 1995–2012, from vertical tows of a 20-cm diameter Wisconsin net (243-μm mesh) at the standard sampling station. Invertebrate samples were preserved and enumerated according to Patoine et al. (2006). Individual species densities (ind./L) were summed as total zooplankton, copepods, large cladocerans and small cladocerans (see above for species). Rotifers were not enumerated.

Phytoplankton abundance and community composition in the Qu’Appelle arm was estimated 1995–2012 using standard trichromatic and high performance liquid chromatographic (HPLC) analysis of carotenoid and chlorophyll pigments (Leavitt and Hodgson, 2001; Vogt et al., 2011). Briefly, particulate organic matter (POM) from depth-integrated water samples (see above) was collected on GF/C glass fiber filters (nominal pore 1.2-μm) and extracted using either pure acetone (trichromatic) or a mixture of acetone:methanol:water (80:15:5, by volume) (HPLC). Trichromatic estimates of chlorophyll a (Chl a) concentrations were used as an index of total phytoplankton abundance (μg Chl/L). In contrast, carotenoids, chlorophylls and their derivatives were isolated and quantified (nmol pigment/L) using an Agilent model 1100 HPLC system (Agilent Technologies Inc., Mississauga, Canada) fitted with photodiode-array and fluorescence detectors and calibrated using authentic standards (Leavitt and Hodgson, 2001). Historical changes in phytoplankton community composition were estimated using pigment biomarkers from siliceous algae (mainly diatoms and chrysophytes; fucoxanthin), cryptophytes (alloxanthin), dinoflagellates (peridinin), chlorophytes (Chl b), colonial cyanobacteria (myxoxanthophyll), and N₂-fixing cyanobacteria (aphanizophyll). As shown by Donald et al. (2013), trichromatic- and HPLC-based analyses provide equivalent estimates of gross phytoplankton abundance and composition as do enumerations of cellular biovolume using light microscopy.

**Data analysis**

For modeling purposes, historical changes in water quality were assessed using estimates of total phytoplankton abundance (Chl a) and water clarity (Secchi depth) during 1995–2010, the interval in which complete predictor data were available. First, linear regression models were developed for both explanatory and response variables to assess the mode of variation of each time series. Time series were detrended using first-difference procedures if temporal autocorrelation was detected. Second, multiple regression models were developed for both water quality indices using forward selection of predictors with two stopping criteria (α and R²adj; 9999 permutations) from the full suite of climatic, meteorological, hydrological and limnological variables (Blanchet et al., 2008). As our goal was to identify potential regulatory mechanisms rather than develop the most parsimonious model, final model composition was not based solely on Akaike’s Information Criterion (AICc), although typically the final model also exhibited the lowest AICc (analysis not shown). The relative contribution of each predictor was quantified using a type III sum of squares analysis of variance (ANOVA) in which variation explained by each predictor was summed into classes representing climate, meteorology, hydrology and internal lake characteristics. Subsequently, regression models were developed for the statistically significant predictors of water quality and clarity, thereby allowing us to evaluate the hierarchical relationships among potential regulatory variables. This approach avoids over-fitting with complex models of poor predictive capabilities (Sharma et al., 2013). Finally, regression analyses were repeated using time series with monthly resolution to assess seasonal variation in potential regulatory processes. Variables were transformed (log₁₀) as necessary to produce normal distributions and co-linear parameters were excluded from final models.
All data manipulation and statistical analyses were performed in the R-language environment using the `lm` (linear regression), `acf` (auto-correlation) and `forward.sel` (packfor) (forward selection) functions (R Development Core Team, 2014).

