

# Direct and interactive effects of climate, meteorology, river hydrology, and lake characteristics on water quality in productive lakes of the **Canadian Prairies**

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22	Running head: Regulation of landscape-scale water quality
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### 24 Abstract

25 Aquatic ecosystems are subject to multiple interacting stressors that obscure regulatory mechanisms and reduce the effectiveness of management strategies. Here we estimate the unique 26 27 and interactive effects of continental climate systems, regional meteorology, river hydrology, and 28 internal lake characteristics on patterns of landscape-scale water quality in six productive lakes within a 52,000 km<sup>2</sup> catchment. We quantify variation in mean summer and monthly algal 29 30 abundance, surface bloom intensity, water clarity, and density of potentially-toxic cyanobacteria 31 during 16 years on the Canadian Prairies. Internal lake characteristics best predicted overall 32 water quality change, while climate systems, regional weather, and river hydrology characterized 33 indirect pathways that influenced physico-chemical environments. Scenario analysis of future 34 environmental change predicted that atmospheric warming  $(3-5^{\circ}C)$  will have the strongest effect 35 on water quality in these productive lakes, but unexpectedly predicted that even severe industrial 36 water extraction (1% of inflow) will have negligible effects on transparency or algal abundance. 37 Instead, nutrient management represents the only practical means to sustain water quality, 38 although atmospheric and lake warming may override re-oligotrophication of eutrophied sites in 39 future decades.

### 40 Introduction

41 Accurate prediction of the unique and interactive effects of climate and humans on 42 aquatic ecosystems will require an improved mechanistic understanding of how ecosystems 43 interact with and respond to environmental variability (Leavitt et al. 2009; Vogt et al. 2011). 44 Among the many challenges associated with such ecological forecasting is the mounting 45 evidence that threats to water quality (e.g., climate, nutrients, toxins, hydrologic flow, exotic 46 species) vary in space and time and can interact through complex pathways (Christensen et al. 47 2006; Palmer and Yan 2013). Development of effective management strategies to protect aquatic 48 ecosystems will require analytical frameworks suitable for large landscapes and that organize 49 anthropogenic and climatic stressors into hierarchies of threat (Brown et al. 2011) by identifying 50 the pathways by which environmental change degrades water quality. This need may be 51 particularly pronounced for lakes in central North America and other continental interiors where 52 dry conditions (Barrow 2009) combine with intensive agriculture (Hall et al. 1999; Bunting et al. 53 2016), urbanization (Leavitt et al. 2006; Waiser et al. 2010), and high climatic variability (Pham 54 et al. 2009; Pomeroy et al. 2007) to create multifaceted controls of water quality (Schindler and 55 Donahue 2006; Leavitt et al. 2009; Bunting et al. 2016).

Decades of research have shown that cultural eutrophication remains among the greatest threats to sustainable water quality (Carpenter et al.1998; Schindler 2006). For example, lakes in continental interiors often lie in large flat fertile agricultural catchments that deliver high nutrient influx (Leavitt et al. 2006; Patoine et al. 2006) and characteristically exhibit high algal productivity, low N:P ratios, and frequent blooms of nitrogen-fixing cyanobacteria (Haertel 1976; Patoine et al. 2006; Orihel et al. 2012). Agricultural development is pervasive in these regions (>75% of land area) such that eutrophication has been favoured by increased tillage, crop

63 fertilization, and industrial livestock activities (Hall et al. 1999; Bunting et al. 2016). Similarly, 64 the low density and discharge of most regional rivers in dry interior regions (Bonsal and Shabbar 65 2008) can lead to disproportionate effects of nutrients and other contaminants from urban centres 66 (Leavitt et al. 2006; Waiser et al. 2010). Pollution of these phosphorus (P)-rich lakes with 67 nitrogen (N) has been shown to increase production and toxicity of cyanobacteria by up to 500% 68 (Leavitt et al. 2006; Donald et al. 2011; Orihel et al. 2012), with unambiguous evidence that 69 water quality has been degraded substantially by nutrients from agricultural and urban activities 70 during the past century (Hall et al. 1999; Maheaux et al. 2015; Bunting et al. 2016). 71 Climate variability has pronounced effects on lakes within continental interiors (Barrow 72 2009; Schindler and Donahue 2009). In the Canadian prairie region of the northern Great Plains, 73 climate variability arises from the interaction of three major climate systems and three air masses 74 (Arctic, Pacific, Gulf of Mexico) that supply moisture into the continental interior (Bonsal and 75 Shabbar 2008). The Pacific Decadal Oscillation (PDO) (Mantua et al. 1997) and El Niño-76 Southern Oscillation (ENSO) (Trenberth and Hurrell 1994) both influence the influx of Pacific 77 precipitation to the Prairies and runoff from western mountains (St. Jacques et al. 2010; Shabbar 78 et al. 2011), with synergism among climate systems producing mild and arid conditions in winter 79 and spring (Mantua et al. 1997; McCabe et al. 2004; Bonsal et al. 2006), 10-fold variation in 80 spring runoff (Pomeroy et al. 2007), and up to 50-day variation in timing of plankton phenology 81 (McGowan et al. 2005; Dröscher et al. 2009). Similarly, the North Atlantic Oscillation (NAO; 82 computed using winter months) regulates annual cyclonic activity and winter breakouts of the 83 Arctic air mass into the Prairies (Hurrell 1995; Wang et al. 2006), timing of ice melt, and development of the clear water phase during spring (McGowan et al. 2005; Dröscher et al. 2009). 84 85 Such strong climatic forcing is forecast to intensify in the future, with a  $\sim 4^{\circ}$ C increase in mean

annual temperature of the Canadian Prairies by 2050 (Barrow 2009; Lapp et al. 2012; IPCC
2013), combining with lower snowfall and runoff (Cohen et al. 2015) to intensify both droughts
and extreme pluvial periods (van der Kamp et al. 2008; Lapp et al. 2013). Together, these events
increase the variability of water chemistry (Pham et al. 2009), regional hydrology (Schindler and
Donahue 2006; Pomeroy et al. 2007), and energy budgets (Dröscher et al. 2009) resulting in
altered planktonic production, community composition, and cyanobacterial abundance (Huisman
et al. 2004; Paerl and Otten 2013).

93 Lakes in continental interiors may be further subjected to intensive hydrologic 94 management to regulate water supplies for urban, agricultural, and industrial applications 95 (Saskatchewan Water Security Agency, SWSA, 2013). For example, low elevation gradients  $(\sim 0.4 \text{ m km}^{-1})$  and high precipitation deficits (20-60 cm yr<sup>-1</sup>) (Pham et al. 2009), combine with 96 97 strongly seasonal precipitation (75% during summer) and runoff mainly (75% of annual 98 discharge) within a three-week interval during spring (Akinremi et al. 1999; Fang and Pomeroy 99 2007), to create low densities of small rivers through much of the northern Great Plains. In the 100 central Canadian Prairies, potash solution mines also alter regional hydrology by each consuming up to  $20 \times 10^6 \text{ m}^3 \text{ yr}^{-1}$  of surface water at full production (J. Hovdebo, Director Licensing and 101 102 Water Use, SWSA, pers. comm.). When combined with similar magnitudes of urban and 103 agricultural uses, industrial applications could effectively eliminate flow in all but the largest 104 regional rivers (SWSA 2013). Although compensatory increases in water conveyance alleviate 105 shortfalls, perpetually augmented flows to offset year-round industrial water extraction can 106 favour vernal flooding and facilitate lotic transport of urban pollutants to downstream lakes 107 (Leavitt et al. 2006; Wyn et al. 2007). Given that these rivers also supply most of the potable 108 water to urban populations on the Canadian Prairies (Hall et al. 1999), an improved

understanding of the effects of hydrologic regime on water quality is essential to developing
sustainable management strategies (Gober and Wheater 2014).

111 Here we use decadal time series from six productive lakes within the Canadian Prairies to 112 quantify the unique and shared effects of variation in continental climate systems, regional 113 meteorological conditions, hydrologic flow regimes, and internal lake characteristics on four 114 indices of regional water quality in eutrophic lakes: total algal abundance, incidence of algal 115 surface blooms, density of potentially-toxic cyanobacteria, and water clarity. We also outline an 116 analytical framework wherein we quantify how water quality parameters have changed over the 117 past 16 years, and apply a generalized numeric approach to determine which classes of predictors 118 have the greatest influence on prairie water quality. These empirical models are then used in a 119 scenario analysis to explore future water quality change in eutrophic hard water lakes in response 120 to expected climate warming, management of nutrients fluxes, and hydrologic modification. 121 Such models are needed to develop a roadmap for adaptive management of aquatic ecosystems, 122 while allowing for continued social and economic development.