**Results**

**Water quality time-series**

Linear regression analysis revealed no significant linear trends in total phytoplankton abundance or water clarity (Fig. 1a, Table 2). When highly productive 1995 was not considered, a small but significant increase in total phytoplankton abundance was recorded for the interval 1996–2012 ($R^2_{adj} = 0.17, \ p = 0.05$) (Fig. 1a). Regression analysis of time series with monthly resolution showed the increase in phytoplankton abundance was restricted to July ($R^2_{adj} = 0.26, \ p = 0.019$) only if 1995 was eliminated, and was not observed in any analyses of data derived solely from May, June or August (all $R^2_{adj} = 0.00, \ p > 0.34$). In contrast, there were no significant linear trends in water clarity recorded in any month ($R^2_{adj} = 0.00–0.07, \ p > 0.15$), though the greatest water clarity occurred during August and the least during June in most years (Fig. 1c).

**Phytoplankton community composition**

HPLC analysis of phytoplankton community composition revealed that siliceous algae (diatoms and chrysophytes) composed 50–80% total algal biomass in the Qu'Appelle arm of Lake Diefenbaker in each year (Fig. 2). In general, relative abundance of these taxa peaked during May, before being partly replaced by cryptophytes (most years), dinoflagellates (9 years) and colonial cyanobacteria (14 years). Overall, diazotrophic cyanobacteria were abundant early (1996–1999) and late (2007–2012) in the time series, whereas non-N2-fixing colonial cyanobacteria were more common in other years (Fig. 2). Cyanobacteria were uncommon in 2001, 2004 and 2006, whereas this group exhibited its maximum abundance within the QU-LTER during 2012.

**Environmental time series**

Regression-based analysis of time series of physico-chemical, climatic, meteorological and hydrological parameters (Table 1) revealed...
few significant trends during the past 20 years. Total zooplankton densities declined significantly and substantially since the mid-1990s ($R^2_{adj} = 0.38 \ p = 0.004$), with a particularly steady rate of decrease since 2000 ($R^2_{adj} = 0.78 \ p < 0.001$) (Fig. 3a). This trend was driven by concomitant reductions in mean summer densities of large-bodied cladocerans ($R^2_{adj} = 0.69, \ p < 0.001$) and copepods ($R^2_{adj} = 0.47, \ p = 0.002$), but not small cladocerans ($R^2_{adj} = 0.00, \ p = 0.46$) (Fig. 3b). Similarly, the pH of Lake Diefenbaker surface waters increased nearly 1.0 unit since 1995 ($R^2_{adj} = 0.37, \ p = 0.008$), similar to patterns recorded in other prairie lakes (Finlay et al., 2009; Vogt et al., 2011). Of the 20 remaining variables, only concentrations of oxygen (increase; $R^2_{adj} = 0.31, \ p = 0.015$) and NH$_4$ (decline; $R^2_{adj} = 0.37, \ p = 0.007$) exhibited significant directional changes during the monitoring period.

Models of summer water quality

Intrinsic limnological characteristics were the strongest predictors of total phytoplankton abundance during 1995–2010, accounting for 48% of historical variation in concentrations of Chl a (Fig. 4a). Specifically, mean phytoplankton abundance during summer was correlated positively to SRP concentration (29% variation explained), and negatively to total zooplankton abundance (19% variation) (Fig. 4b, Table 2). Analysis of models based on monthly data (not shown) suggested that SRP was a significant predictor ($p < 0.05$) of phytoplankton abundance late in summer (July–August), while effects of zooplankton were restricted to July (analysis not shown). In contrast, changes in mean summer water clarity (52% variation explained) were predicted by hydrologic inflow (37% variation) and the prevalent climate system (ENSO-PDO; 15% variation), but not by limnological or meteorological parameters (Fig. 4b, Table 2).

Additional regression models suggested that the controls of water quality (SRP, zooplankton) were themselves under independent regulation. For example, water-column concentrations of SRP were correlated negatively to oxygen content and positively to concentrations of inorganic C ($R^2_{adj} = 0.48 \ p = 0.006$), whereas total zooplankton abundance was correlated negatively to concentrations of DOC ($R^2_{adj} = 0.21 \ p < 0.05$) (Table 2). Regression models were not developed for the principal predictors of water clarity (hydrologic inflow, ENSO-PDO), because those factors are regulated by processes outside the spatial domain of our data collection (snowmelt in Rocky Mountains and Pacific seafloor-surface temperature, respectively) (Lapp et al., 2013; St. Jacques et al., 2010).