### 123 Methods

124 *Site Description* – The six productive study lakes are situated within the Qu'Appelle River catchment, a system that drains  $\sim$ 52,000 km<sup>2</sup> of mixed grassland in southern Saskatchewan 125 126 (SK), Canada (Fig. 1). This chain of lakes extends ~400 km eastward from mesotrophic (Lake 127 Diefenbaker) and eutrophic reservoirs (Buffalo Pound) to hyper-eutrophic downstream lakes 128 (Katepwa, Crooked), with sub-saline Last Mountain Lake and hyper-eutrophic Wascana Lake 129 reservoir draining into the Qu'Appelle River through small tributaries near the City of Regina. 130 Regional climate is characterized as cool-summer humid continental (Köppen Dfb classification), 131 with short summers (mean 19°C in July), cold winters (mean -16°C in January), and low annual

temperatures (~1°C) with high seasonal variability. Average annual precipitation is ~380 mm,
with most rain falling between May and July, and most runoff occurs during a short snowmelt
period in spring (Akinremi et al. 1999; Fang and Pomeroy 2007). This region experiences high
hydrologic variability, such that river inflow to lakes varies by an order-of-magnitude between
years and across the catchment. The surrounding landscape is largely agricultural (~75%; grains
and pasture), with smaller sections remaining as undisturbed grassland (~12%) and surface
waters (~5%) (Hall et al. 1999; Finlay et al. 2015).

Study lakes are all productive, but vary up to 10-fold in most morphometric and
limnological parameters (Table 1; Supporting Information, SI, Table S1). Lakes are polymictic,

141 although Katepwa and Diefenbaker can exhibit limited thermal stratification during some

142 summers. Lakes share a common plankton composition distinguished by diverse summer

143 assemblages of cyanobacteria and abundant cyclopoid copepods (Patoine et al. 2006; Vogt et al.

144 2011). Regional fish communities include walleye (*Sander vitreus*), northern pike (*Esox lucius*),

145 yellow perch (Perca flavescens), cisco (Coregonus artedi), bigmouth buffalo (Ictiobus

146 *cyprinellus*), and white sucker (*Catostomus commersoni*), although precise community

147 composition and population densities are not known for most years.

148 *Climate data* - Time series of climate variables (1995-2010) were compiled from public 149 archives, including the US National Oceanic and Atmospheric Administration (North Atlantic 150 Oscillation index, NAO), the Australian National Climate Centre (Southern Oscillation Index, 151 SOI), and the University of Washington Joint Institute for the Study of the Atmosphere and 152 Ocean (PDO). Additionally, we estimated potential interactions between the PDO and El Niño 153 Southern Oscillation (ENSO; as SOI) as the product of the respective indices because low-flow 154 hydrological events are amplified by a synergistic interaction between El Niño phases of ENSO

155	and positive phases of the PDO (Bonsal and Shabbar 2008; Shabbar and Yu 2012). The calendar
156	day of year (DOY) of spring ice melt 1995-2010 was obtained from Vogt et al. (2011).
157	Meteorology - Meteorological measurements (1995-2010) within the catchment were
158	obtained from the Environment Canada National Climate Archives
159	(http://www.climate.weatheroffice.gc.ca/ climateData) for four weather stations that occupy the
160	same latitudinal and longitudinal gradients as the study lakes (Fig. 1). Mean monthly air
161	temperature (°C), precipitation (mm), and daily wind speed (km h <sup>-1</sup> ) were acquired for May-
162	August and were used to compute a mean summer value that overlapped with the limnological
163	sampling regimen (described below). Snow accumulation was estimated as the sum of monthly
164	precipitation from January-March in each calendar year. Variation in solar irradiance was
165	quantified by Environment Canada for each meteorological site (Vogt et al. 2011); however,
166	because of discontinuous data availability, energy fluxes could not be estimated for all lakes and
167	years, and irradiance data were not used in statistical models.
168	Hydrology - Hydrologic data were collected by the Saskatchewan Water Security Agency
169	(SWSA) and were assessed as the total monthly or summer inflow to each lake $(m^3 d^{-1})$ . Inflows
170	were estimated using flow gauges on streams, measurements of lake levels, and estimates of net
171	evaporation. Inflow data and lake volume were used to compute residence time for each lake and
172	year. In contrast, the nutrient content of river water was not available for most sites (c.f., Donald
173	et al. 2015), such that annual variation in allochthonous N and P influx could not be estimated for
174	all lakes and years, and were not included in statistical models. However, earlier mass balance
175	studies comparing the outflow of upstream lakes with the inflow of basins immediately
176	downstream (Patoine et al. 2006; Leavitt et al. 2006; Finlay et al. 2010) suggest that historical

variations in water-column nutrient concentration (see below) can be used to approximatehistorical changes in nutrient influx during the ice-free period.

179 Internal Lake Variables - Study lakes were sampled bi-weekly using standard protocols 180 from May to August during 1995-2010, except for Wascana Lake (1996-2010) (Patoine et al. 181 2006; Vogt et al. 2011). Depth-integrated samples were collected at midday at a standard geo-182 positioned station in each lake by pooling casts of a 2-L Van Dorn water bottle taken every meter 183 to a maximum depth of 3 m (Buffalo Pound, Wascana), 6 m (Crooked), or 15 m (Diefenbaker, 184 Last Mountain, Katepwa). These integrated samples were filtered through a 0.45- $\mu$ m pore 185 membrane filter and analyzed at the University of Alberta Water Chemistry Laboratory for concentrations of soluble reactive phosphorus (SRP,  $\mu g P L^{-1}$ ) and total dissolved phosphorus 186 (TDP,  $\mu$ g P L<sup>-1</sup>), as well as total dissolved nitrogen (TDN), ammonium (NH<sub>4</sub><sup>+</sup>), and the sum of 187  $NO_2^{2-}$  and  $NO_3^{2-}$  (all  $\mu$ g N L<sup>-1</sup>). Total inorganic (TIC) and dissolved organic carbon (DOC) 188 concentrations (mg C  $L^{-1}$ ) in filtered samples were quantified using a Shimadzu model 5000A 189 190 (Shimadzu, Kyoto, Japan) total carbon analyzer following Finlay et al. (2009). Water temperature (°C;  $T_{water}$ ) and oxygen content (mg  $O_2 L^{-1}$ ) were computed as average values of 191 192 depth profiles collected every 1 m using a YSI model 85 meter (YSI, Yellow Springs, Ohio, 193 USA), while pH was measured at the surface (0.5 m) using a calibrated handheld probe. 194 Zooplankton densities were estimated bi-weekly (May-August 1995-2010) from vertical 195 tows of a 20-cm diameter Wisconsin net (243-µm mesh) at the standard sampling station in each 196 lake. Invertebrate samples were preserved and enumerated according to Patoine et al. (2006). Densities of individual species (ind.  $L^{-1}$ ) were summed by month and for each year for a set of 197 198 taxonomic categories that included total zooplankton (all species), herbivorous or omnivorous 199 taxa (carnivores excluded), large-bodied cladocerans (Daphnia galeata mendotae, D. magna, D.

200 pulex, Diaphanosoma birgei), small-bodied cladocerans (D. retrocurva, Bosmina longirostris,

201 Ceriodaphnia sp., Chydorus, sp.), and copepods (Leptodiaptomus siciloides, Diacyclops

202 *thomasii*). We anticipated that landscape-scale changes in planktivory by fish and invertebrates

- 203 (Vogt et al. 2013, 2015) would be evident as changes in the densities of large and small
- 204 zooplankton due to size-selective trophic interactions (Carpenter and Kitchell 1993).

205 Water Quality Indices - Water clarity was measured using a 20-cm diameter Secchi disk, 206 lowered in shade at a standard sampling station. Total algal abundance (total algae) was 207 estimated from depth-integrated water-column concentrations of chlorophyll a (Chl a), collected 208 from pooled Van Dorn samples taken at 1-m intervals, and quantified using standard trichromatic 209 techniques (Vogt et al. 2011). Surface chlorophyll a (surface bloom intensity) was measured 210 similarly based on samples collected only in the uppermost 1 m of the water column. 211 Concentrations of colonial cyanobacteria were assessed based on the depth-integrated 212 concentrations of the taxonomically diagnostic carotenoid myxoxanthophyll, a biomarker for 213 colonial and potentially toxic cyanobacteria. Microscopic analysis shows that Microcystis and 214 Anabaena spp. are common phytoplankton in Qu'Appelle lakes, that these taxa produce hepatotoxic microcystin (MC), and that toxin levels can exceed Canadian (1.5  $\mu$ g L<sup>-1</sup>) and World 215 Health Organization (1.0  $\mu$ g L<sup>-1</sup>) drinking water guidelines by 10-fold (Donald et al. 2011; Orihel 216 et al. 2012). Myxoxanthophyll concentration (nmoles  $L^{-1}$ ) was measured using an Agilent model 217 218 1100 high performance liquid chromatography (HPLC) system (Agilent, Palo Alto, California, 219 USA) calibrated with authentic standards as described by Leavitt et al. (2006).

Data Analysis - Identification of hierarchical relationships among multiple environmental
 stressors requires a diverse suite of statistical tools and a stepwise sequence of analytical
 decisions (Sharma et al. 2008, 2013). Here we outline a general framework for such analysis that

incorporates considerations of both temporal and spatial autocorrelation, model selection, and variation-partitioning procedures, and which estimates the relative influence of diverse potential regulators on environmental quality. We apply this three-step framework to the lake ecosystems described above, but anticipate that our approach will be suitable for other ecosystems with long time series.

228 In the first step, linear regression models were developed for both explanatory and 229 response variables to assess the mode of variation of each time series. For example, the 230 autocorrelation function (ACF) was used to quantify the series correlations in time series 231 residuals over a range of time lags (Carpenter 1993). In the presence of a significant linear trend, 232 time series were first detrended using first-difference procedures. In this paper, predictor and 233 response time series exhibited no statistically significant evidence of autocorrelations, thresholds, 234 discontinuities, nonlinearities, or oscillatory dynamics. As a result, there was no requirement for 235 subsequent models to include advanced time series procedures, such as autoregressive moving-236 average components (Hampton et al. 2013).

In the second step, multiple regression models were developed independently for all waterquality indices using forward selection of predictors from the full suite of climatic,

meteorological, hydrological, and limnological variables (Sharma et al. 2013). 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 adjusted for small sample sizes (AICc), although forward selection typically also produced the model with lowest AICc (analysis not shown). Instead, we used a forward selection based on two-stopping criteria to identify variables that would be included in the multiple regression model. Variables were selected to be included in the model using significant alpha values less than 0.05, and

adjusted  $R^2$  values ( $R^2_{adi}$ ) that significantly increased explained variation (Blanchet et al. 2008). 246 247 The relative contribution of each predictor was quantified using a type III sum of squares analysis 248 of variance (ANOVA) in which variation explained by each predictor was summed into classes 249 representing climate, meteorology, hydrology, and internal lake characteristics. In addition to the 250 four water quality indices, regression models were developed for their most influential predictors 251 (T<sub>water</sub>, SRP, TIC, pH; see below) to assess indirect controls of water quality. Initial analyses 252 focused on mean summer values, but data with monthly resolution were also used to quantify 253 seasonal differences in potential regulatory mechanisms. Preliminary correlation analysis 254 revealed that the only significant interaction between response variables was that of total algal 255 abundance and water clarity; hence it alone was included in the final models.

256 In all models, variables were transformed  $(\log_{10})$  as necessary to produce normal 257 distributions and multi-collinear parameters were excluded from final models (VIF>10, r>0.7). 258 Significant (p < 0.05) model parameters were selected using a Monte-Carlo forward selection 259 procedure with 9999 permutations (Blanchet et al. 2008) and model explanatory power was summarized using adjusted coefficient of determination  $(R^2_{adi})$ . The potential influence of 260 261 landscape position and site-specific, but un-measured, limnological variables on regression 262 models was estimated using a categorical lake identification code as a covariate; however, as lake 263 identity did not substantially influence model fit, this code was not retained in the final models (analysis not shown). Similarly, time series were evaluated for the possibility of applying 264 265 regression tree analysis (Orihel et al. 2012), but this approach was not employed here because the predictive power of such models was too low ( $R^2 < 0.25$ ), likely owing in part to the number of 266 267 sites and length of time series. All data manipulation and statistical analyses were performed in 268 the R-language environment (R Development Core Team 2013).

269 In the third step, regression models were used to explore the effects of future scenarios of 270 regional environmental change on water quality and to identify potential management strategies. 271 Ensemble forecasts from general circulation models suggest that regional air temperatures will 272 increase 1.5-4°C by 2046-2065 CE (5°C by 2100 CE) (IPCC 2013), while industrial water 273 extraction could nearly eliminate flow of all but the largest rivers if not augmented by 274 conveyance from headwater reservoirs (SWSA 2013). In addition, nutrient concentrations could 275 both decrease or increase in the near future, as regional runoff has declined 25% due to 276 diminished winter precipitation (Akinremi et al. 1999; St. Jacques et al. 2010) and the City of 277 Regina was required by Canadian federal law to upgrade wastewater facilities by 2017, but high 278 regional economic growth (~5% year<sup>-1</sup>) may increase non-point fluxes of nutrients. To forecast 279 how these factors may influence water quality, we applied the regression models to scenarios in 280 which we estimated values for total algae, surface blooms, and water clarity for a range of 281 potential increases in water temperature (1- 5°C), inflow regimes (1%, 25%, 50%, 150%, 200%, 282 and 1000% of current mean summer inflow), and nutrient fluxes (10%, 25%, 50%, 200% and 283 300% of water column means). This scenario analysis included both the unique effects of each 284 stressor and factor interactions. Even though the multiple regression procedure generated a 285 statistically significant model abundances of colonial cyanobacteria, it was not included in this 286 forecast analysis because of its comparably weaker fit relative to the other water quality metrics 287 (see below).

288 **Results** 

*Time-series characteristics* - There were no significant linear trends in mean summer
 values for any of the four water quality parameters during 1995-2010 (Fig. 2, SI Table S2).
 Similarly, time series showed no evidence of auto-correlation, despite an apparent 5-yr cycle in

colonial cyanobacteria in the shallowest lakes (Wascana, Buffalo Pound). When analyzed with data collected in May, total algal abundance ( $R^2_{adj} = 0.06$ , p=0.008), surface bloom intensity ( $R^2_{adj}$ = 0.05, p=0.02), and densities of colonial cyanobacteria ( $R^2_{adj} = 0.04$ , p=0.04) all increased slightly through time, whereas water transparency did not exhibit significant change (analysis not shown). There were no significant temporal trends for any water quality variable for analyses restricted to data from June, July, or August.

Among internal lake characteristics, only mean summer pH increased significantly ( $R^2_{adj}$ = 0.28, *p*<0.0001) during the 16-year sampling period (Finlay et al. 2009, 2015), although this trend was statistically significant only during the months of May and July. Water temperature, SRP, and TIC did not exhibit statistically significant trends in either summer or monthly mean values. All limnological and environmental time series lacked significant temporal autocorrelation over the period studied.