Discussion

Analysis of a comprehensive suite of limnological and environmental variables from the lacustrine zone of a major continental reservoir (Table 1) demonstrated that phytoplankton abundance, community

![Fig. 2](image-url). Mean monthly (May–August) relative abundance of the major phytoplankton groups in the Qu’Appelle arm of Lake Diefenbaker, Canada (1995–2012). Absolute and relative abundance of phytoplankton groups was determined by high performance liquid chromatography of their diagnostic pigments. Phytoplankton groups (and pigments) include N$_2$-fixing cyanobacteria (aphanizophyll), colonial cyanobacteria (myxoxanthophyll), chlorophytes (chlorophyll b), siliceous algae (diatoms and chrysophytes; fucoxanthin), cryptophytes (alloxanthin), and dinoflagellates (peridinin).

### Table 1

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composition and water clarity have been resilient to climatic and anthropogenic stressors during the past 20 years (Figs. 1, 2). All three parameters show little evidence of directional change during 1995–2013, consistent with recent paleolimnological quantification of phytoplankton abundance in lacustrine regions since 1967 (Tse et al., 2015) and 30 years of Landsat imagery (Yip et al., 2015), but in contrast to continued increases in regional population, agricultural production and climate warming, and to declining river discharge (Bunting et al., 2011; Leavitt et al., 2006; St. Jacques et al., 2010). Instead, half of observed inter-annual variation in mean-summer phytoplankton abundance (mainly diatoms, flagellates) was explained by trophic processes (nutrient availability, herbivory) (Table 2, Fig. 3), whereas a similar proportion of changes in water clarity were explained mainly by physical controls (ENSO-PDO, river inflow) (Table 2). Given that the food-web structure and hydrological cycle of Lake Diefenbaker are similar to those observed for many of the largest reservoirs in the United States (Bolgrien et al., 2009; Bowersox et al., 2014; Lynott et al., 1995), we suggest that our findings provide a useful model for lacustrine regulatory processes in reservoirs in much of central and western North America. Specifically, we forecast that future declines in river inflow from mountain snowfields (Lapp et al., 2013; St. Jacques et al., 2010) should reduce the inorganic turbidity, whereas continued economic development that elevates nutrient supply will likely favor increased phytoplankton abundance and possibly cyanobacterial outbreaks in lacustrine embayments (Donald et al., 2011; Leigh et al., 2010). Consequently, selection of the appropriate management strategy will depend on whether such reservoirs are exploited principally for industrial, recreational or domestic uses.

**Phytoplankton abundance**

Moderate phytoplankton abundance (Fig. 1) and diatom-rich community composition (Fig. 2) are consistent with observations in other large temperate reservoirs in the Great Plains of North America (Bolgrien et al., 2009; Joeckel and Diffendal, 2004). In these large lakes, hydrologic and nutrient influx (Finlay et al., 2009; Patoine et al., 2006) is controlled mainly by snowmelt in westerly mountain ranges during early summer (Lapp et al., 2013; St. Jacques et al., 2010), rather than local snowmelt during March and April (Fang and Pomeroy, 2007; Pham et al., 2009; Quiñones-Rivera et al., 2015). Typically, water from mountain ranges is cold, has lower nutrient content than seen in natural prairie lakes (Pham et al., 2008, 2009), and exhibits high turbidity associated with suspended inorganic particulates, leading to low algal production (Dubourg et al., 2015). Diatoms predominate when turbulence related to inflow is greatest (spring, early summer) (Hall et al., 1999a), while flagellates (cryptophytes, chlorophytes, dinoflagellates) are increasingly common as inflow slows, turbulence declines, and thermal stratification may occur (Abirhie et al., 2015; Dröscher et al., 2009; McGowan et al., 2005b). These patterns are in marked contrast to many natural lakes in the prairie ecorezone (Donald et al., 2013; Leavitt et al., 2006; Pham et al., 2008), as well as some large reservoirs from continental interiors of China (Lv et al., 2014), Australia (Bowling et al., 2013), and South America (Fernandez et al., 2014), where high turbidity reflects dense blooms of cyanobacteria arising from excessive supply of P and N (Leigh et al., 2010; Sukenik et al., 2012). Differences in production between the large reservoirs of western North America and natural prairie lakes may reflect differences in the predominant source of nutrients to the water-column of artificial (alochthonous, riverine) and natural aquatic ecosystems (autochthonous, sedimentary) (e.g., Leavitt et al., 2006; Abirhie et al., 2015; Patoine et al., 2006).