304 Models of summer water quality – Multiple regression models explained 26-75% of variation (as  $R^2_{adi}$ ) in mean summer water quality parameters (Fig. 3a). In general, intrinsic 305 306 limnological characteristics were the strongest predictors of total algae, surface blooms, water 307 clarity, and abundance of colonial cyanobacteria, accounting for 53-80% of explained variation. 308 River hydrology played a secondary role in predictive models, accounting for an additional 9-309 25% of explained variation, while climate systems usually accounted for lower fractions of 310 explained variation in models of total algae (~11%), water clarity (~7%), and colonial 311 cyanobacteria (~15%). Regional meteorology was a substantial predictor for models of colonial 312 cyanobacterial abundance (~33% of explained variation) (Fig. 3a). 313 Total algal abundance and surface bloom intensity were both correlated positively with

changes in  $T_{water}$ , SRP, and pH, and negatively with river inflow to lakes (SI Table S2). In

315 addition, total algal abundance was related inversely to the NAO index. In contrast, water clarity 316 was correlated positively to lake inflow, TIC content, and PDO×ENSO interactions, and 317 negatively to T<sub>water</sub> and concentrations of Chl a and SRP. Densities of colonial cyanobacteria 318 were correlated positively to T<sub>water</sub> and negatively to wind speed and the ENSO (SI Table S2). In 319 all cases, model performance was equivalent when NH<sub>4</sub><sup>+</sup> replaced SRP as a predictor (analysis 320 not shown), suggesting that the effects of these dissolved nutrients could not be distinguished. 321 Given the relative importance of select physico-chemical characteristics (T<sub>water</sub>, dissolved 322 nutrients, TIC, pH) as predictors of water quality, we built additional regression models to 323 investigate how these limnological parameters responded to variation in the climate systems, 324 regional meteorology, hydrological regimes, and other lake characteristics (Fig. 3b, SI Table S3). These new models explained 23-51% ( $R^{2}_{adi}$ ) of mean summer variation in limnological drivers of 325 326 water quality, with river hydrology (~22-83% of explained variation), climate (~20-76%), and 327 meteorological conditions (~10-40%) making important model contributions. Specifically, T<sub>water</sub> 328 was correlated positively to air temperature, but negatively to volume of inflow, ice-off date, and 329 snow accumulation, whereas SRP concentration was correlated negatively to river inflow and 330 wind speed, and TIC content was correlated positively to ice-off date and inversely to inflow 331 (Table 4). Only variation in mean summer pH was predicted by changes in other internal lake 332 characteristics (~54% of explained variation) (Fig. 3b), with a positive correlation to water-333 column DOC content, and a negative relationship with TIC concentration, NAO index, summer 334 precipitation, and date of ice melt.

Monthly models of water quality - Model performance varied substantially by month and among water quality parameters (Fig. 4). For example, regression models based on data from May explained 65-78% of variation in all water quality parameters except for colonial

338 cyanobacteria, while more modest (26-70%), but still statistically-significant, models could be 339 constructed for all parameters when models were based on data from July or August alone. In 340 contrast, only the models for water clarity and algal abundance were significant during June  $(R^2_{adi})$ = 0.65,  $R_{adi}^2$  = 0.30). Similar to models of mean summer conditions, internal lake characteristics 341 342 exerted the greatest influence on monthly water quality, accounting for 80-100% of explained 343 variation during May-July and a reduced, but still paramount, proportion in August (Fig. 4). 344 Once again, T<sub>water</sub>, dissolved nutrients, TIC, and pH were the most important predictors of algal 345 abundance. Interestingly, river hydrology and regional meteorological conditions were correlated 346 with water-column Chl a concentration, but not with the abundance of colonial cyanobacteria. 347 Overall, food-web processes were only significant in the water clarity models of May and June, 348 when large-bodied cladocerans were significant predictors of changes in secchi depth (15% and 349 3% of explained variance, respectively).

350 Forecasting future water quality – Scenario analysis with regression models suggested 351 that increases in water temperature due to climate warming will have a greater effect on total 352 algal abundance and surface bloom intensity in these productive lakes than will either regional 353 management of nutrient sources or changes in hydrology resulting from industrial extraction or 354 compensatory increases in river conveyance (Table 2). For example, models predicted that total 355 algal abundance will increase by  $\sim$ 75% with a 5°C increase in T<sub>water</sub>, whereas Chl *a* content is 356 expected to vary little  $(\pm 7\%)$  if inflow is either doubled or declines to 1% of mean summer 357 inflow. Instead, algal abundance only declined appreciably (~65%) when hydrologic input to 358 lakes was increased 1000% over mean summer conditions, a value which exceeds conveyance 359 capacity of the Qu'Appelle River. Algal responses to changes in nutrient sources were of 360 intermediate intensity, with models predicting a 64% increase with three-fold higher

361 concentrations, and a 29% decline if nutrient content was reduced to 10% of current mean 362 summer values. Similarly, the intensity of surface blooms increased progressively with T<sub>water</sub> 363 (~60% for 5°C warming) and nutrients (~50% for 300% increase), while a 200% change in mean 364 river flow altered such blooms by <10%. In contrast, water clarity is expected to change less 365 than 3% with even extreme atmospheric warming, 10-fold variation in nutrient content, or a 366 doubling of hydrologic inflow (Table 2). In all cases, interactions between temperature, nutrient, 367 and river flow scenarios were purely additive and there was no evidence of either synergistic or 368 antagonistic interactions when multiple parameters were manipulated.

369

### 370 **Discussion**

371 Analysis of 25 decadal time series demonstrated that water quality in eutrophic lakes of 372 the Canadian Prairies is regulated mainly by variation in internal lake characteristics (water 373 temperature, dissolved nutrients, pH) (Fig. 3a), but that these limnological parameters are 374 correlated in turn to variations in large-scale climate systems, regional meteorology, and river 375 hydrology (Fig. 3b). Unexpectedly, the composition of predictive models varied substantially 376 among closely related measures of phytoplankton communities (SI Table S2) and among months 377 (Fig. 4), underscoring the need to explicitly evaluate both direct and indirect pathways for each 378 ecological stressor and response parameter (Palmer and Yan 2013). Further, application of these 379 models to realistic scenarios of future environmental change (Table 2) showed that potential 380 regulatory mechanisms with the greatest effect on water quality (temperature increase) or the 381 greatest ease of management (1000% variation in river conveyance) did not represent the most 382 effective means of sustaining regional water quality in the coming decades (nutrient diversion). 383 Such quantitative assessment of the relative effects of multiple forcing mechanisms is important

to allow scientists and managers to develop effective and adaptive management strategies to
 protect aquatic resources (Schindler 2001; Gober and Wheater 2014).

386 Controls of summer water quality - Regression analysis suggested that water quality 387 change during the past two decades was explained best by variation in T<sub>water</sub>, solute content, and 388 inflow regimes, factors that were ultimately under climatic control (SI Table S2). Elevated T<sub>water</sub> 389 increases algal growth (Paerl and Otten 2013; Winder and Sommer 2012) and intensifies the 390 thermal stratification that favours buoyancy-regulating, bloom-forming cyanobacteria in 391 eutrophic lakes (Huisman et al. 2004; Cantin et al. 2011). Warmer surface waters arise from 392 changes in the net energy budget of a lake (e.g., MacIntyre et al. 2014), which, for polymictic 393 prairie lakes, is mainly due to altered transmission of solar irradiance (O'Reilley et al. 2015), 394 variation in air mass and its temperature (Bonsal et al. 2006; Bonsal and Shabbar 2008), and 395 influx of discrete water sources (Dröscher et al. 2009). Although direct irradiance measures were 396 not available for all lakes and years as required for regression model analysis, previous analysis 397 of data from six regional meteorological stations (Vogt et al. 2011) reveals a slow increase in 398 regional receipt of solar energy and extremely low interannual variation (coefficient of variation 399 = 6%), in contrast to stable but more annually-variable lake parameters (Fig. 2). As well, earlier 400 analysis of energy budgets for regional lakes reveals that interannual variation in the rate of 401 summer heat accumulation in lakes (~50 days) is controlled by interactions between the mass of 402 snow received the preceding winter, timing of spring ice melt, and the volume of cold-water 403 runoff during the vernal freshet (Dröscher et al. 2009), all of which were identified as important 404 predictors in our regression analysis (SI Table S3). Spring runoff also influences algal density by 405 altering water renewal rates (dilution) in central North American lakes, as ~75% of regional river 406 discharge occurs during 3 weeks of March-April, yet runoff volume varies by 10-fold among

407 years (Fang and Pomeroy 2007; Pham et al. 2009). The importance of interannual variation in
408 seasonal properties is underlined by the fact that regression models explained up to 75% of
409 interannual variation in water quality parameters, despite the fact that there were no linear or
410 discontinuous changes in mean summer algal abundance, bloom characteristics, or water clarity
411 (Fig. 2).