Absence of decadal-scale trends in water quality is consistent with observations from other large prairie lakes (Bunting et al., 2011; Patoine et al., 2006), Landsat analysis of this reservoir (Yip et al., 2015), and recent paleolimnological analysis of phytoplankton fossils in Lake Diefenbaker sediments (Yip et al., 2015). Although phytoplankton abundance has increased >300% above baseline in many large prairie lakes, most cultural eutrophication occurred by 1990 mainly due to intensification of grain and livestock production during the 20th century (Bunting et al., 2011; Hall et al., 1999a). Similarly, although the downstream reaches of Lake Diefenbaker experienced a small trophic surge for several years following inundation of the valley in 1967 (Hall et al., 1999a; Lucas et al., 2015), phytoplankton abundance declined before expanding again to a stable plateau in the late 1980s and early 1990s (Tse et al., 2015). Although speculative, recent research suggests that modern water quality conditions may be the result of an interaction between long-term land-use patterns and a sudden persistent change in climatic forcing within the northern Great Plains (McCullough et al., 2012).

Multiple regression models suggest that nutrient supply from reservoir sediments during summer may be an important control of decadal variability in total phytoplankton abundance. Specifically, depth-integrated estimates of phytoplankton abundance were correlated positively with that of SRP, whereas the latter was correlated negatively with water-column oxygen level and positively with DIC content (Table 2). Bottle bioassays conducted biweekly during summers

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**Table 2.** Mean summer phytoplankton abundance in Lake Diefenbaker, Canada, during May–August 1995–2012.

<table>
<thead>
<tr>
<th>Year</th>
<th>Zooplankton (ind/L)</th>
<th>Copepods (ind/L)</th>
<th>Leptodiaptomus siciloides</th>
<th>Diacyclops thomasii</th>
</tr>
</thead>
<tbody>
<tr>
<td>1995</td>
<td>10.00</td>
<td>10.00</td>
<td>10.00</td>
<td>10.00</td>
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<tr>
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<td>2007</td>
<td>30.00</td>
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<td>30.00</td>
<td>30.00</td>
</tr>
<tr>
<td>2010</td>
<td>35.00</td>
<td>35.00</td>
<td>35.00</td>
<td>35.00</td>
</tr>
<tr>
<td>2013</td>
<td>40.00</td>
<td>40.00</td>
<td>40.00</td>
<td>40.00</td>
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</tbody>
</table>

**Fig. 3.** Mean summer density of (A) total zooplankton density (ind./L) and (B) copepods (Leptodiaptomus siciloides, Diacyclops thomasii), large cladocerans (Daphnia spp.) and small cladocerans collected from the Qu’Appelle arm of Lake Diefenbaker, Canada, during May–August 1995–2012.
since 1994 as part of the QU-LTER program reveal that while most down-
stream Qu’Appelle lakes exhibit pronounced algal limitation by supply of N (Donald et al., 2011; Leavitt et al., 2006), instantaneous algal growth in the lacustrine portion of Lake Diefenbaker is regulated mainly by P supply (Dubourg et al., 2015; Hecker et al., 2012; Quiñones-Rivera et al., 2015). Further, diazotrophic cyanobacteria are rare (Fig. 2) (Abirhire et al., 2015; McGowan et al., 2005b) and there is no net fixation of atmospheric N₂ in most years (Patoine et al., 2006). Instead, Lake Diefenbaker is a substantial net sink for P flux through the South Saskatchewan River drainage basin (North et al., 2015). As shown by Nürnberg (1998), water-column P concentrations are thought to be influenced by the development of deepwater hypoxia (but see Hupfer and Lewandowski, 2008), mainly due to declines in the effectiveness of the oxidized microzone as a P trap with loss of O₂ (reviewed in Wetzel, 2001). Consistent with this hypothesis, sediments of the Qu’Appelle arm of Lake Diefenbaker are over 50% inorganic carbonate by mass (Finlay et al., 2010) and appear to be a significant source of P to the water column (North et al., 2015).