412 Identification of separate influences of climate systems and regional meteorology on 413 water quality in eutrophic ecosystems is consistent with mechanisms known to regulate 414 atmospheric conditions in central Canada. Regional warming occurs most commonly when El 415 Niño and positive-phase PDO events interact to increase sea surface temperatures in the eastern 416 North Pacific Ocean and force jet-stream position northward beyond the Prairies (Shabbar et al. 417 2011). Similarly, introduction of synoptic precipitation into central Canada is influenced by the 418 position of continental jet streams that variously import water from the northern Pacific Ocean, 419 the Gulf of California, and the Gulf of Mexico (Higgins et al. 1997; Liu and Stewart 2003). 420 Finally, timing of ice melt is influenced strongly by atmospheric teleconnections, as warm spring 421 conditions are common during synergistic interactions between El Niño events and the PDO 422 (Bonsal et al. 2006), while winter extreme temperatures and ice cover are influenced by changes 423 in atmospheric circulation in the Arctic (as NAO) (Dröscher et al. 2009). Thus, while regional air 424 and water temperatures vary synchronously as a result of seasonal cycles of solar irradiance and 425 direct water-column heating, interactions among climate systems provide additional indirect 426 controls of lake warming through hydrologic variability (Dröscher et al. 2009).

Interactions between river hydrology, nutrient status, and lake production revealed by
regression models (SI Tables S2, S3) are consistent with regulatory mechanisms identified by
decadal-scale macronutrient budgets (Patoine et al. 2006; Leavitt et al. 2006; Finlay et al. 2010).

430 For example, regression models suggest that algal abundance is stimulated by nutrient content, 431 but reduced by river inflow (Table 2), despite allochthonous nutrient influx being a ubiquitous 432 predictor of lentic Chl content (Schindler 2006). Analysis of mass-balance budgets reconciles 433 these observations by demonstrating that lake sediments presently account for up to 85% of 434 nutrient supply to the water column of these eutrophic lakes (Patoine et al. 2006). In addition, 435 cold-region hydrological models (Pomeroy et al. 2007) and stable isotope analyses (Pham et al. 436 2009) both reveal that the brief snow melt in spring is the predominant source of water to 437 regional rivers and lakes and that the volume of runoff is greatest when rapid snow melt occurs 438 over frozen soils, conditions that favour water, but not necessarily nutrient, mobilization. As 439 well, we note that flow in the Qu'Appelle River is subject to engineered conveyance from 440 upstream lakes and that such channelized flow can decouple the relationships between climate, 441 runoff, and lotic nutrient concentrations seen elsewhere (McCullough et al. 2012; Bunting et al. 442 2016). Thus, while it remains necessary to be cautious about inference of regulatory mechanisms 443 from a regression-based analysis, the strong support of our models by whole-lake mass balance 444 budgets, catchment-scale nutrient transport studies, and centennial-scale paleoecological research 445 provides a solid mechanistic basis for our findings and their application to eutrophic lakes. 446 Comparison of regression model composition (SI Table S2) suggests that regulatory 447 pathways may differ substantially among even highly correlated water quality parameters or 448 limnological characteristics (Fig. 5). For example, models of total algal abundance and water 449 clarity were complex, of similar predictive power, and influenced by combination of climate 450 systems, hydrologic characteristics, and limnological properties, as described above. In contrast, 451 the model for colonial cyanobacteria included only variables related to energetic characteristics of lakes (temperature, wind speed, ENSO), a combination of variables that is consistent with 452

453 other research showing that colonial cvanobacteria are most abundant in eutrophic sites during 454 years when waters are warm, wind speed is low, and lakes exhibit stronger thermal stratification 455 (Huisman et al. 2004; Zhang et al. 2012; Paerl and Otten 2013). All these conditions are 456 enhanced during El Niño events and, accordingly, we note that both shallow lakes (Wascana, 457 Buffalo Pound) exhibited ~5 year cycles of colonial cyanobacteria abundance (Fig. 2) which, 458 while not statistically significant, peaked during known El Niño events (e.g., 1997). Such 459 marked differences among predictive models are important to document, as they suggest that 460 eutrophic lake management strategies will vary according to the precise regulatory goal (e.g., 461 increased transparency, reduced cyanobacteria).

462 Seasonal variation in predictive models - Pronounced variation in the predictive power of 463 water-quality models developed with monthly data (Fig. 4) is consistent with known patterns of 464 plankton phenology in the Qu'Appelle catchment. For example, algal abundance and water clarity models were strong in May ( $R^2_{adi} > 0.65$ ) when phytoplankton communities are composed 465 466 of diatoms and flagellates and complete water-column mixing eliminates vertical zonation of 467 phytoplankton (McGowan et al. 2005; Vogt et al. 2011). In contrast, colonial cyanobacteria are 468 rare in Qu'Appelle lakes during spring (Patoine et al. 2006), consistent with non-significant 469 model for their characteristic biomarker, myxoxanthophyll, during May. Overall, statistical 470 models suggested a role of herbivory in regulating water quality in early summer (but not all 471 summer), with the inclusion of large-bodied herbivores as predictors of water clarity in May and 472 June, the months in which intense grazing by large-bodied *Daphnia* spp. reduces algal biomass 473 and increases Secchi depth by up to 10-fold (Dröscher et al. 2009). In addition, while all water 474 quality models were significant when developed with data from either July or August, the latter 475 models were uniformly more predictive than those based on July data, possibly reflecting the fact that the high thermal capacity of very large lakes can extend cooler waters and clear water phases
later into the summer (Dröscher et al. 2009). Instead, parameters related closely to elevated
temperatures played a more important role in regression models developed with data from August
(Fig. 4d).

480 Landscape management of lakes - The analytical framework employed here allows us to 481 differentiate among global climate systems, regional meteorology, river hydrology, and site-482 specific limnological features as potential controls of water quality in productive lakes at the 483 landscape scale. Although our models were based solely on linear regression analysis, this 484 simple approach was warranted by the data structure, and more complicated analytical 485 approaches were unnecessary (e.g., detrending, regression trees, multivariate autoregressive 486 models, spectral analysis) (Hampton et al. 2013). Regardless, our analysis explained on average 487  $\sim$ 50% of observed interannual variation in algal abundance (SI Table S2), despite the absence of 488 any progressive trend in lake production during the past two decades (Fig. 2). Instead, 489 application of these models allowed us to develop a roadmap for adaptive management of 490 continental lakes in the face of future warming of 1.5-5°C (IPCC 2013), nutrient pollution from 491 farms and cities (Leavitt et al. 2006; Bunting et al. 2016), and industrial extraction of water by 492 agriculture or solute mines (SWSA 2013).

Analysis of model forecasts suggests that resource managers in semi-arid agricultural regions will have few options to improve regional water quality through regulation of energy and water fluxes. For example, while water temperatures were the best predictor of algal production (Table 2), direct reduction of energy influx to lakes is not possible. Similarly, the effectiveness of indirect management of thermal properties by cold water runoff is likely to be limited to early summer (Dröscher et al. 2009) due to high seasonality of discharge (Pomeroy et al. 2007; Fang

499	and Pomeroy 2007) and long hydrological transit times among lakes (Fig. 1). In addition,
500	although water conveyance though the Qu'Appelle River has been managed for over a century
501	via reservoirs (Diefenbaker, Buffalo Pound, Wascana) and outlet dams on natural lakes (Hall et
502	al. 1999; SWSA 2013), the limited channel capacity and low topographic relief (0.4 m km <sup><math>-1</math></sup> )
503	greatly constrains river discharge unless accompanied by re-channelization of the river. Even so,
504	our analysis shows that more than a doubling of lotic conveyance will have negligible effects
505	(<5%) on water quality (Table 2), a pattern which may generalize well to other dry continental
506	regions. In fact, even unrealistically diminished river flow (1% of mean summer values) appears
507	to have only relatively minor effects (<10% reduction) on water quality (Table 2). Further
508	analysis of the independent influx of nutrients and water from discrete sources (livestock
509	operations, cities, crop production) will help refine this observation (Bunting et al. 2016).
510	Application of regression models to realistic scenarios suggests that reductions in nutrient
511	influx may be the most practical means of preserving regional water quality in the immediate
512	future. Consistent with this prediction, previous research shows that algal abundance in
513	eutrophic Qu'Appelle lakes has increased up to 300%, and cyanobacteria by >500%, as a linear
514	function ( $r^2 > 0.70$ , $p < 0.05$ ) of the influx of dissolved N (mainly NH <sub>4</sub> <sup>+</sup> ) from urban centres during
515	1900-1980 (Hall et al. 1999; Leavitt et al. 2006, 2009). Presently, urban point sources represent
516	~70% of total ecosystem N in downstream lakes (Leavitt et al. 2006); however, wastewater
517	treatment plants are mandated by federal legislation to reduce $NH_4^+$ pollution to ~15% of current
518	discharge by 2017, and are already operational in the City of Regina. Because fertilization with
519	$NH_4^+$ increases algal bloom density and toxicity by up to 400% in these SRP-rich lakes (reviewed
520	in Donald et al. 2011), substantial diversion of N is expected to improve water quality.
521	Interestingly, our models forecast less improvement in water quality (Table 2) than would be