Internal nutrient loading is also hypothesized to be responsible for decade-long surges in planktonic production in reservoirs. In this case, flooding of dry river valleys leaches soluble nutrients from formerly terrestrial soils, erodes newly formed shorelines, and decomposes inundated vegetation (reviewed in Thornton et al., 1990). Oxygen consumption during vegetation decomposition favors deepwater anoxia, further increasing nutrient flux from sediments (see above). However, continued erosion of shorelines also buries submerged organic substrates, reduces oxygen demand and nutrient release, and reduces production by benthic communities in favor of planktonic assemblages, leading to a decline in lake production (Hall et al., 1999a; Hewlett et al., 2015; Thornton et al., 1990). Although this ontogenetic pattern can be modified by differences in the original habitat type (terrestrial, wetland, etc.) and/or the rate of erosion, the direction of change is consistent with a shift from bottom-up to top-down control of primary production.

![Fig. 4.](image-url) (A) Proportion of total explained variation (open bars) and sources of explained variation (filled bars) in total phytoplankton abundance (as μg Chl a/L) and water clarity (as Secchi depth, m) as identified in multiple regression analysis of mean summer (May-August) conditions in the Qu’Appelle arm of Lake Diefenbaker, Canada, 1995–2010. Model performance was evaluated by adjusted coefficient of determination ($R^2_{adj}$). Significant ($p < 0.05$) explanatory variables were selected by forward selection multiple regression based on 9999 permutations and were classified into categories associated with variation in climate systems (black), river hydrology (dotted), and internal lake characteristics (waves). (B) Potentially-causal relationships among water quality variables and independent predictors were identified from multiple regression models (Table 2). Predictors include soluble reactive phosphorus (SRP), mean total zooplankton density (Zoop.), indices of interactions between the Pacific Decadal Oscillation (PDO) and El Niño-Southern Oscillation (ENSO), and riverine inflow to Lake Diefenbaker (Inflow). Numbers and signs reflect the proportion of explained variation in water quality parameters (ovals) attributable to variation in predictor variables (squares) due to inhibitory (−) or stimulatory (+) interactions.
aquatic), area of flooded land, degree of shoreline development, valley geometry, water turbidity and magnitude of water level fluctuations (Hecky and Guildford, 1984; Thornton et al., 1990), studies generally agree that autochthonous nutrient sources can be important controls of decadal-scale development of reservoir productivity independent of allochthonous sources (Thornton et al., 1990). Better estimation of the importance of internal nutrient sources is essential for Lake Diefenbaker and other large reservoirs in central North America (North et al., 2015), as these water bodies supply much of the potable water to urban centres in the continental interior (e.g., Saskatchewan Water Security Agency, SWSA, 2012).

Recent changes in the grazing regime in Lake Diefenbaker may have also had an important effect on phytoplankton abundance during the past 20 years (Table 2, Fig. 3). While quantitative estimates of fish abundances are not available, the marked and persistent decline in density of large zooplankton (Fig. 3) coincides with a documented escape of ~360,000 rainbow trout from a local fish farm in the year 2000 (Saskatchewan Water Security Agency, SWSA, 2012; Saskatchewan Environment, unpublished data). This event was one of a series of unintended releases during the past 15 years. Rainbow trout have a varied diet in large reservoirs of central North America, but prefer large-bodied zooplankton and other invertebrates when fish are up to 46 cm in length (Lynott et al., 1995). Consistent with the effects of size-selective predation by visually-orienting fish, densities of large-bodied Daphnia and copepods declined nearly 75% between 2000 and 2012 (Fig. 3a), whereas the abundance of small cladocerans was unchanged (Fig. 3b). Similarly, research on other large western lakes (e.g., L. Tahoe) reveals that stocked rainbow trout prefer much of the potable water to urban centres in the continental interior (e.g., Saskatchewan Water Security Agency, SWSA, 2012). Recent changes in the grazing regime in Lake Diefenbaker may have also had an important effect on phytoplankton abundance during the past 20 years (Table 2, Fig. 3). While quantitative estimates of fish abundances are not available, the marked and persistent decline in density of large zooplankton (Fig. 3) coincides with a documented escape of ~360,000 rainbow trout from a local fish farm in the year 2000 (Saskatchewan Water Security Agency, SWSA, 2012; Saskatchewan Environment, unpublished data). This event was one of a series of unintended releases during the past 15 years. Rainbow trout have a varied diet in large reservoirs of central North America, but prefer large-bodied zooplankton and other invertebrates when fish are up to 46 cm in length (Lynott et al., 1995). Consistent with the effects of size-selective predation by visually-orienting fish, densities of large-bodied Daphnia and copepods declined nearly 75% between 2000 and 2012 (Fig. 3a), whereas the abundance of small cladocerans was unchanged (Fig. 3b). Similarly, research on other large western lakes (e.g., L. Tahoe) reveals that stocked rainbow trout prefer

### Table 2

<table>
<thead>
<tr>
<th>Water quality variable</th>
<th>Linear regression</th>
<th>Multiple regression</th>
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<tbody>
<tr>
<td></td>
<td>𝑅^2_adj</td>
<td>𝑝</td>
</tr>
<tr>
<td>Total phytoplankton (μg Chl/L)</td>
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<td>0.09</td>
</tr>
<tr>
<td>Water clarity (m)</td>
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<tr>
<td>Soluble reactive phosphorus (μg P/L)</td>
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<td>0.33</td>
</tr>
<tr>
<td>Total zooplankton (ind./L)</td>
<td>0.38</td>
<td>0.004</td>
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</tbody>
</table>

### Water clarity

Multiple regression analysis shows that inter-annual variation in water clarity is regulated mainly by changes in climatic conditions that regulate river discharge and inorganic turbidity (Table 2). Specifically, the Qu’Appelle arm of Lake Diefenbaker was more transparent in years with dry winters (ENSO-PDO) and low discharge of the South Saskatchewan River (inflow). Runoff to reservoirs in the Northern Great Plains is derived from two main water sources; local snowmelt during March–April (Fang and Pomeroy, 2007; Pham et al., 2009), and influx of alpine meltwaters via east-flowing rivers in June (e.g., South Saskatchewan, Missouri) (Quiñones-Rivera et al., 2015; St. Jacques et al., 2010). While the former combines with regional groundwater sources to sustain natural lakes in the Canadian Prairies (Pham et al., 2009; van der Kamp et al., 2008), discharge of large prairie rivers that regulate reservoir hydrology is controlled mainly by release in alpine snow packs and upstream hydrologic management (Lapp et al., 2013).