522 expected on the basis of paleolimnological, mass-balance, and experimental studies (Hall et al. 523 1999; Leavitt et al. 2006; Donald et al. 2011), possibly because our regression-based approach 524 cannot estimate centennial-scale changes in nutrient regimes, sedimentary sources may reduce 525 lake sensitivity to allochthonous nutrient influx (Jeppesen et al. 2005; Patoine et al. 2006), or 526 because some Qu'Appelle lakes are not impacted by urban wastewater (Leavitt et al. 2006). 527 Regulatory mechanisms and management strategies indentified here should generalize 528 well to continental landscapes with similar climatic, edaphic, and limnological characteristics. 529 Long-term changes in carbon fluxes (Finlay et al. 2010, 2015), nitrogen biogeochemistry (Bogard 530 et al. 2012), water sources (Pham et al. 2009), and climatic forcing (Pham et al. 2009, Vogt et al. 531 2011) are highly synchronous among Qu'Appelle and other lakes within a 235,000 km<sup>2</sup> prairie 532 region, irrespective of basin hydrology (open or closed drainage). Although less well studied than boreal regions, such continental interiors account for  $\sim 8.000,000 \text{ km}^2$  (Finlay et al. 2015) 533 534 and their freshwaters are critical resources for social and economic development (Barica 1987; 535 Schindler 2001) as well as regulation of climatic processes (Finlay et al. 2015). The models 536 presented here represent an important first step in establishing a predictive understanding of 537 relative importance of environmental and human mechanisms threatening lakes in these districts 538 (Brown et al. 2011). Collectively, the analyses presented here suggest that regional management 539 of continental lakes should focus on nutrient regulation as a means of mitigating cultural eutrophication, but caution that improvements on the decadal scale may be offset by continued 540 541 climate warming (Table 2). 542

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Table 1. Morphometric characteristics of study lakes are listed for the Qu'Appelle River catchment, Saskatchewan, Canada.

7	2	7
7	2	8

	Buffalo Pound	Crooked	Diefenbaker	Katepwa	Last Mountain	Wascana
Latitude (°N)-Longitude (°W)	50.65 - 105.50	50.6 - 102.73	51.12 - 106.63	50.7 - 103.65	51.08 - 105.23	50.45 - 104.61
Elevation (m)	509.30	451.70	552.00	478.20	490.10	570.50
Lake Area (km <sup>2</sup> )	29.10	15.00	500.00	16.20	226.60	0.50
Mean Depth (m)	3.00	8.06	33.00	14.30	7.90	1.50
Max Depth (m)	5.50	16.50	62.00	23.20	30.80	3.00
Volume (m <sup>3</sup> )	$8.75 \times 10^7$	$1.21 \times 10^{8}$	9.40x10 <sup>9</sup>	2.33x10 <sup>8</sup>	1.81x10 <sup>9</sup>	$7.00 \times 10^5$
Water Residence Time (year)	0.70	0.50	1.30	1.34	12.60	0.05
Gross Drainage Area (km <sup>2</sup> )	$3.36 \times 10^3$	$5.32 \text{x} 10^4$	1.36x10 <sup>5</sup>	$4.86 \text{x} 10^4$	$2.33 \text{x} 10^4$	$2.68 \times 10^3$
Effective Drainage Area km <sup>2</sup> )	$1.28 \times 10^3$	$1.38 \text{x} 10^4$	$8.69 \times 10^4$	$1.22 \text{x} 10^4$	$2.90 \times 10^3$	$1.25 \times 10^{3}$

Table 2. Summary of scenario analysis depicting changes in total algae, surface bloom 730 731 intensity, and water clarity under different hydrologic regimes, increases in water 732 temperature, or water-column nutrient content. Changes are depicted with estimated values of total algae ( $\mu$ g Chl L<sup>-1</sup>), surface blooms ( $\mu$ g Chl L<sup>-1</sup>), and water clarity (depth, 733 m) and percentage change in each response variable under each scenario. Further, values 734 735 are given for each variable as estimates of current conditions from the model, and as 736 measured averages of current conditions. Factor interactions were linear combinations of 737 expected change and are not presented. 738

	T . 1 . 1	<u>.</u>	Surface	0/	XX /	<u>0</u> (
	Total Algae $(127 \text{ J}^{-1})$	%	Blooms $(1, 2, 1, -1)$	%	Water	%
	(µg L)	change	(µg L )	change	Clarity (m)	change
1% of inflow	20.3	7.3	23.5	10.1	1.5	3.3
25% of Inflow	19.9	5.6	22.9	7.7	1.6	2.5
50% of Inflow	19.6	3.7	22.4	5.1	1.6	1.7
150% Inflow	18.2	-3.7	20.3	-5.1	1.6	-1.7
200% Inflow	17.5	-7.4	19.2	-10.2	1.7	-3.3
1000% of Inflow	6.3	-66.7	1.7	-91.9	2.1	-29.9
1 °C Temp. Increase	21.7	14.6	23.8	11.5	1.6	0.2
2 °C Temp. Increase	24.4	29.3	26.3	22.9	1.6	0.4
3 °C Temp. Increase	27.2	43.9	28.7	34.4	1.6	0.6
4 °C Temp. Increase	29.9	58.6	31.2	45.9	1.6	0.8
5 °C Temp. Increase	32.7	73.3	33.6	57.4	1.6	0.9
10% current nutrients	13.4	-29.0	16.2	-23.9	1.6	-0.6
25% current nutrients	14.3	-24.2	17.1	-19.9	1.6	-0.5
50% current nutrients	15.8	-16.1	18.5	-13.3	1.6	-0.3
200% current nutrients	25.0	32.2	27.0	26.5	1.6	0.6
300% current nutrients	31.1	64.5	32.7	53.1	1.6	1.2



Fig. 1. The Qu'Appelle River catchment, Saskatchewan, Canada, originates at Lake
Diefenbaker and flows eastward through Buffalo Pound, Katepwa, and Crooked lakes.
Last Mountain Lake and Wascana Lake enter the river through tributary creeks.
Limnological characteristics of study lakes were monitored bi-weekly during the ice-free
season (May-August) from 1995-2010. Four climate stations indicated with crosses
provided weather data for the same interval (1995-2010).





**Fig. 2.** Time series of four indices of water quality: total algae ( $\mu$ g L<sup>-1</sup>), surface blooms ( $\mu$ g L<sup>-1</sup>), water clarity (m), and colonial cyanobacteria (nmoles myxoxanthophyll L<sup>-1</sup>). Data are based on seasonal (May-August) means ± standard error (SE) for the interval 1995-2010 and were collected from six study lakes; Buffalo Pound, Crooked, Diefenbaker, Katepwa, Last Mountain, and Wascana. There were no statistically significant trends in any time series (see Methods).

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799 Fig. 3. Total explained variation (white) and proportion of non-residual variation 800 explained (filled) by multiple regression models describing variation in mean summer 801 (May-August) (A) water quality parameters, including total algae, surface blooms, water 802 clarity, and potentially-toxic colonial cyanobacteria, or (B) key limnological characteristics, including water temperature (T<sub>water</sub>), soluble reactive phosphorus 803 804 concentration (SRP), total inorganic carbon content (TIC), and pH. Model performance was evaluated by adjusted coefficient of determination ( $R^2_{adj}$ ). Significant (p < 0.05) 805 806 explanatory variables were selected by forward selection multiple regression based on

- 807 9999 permutations and were classified into categories associated with variation in climate
- 808 systems (black), regional meteorology (diagonal lines), river hydrology (dotted), and
- 809 internal lake characteristics (waves).
- 810
- 811



826 Fig. 4. Total explained variation (white) and proportion of non-residual variation 827 explained (filled) by multiple regression models describing variation in mean monthly 828 estimates of total algal abundance, surface bloom intensity, water clarity, and density of 829 colonial cyanobacteria for data from (A) May, (B) June, (C) July, or (D) August. Model performance was evaluated by adjusted coefficient of determination  $(R^2_{adi})$ . Significant 830 831 (p < 0.05) explanatory variables were selected by forward selection multiple regression 832 and were classified into categories associated with variation in climate systems (black), 833 regional meteorology (diagonal lines), river hydrology (dotted), and internal lake 834 characteristics (waves).