Timing and magnitude of release of water from mountain sources appears to be controlled in part by variation in the PDO (Lapp et al., 2012, 2013; Schindler and Donahue, 2006), with anomalously low discharge occurring when ENSO and PDO systems reinforce each other to split the winter jet stream and induce warm dry winters in western Canada and northern USA (Mantua et al., 1997; McCabe et al., 2004; Shabbar et al., 2011). In general, years with low river discharge result in lower turbidity associated with suspended solids (Thornton et al., 1990), because of both lower influx and reduced erosion of reservoir shorelines (Coakley and Hamblin, 1969; Hewlett et al., 2015). Interestingly, although both ENSO and PDO systems are known to regulate spring climate, trophic interactions, phytoplankton composition and primary production (Dröscher et al., 2009; Weyhenmeyer et al., 1999), our regression analysis revealed no evidence of direct effects of climate, hydrology or regional meteorological condition on mean summer phytoplankton abundance or composition within the Qu’Appelle arm (Table 2). Instead, we conclude that water clarity and phytoplankton abundance in large lacustrine reaches are under parallel but largely independent regulatory mechanisms (physical and trophic, respectively).
Forecasts of reservoir response to climate and anthropogenic stressors

General circulation models and downscaled regional climate models predict that the North American grasslands will warm ~4 °C within 40 years (Barrow, 2009). Such effects may be particularly noticeable in central Canada, where minor changes in mean annual temperatures (~1 °C) change the state of water (solid, liquid). Although precipitation on the northern Great Plains is expected to increase and become more variable in coming decades, elevated evaporation associated with atmospheric warming is expected to offset increased receipt of snow and rain, producing a more arid climate (Lapp et al., 2012). We infer that river inflow to large prairie reservoirs (Diefenbaker, Oahe, Sakakawea, Fort Peck) will remain a key regulatory mechanism in the future, given that base flow in prairie rivers has already declined nearly 50% since 1900 due to climate change and industrial use (St. Jacques et al., 2010), future PDO systems may be weaker than at present (Lapp et al., 2012), and the snowmelt in the Rockies is expected to occur earlier and decline in magnitude (St. Jacques et al., 2010). Based on our analyses, we anticipate that these declines will favor less turbid water suitable for domestic and agricultural consumption, particularly in downstream lacustrine regions.

Continued strong urban and industrial growth in much of the Canadian Prairies, combined with expected economic recovery in the central United States, may increase nutrient influx to regional reservoirs. For example, application of agricultural fertilizers has risen steadily since 1960 and is expected to nearly double again by 2050 (Bogard et al., 2011). Similarly, stronger commodity prices (grain, oil, potash), combined with plentiful regional reserves, suggest that anthropogenic nutrient influx to large reservoirs will continue to increase due to future economic development. While these nutrient sources do not appear to have degraded water quality in eastern Lake Diefenbaker during the past 20 years (Fig. 1, Table 2) (Tse et al., 2015; Yip et al., 2015), modern and paleolimnological analysis of large regional water bodies suggest that anthropogenic effects may develop slowly, before reaching a tipping point beyond which water quality changes suddenly (Bunting et al., 2011). Further research is needed to determine whether increased phytoplankton production after 1990 reflects such a threshold effect (Bunting et al., 2011), the result of a trophic upsurge during reservoir ontogeny (Hall et al., 1999a; Thornton et al., 1990), or a sudden change in regional climatic forcing mechanisms (McCullough et al., 2012).

Regression analysis of nearly two decades of limnological monitoring suggests that optimal management strategy for lacustrine reaches of large reservoirs within central North America may depend on the relative importance of industrial, recreational and domestic uses of the ecosystem, as well as whether the reservoir is managed to optimize phytoplankton abundance or water clarity. Longer reservoir residence times will favor less turbid water suitable for consumption by livestock and humans, although this strategy will likely reduce generation of hydroelectric power (Saskatchewan Water Security Agency, SWSA, 2012) and may favor potentially-toxic blooms of cyanobacteria (Fig. 2) because of reduced dilution of internal nutrient sources and increased water clarity (Dubourg et al., 2015). Similarly, management for industrial aquaculture will likely increase nutrient supply (Figueroed and Giani, 2005; Guo and Li, 2002), while reducing herbivore control of phytoplankton (Fig. 3, Table 2). Finally, managers must recognize that specific strategies are likely to interact with continued economic growth and climatic variability to produce complex, hierarchical pathways of ecosystem regulation (Leavitt et al., 2009).

Acknowledgments

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