849 Fig. 5. A schematic representation of the predictive relationships between explanatory 850 and response variables for (A) water quality and (B) important internal lake 851 characteristics. Water quality response variables are depicted with open ovals. All 852 predictor variables are depicted with shaded rectangles and are classified by general 853 category: climate systems (black), regional meteorology (diagonal lines), river hydrology 854 (dotted), and internal lake characteristics (waves). Arrow thickness increases with 855 percentage of non-residual variation explained for each model. Interactions between 856 water quality variables were not measured except for that between total algal abundance 857 and water clarity.

Supporting Information Table S1. Variables initially included in regression models. Categories include large-scale climate systems, regionalmeteorology, river hydrology, and internal lake characteristics. Mean values were computed at seasonal resolution (May-August), from 1995-2010  $\pm$ standard deviation (SD). Ranges are presented as the maximum and minimum seasonal values from 1995-2010. PDO = Pacific decadal Oscillationindex, ENSO = El Niño-Southern Oscillation index, NAO = winter North Atlantic Oscillation index, SRP = soluble reactive phosphorus, TDP = total

dissolved phosphorus, DOC = dissolved organic carbon, DIC = dissolved inorganic carbon, and zoop. = zooplankton.

Category	Explanatory variable		Buffalo Pound	Crooked	Diefenbaker	Katepwa	Last Mountain	Wascana
Climate	Ice Out, day of year (DOY)	Mean ± SD	$110.38\pm6.40$	$114.02\pm5.05$	$120.69\pm8.76$	$114.06\pm7.36$	$112.94 \pm 6.59$	$105.97\pm3.09$
		Range	95-120	107-123	108-121	103-128	105-128	100-110
	Climate Teleconnections		PDO	ENSO	NAO	_		
		Mean ± SD	$0.03 \pm 0.74$	$0.54 \pm 6.24$	$-4.82 \pm 12.79$			
		Range	-1.29-1.46	-11.76-10.17	-41.74-0.39			
Meteorology	Summer Temperature (°C)	Mean $\pm$ SD	$15.62 \pm 1.06$	$15.17 \pm 1.03$	$15.89\pm0.97$	$14.72 \pm 1.11$	$15.62 \pm 1.06$	$15.62 \pm 1.06$
		Range	$\begin{array}{c} 13.20\text{-}17.08 \\ 56.95 \pm 14.49 \end{array}$	$\begin{array}{c} 12.60\text{-}16.83 \\ 64.85 \pm 20.48 \end{array}$	$\begin{array}{c} 14.08\text{-}17.33 \\ 50.50 \pm 16.53 \end{array}$	$\begin{array}{c} 12.20 - 16.25 \\ 56.34 \pm 23.07 \end{array}$	13.20 - 17.08 56.95 ± 14.49	13.20 - 17.08 56.95 ± 14.49
	Precipitation (May-August) (mm)	Mean ± SD Range	28.95 - 75.60	25.55 - 99.88	26.5 - 80.53	18.9 - 85.40	28.95 - 75.60	28.95 - 75.60
	Annual Precipitation (mm)	$Mean \pm SD$	$32.32\pm6.43$	$36.87 \pm 8.91$	$29.46\pm8.55$	$33.62 \pm 10.16$	$32.32\pm6.43$	$32.32\pm6.43$
		Range	21.64 - 45.33	19.73 - 57.88	16.54 - 44.51	16.96 - 55.82	21.64 - 45.33	21.64 - 45.33
	Winter Snowfall (mm)	$Mean \pm SD$	$14.91 \pm 4.71$	$15.25\pm8.00$	$13.29\pm5.48$	$17.03 \pm 6.89$	$14.91 \pm 4.71$	$14.91 \pm 4.71$
		Range	6.87 - 25.67	7.07 - 39.87	3.2 - 21.20	4.27 - 30.87	6.87 - 25.67	6.87 - 25.67
	Wind speed (km h <sup>-1</sup> )	$Mean \pm SD$	$14.98 \pm 2.64$	$14.16\pm5.24$	$11.90\pm3.67$	$12.06\pm3.09$	$15.50\pm3.38$	$9.28\pm3.67$
		Range	10.875 - 20.00	6.5 - 22.44	7.12 - 20.71	6.67 - 18.75	9.5 - 21.88	4.25 - 17.03
Hydrology	Annual Inflow (dam <sup>3</sup> )	Mean $\pm$ SD	$1.3E5 \pm 2.2E4$	$2.8E5 \pm 1.7E5$	$7.0E6 \pm 2.6E6$	$2.4\text{E5} \pm 1.5\text{E5}$	1.4E5±6.1E4	3.0E4±3.2E4
		Range	1.0E5 - 1.9E5	7.4E5 - 5.9E5	2.7E6 - 1.2E7	6.0E4 - 5.1E5	7.9E4 - 2.4E5	1.7E3- 1.1E5
	Residence time (yr)	Mean $\pm$ SD	$0.73\pm0.09$	$0.62\pm0.46$	$1.60\pm0.72$	$1.39 \pm 1.04$	$11.62\pm4.20$	$0.08 \pm 0.11$
		Range	0.60 - 0.90	0.10 - 1.94	0.82 - 3.66	0.44 - 4.37	5.08 - 18.01	0.01 - 0.41
Internal Lake	SRP ( $\mu$ g L <sup>-1</sup> )	Mean ± SD	$30.70\pm63.27$	$82.89 \pm 42.84$	$10.52 \pm 12.28$	$108.88\pm54.57$	$24.25 \pm 17.98$	223.79 ±119.63

Characteristics		Range	4.64 - 266.69	9.14 - 149.11	0.1 - 47.53	9.13 - 240.13	3.44 - 72.55	67.44 - 450.67
	TDP ( $\mu$ g L <sup>-1</sup> )	Mean $\pm$ SD	$50.25 \pm 85.82$	$116.07 \pm 42.26$	$18.93 \pm 18.05$	$144.45 \pm 41.06$	$48.30\pm27.32$	301.49±162.23
		Range	15.56 - 370.61	47.24 - 171.38	3.03 - 68.57	58.85 - 233.02	23.31 - 132.55	103.34 - 597.89
	$NO_3 (\mu g L^{-1})$	Mean $\pm$ SD	$76.87 \pm 80.30$	$93.85 \pm 99.44$	$167.22\pm93.67$	$204.83 \pm 183.96$	$61.14 \pm 57.06$	153.78±135.34
		Range	10.22 - 305	0 - 391.43	1 - 307.67	0.56 - 573.44	5.75 - 167.56	7.76 - 436.21
	$NH_4 (\mu g L^{-1})$	Mean $\pm$ SD	$32.86 \pm 44.87$	$30.49 \pm 28.03$	18.55 ±20.94	$75.32\pm84.19$	$28.40 \pm 23.99$	81.42 ± 113.95
		Range	0 - 158.75	0 - 107.14	0.2 - 77.5	1.89 - 351.25	0.2 - 91.25	0.2 - 446.25
	DOC (mg $L^{-1}$ )	Mean $\pm$ SD	$7.49\pm3.30$	$13.28\pm5.95$	$6.76\pm3.16$	$13.70\pm5.10$	$16.44 \pm 7.59$	$17.90\pm6.67$
		Range	3.62 - 17.06	5.78 - 33.02	3.72 - 14.93	6.58 - 30.17	7.01 - 34.05	10.88 - 40.46
	TIC (mg $L^{-1}$ )	Mean $\pm$ SD	$32.29\pm6.17$	$49.82 \pm 7.90$	$33.56 \pm 4.93$	$48.60\pm7.55$	$57.86 \pm 7.85$	$40.16\pm7.81$
		Range	15.94 - 39.47	35.22 - 66.09	27.03 - 45.71	40.94 - 67.69	49.02 - 78.05	27.71 - 54.38
	рН	Mean $\pm$ SD	$8.72\pm0.43$	$8.82\pm0.41$	$8.66\pm0.45$	$8.97 \pm 0.44$	$8.82\pm0.38$	$9.04\pm0.33$
		Range	7.95 - 9.49	8.24 - 9.51	8.03 - 9.43	8.28 - 9.70	8.29 - 9.51	8.36 - 9.69
	Water Temperature (°C)	Mean $\pm$ SD	$17.66\pm0.96$	$16.72 \pm 1.18$	$13.16\pm0.97$	$13.27 \pm 1.09$	$15.31 \pm 1.19$	$17.67 \pm 1.10$
		Range	15.59 - 19.39	14.43 - 18.58	11.41 - 14.59	11.61 - 15.45	13.30 - 17.70	16.35 - 19.97
	$O_2 (mg L^{-1})$	Mean $\pm$ SD	$8.14 \pm 1.40$	$7.94 \pm 1.43$	$8.98 \pm 1.64$	$7.16 \pm 1.01$	$8.04 \pm 1.40$	$8.13 \pm 1.03$
		Range	5.29 - 9.84	4.27 - 9.86	5.39 - 11.05	5.45 -9.34	4.44 - 9.66	6.25 - 9.35
	Conductivity ( $\mu$ S cm <sup>-1</sup> )	Mean $\pm$ SD	$468.7\pm80.5$	$1210.7 \pm 148.7$	$411.0\pm134.7$	$1135.5 \pm 159.3$	1776.2±177.6	900.3±270.7
		Range	377.8 - 704.9	930.5 - 1484.0	309.1 - 697.8	798.6 - 1452.1	1579.2-2178.7	515.1 - 1436.7
	Total Zoopl. (ind L <sup>-1</sup> )	Mean $\pm$ SD	$115.09 \pm 115.78$	$67.26 \pm 25.30$	$23.84 \pm 14.48$	$66.82 \pm 33.74$	$43.89 \pm 13.73$	$67.18 \pm 46.83$
		Range	5.06 - 399.85	29.72 - 117.45	10.41 - 61.17	20.57 - 136.66	23.89 - 70.56	21.60 - 206.73
	Herbivores and Omnivores	Mean $\pm$ SD	$83.43 \pm 83.02$	$58.98 \pm 22.99$	$18.56 \pm 11.55$	$59.91 \pm 28.79$	38.55 ± 13.53	$48.42\pm32.47$
	(ind $L^1$ )	Range	3.77 - 328.26	25.52 - 105.75	7.68 - 44.22	17.16-114.07	20.56 - 65.67	16.67 - 152.78
	Large Cladocera (ind L <sup>-1</sup> )	Mean ± SD	$21.80 \pm 16.91$	$16.47 \pm 10.18$	$4.53 \pm 2.35$	$10.66 \pm 5.30$	$11.21 \pm 4.09$	$14.60\pm9.84$
		Range	1.22 - 51.88	3.87 - 39.64	1.87 - 9.34	3.36 - 20.36	6.10 - 21.78	4.53 - 36.23
	Small Cladocera (ind L <sup>-1</sup> )	$Mean \pm SD$	$23.36\pm45.19$	$1.42 \pm 1.83$	$2.61 \pm 1.61$	$2.22\pm3.07$	$1.94 \pm 1.65$	$6.07 \pm 15.59$
		Range	0.03 - 185.16	0 - 5.76	0.46 - 5.36	0.08 - 11.54	0.28 - 5.64	0.10 - 60.35
	Copepods (ind L <sup>-1</sup> )	$Mean \pm SD$	$31.31\pm26.23$	$43.29 \pm 17.04$	$11.88 \pm 9.56$	$46.79\pm21.62$	$25.43 \pm 10.21$	$28.59 \pm 15.48$
		Range	2.48 - 89.44	22.02 - 76.67	4.80 - 35.87	13.64 - 92.54	12.30 - 50.49	11.44 - 70.69
	Chlorophyll a ( $\mu$ g L <sup>-1</sup> )	$Mean \pm SD$	$30.86 \pm 11.40$	$31.24 \pm 13.54$	$5.38 \pm 2.53$	$26.24\pm5.97$	$17.04 \pm 7.61$	$40.89 \pm 16.99$

 (nmoles myxo. L <sup>-1</sup> )	Range	0.01 - 1.71	0 - 0.68	0 - 0.06	0 - 1.44	0 - 0.64	0 - 4.13
Cyanobacteria density	$Mean \pm SD$	$0.62\pm0.53$	$0.16\pm0.23$	$0.02\pm0.02$	$0.38\pm0.43$	$0.19\pm0.17$	$1.54 \pm 1.54$
	Range	0.57 - 2.87	1.14 - 1.98	2.81 - 4.22	0.88 - 2.07	1.58 - 2.36	0.51 - 1.28
Clarity (Secchi depth m)	$Mean \pm SD$	$1.18\pm0.70$	$1.41\pm0.21$	$3.36\pm0.44$	$1.57\pm0.32$	$2.08\pm0.21$	$0.79\pm0.23$
	Range	13.56 - 56.61	10.18 - 67.65	2.95 - 14.12	19.12 - 41.26	8.69 - 40.88	18.75 - 77.96

**Supporting Information Table S2**. Summary of regression models predicting four indices of water quality; concentrations of total algae, surface blooms, water clarity, and concentrations of colonial cyanobacteria. Models are based on 16 years of monitoring in six study lakes (May-August, 1995-2010). Model performance is summarized using an adjusted coefficient of determination ( $R^2_{adj}$ ), and models were significant with a probability level of *p*. Multiple regression models include predictor variables for each water quality index selected using a Monte Carlo forward selection. SRP = soluble reactive phosphorus concentration, NAO = winter North Atlantic Oscillation index, TIC = total inorganic carbon concentration, wind = mean wind speed, ENSO = El Niño-Southern Oscillation index, and temp. = temperature.

Water Quality Variable	Lin	ear Regre	ssion	Multiple Regression						
	$\mathbf{p}^2$		alono		$\mathbf{p}^2$	n	Productor	Coofficient	% Total Variation	% Explained
Total algae	$\Lambda_{adj}$	<u> </u>	0.60	Water Temperature $\pm$ SPP - NAO - Inflow $\pm$ pH	Λ <sub>adj</sub>	$\frac{p}{<0.00001}$	Water Temp	2 77	23.5	45.6
Total algae	0.02	0.07	0.00		0.51	<0.00001	SRP	3.88	13.1	45.0 25.6
							NAO	-0.22	60	11.7
							Inflow	0.00	4.5	87
							nH	5 70	4.3	8.4
							Residual	0110	48.6	011
							Intercept	-80.50		
Surface Blooms	0.02	0.08	0.77	pH + Water Temperature + SRP - Inflow	0.44	< 0.00001	pH	12.40	15.1	34.2
							Water Temp.	2.45	12.2	27.8
							Log <sub>10</sub> SRP	3.61	9.7	22.0
							Inflow	0.00	7.0	15.9
							Residual		56.0	
							Intercept	-130.00		
Water Clarity	0	0.57	0.00	- Chl a + Inflow - SRP + TIC – Water Temperature +	0.75	< 0.00001	Chl a	-0.01	18.7	24.9
				ENSO*PDO			Inflow	0.00	18.3	24.4
							$\log_{10}$ SRP	-0.06	14.7	19.6
							TIC	0.01	10.4	13.9
							Water Temp.	-0.03	7.9	10.5
							PDO*ENSO	0.01	5.0	6.7
							Residual		25.0	
							Intercept	1.54		
Colonial Cyanobacteria	0	0.63	0.01	Water Temperature - Wind - ENSO	0.26	<0.00001	Water Temp.	0.17	13.7	52.7
							Wind	-0.07	8.5	32.7
							ENSO	-0.03	3.8	14.5
							Residual		74.0	
							Intercept	-1.19		

873 Supporting Information Table S3. Summary of regression models predicting four limnological characteristics; water temperature, soluble reactive

P content, TIC, and pH. Models are based on 16 years of monitoring in six study lakes (May-August, 1995-2010). Model performance is

summarized using an adjusted coefficient of determination ( $R^2_{adj}$ ), and models were significant with a probability level of p. Multiple regression

876 models include predictor variables for each water quality index selected using a Monte Carlo forward selection. Temp. = temperature, ice out = day

of year of ice melt, DOC = dissolved organic carbon concentration, NAO = winter North Atlantic Oscillation index, and precip. = precipitation.

Water Quality Variable	L	inear Regress	ion	Multiple Regression						
	$R^2$ di	p	slope	· · · ·	$R^2$ and	р	Predictor	Coefficient	% Total Variation Explained	% Explained Variation
Water Temperature	0	0.97	0.00	- Inflow + Summer Air Temperature - Ice Out -	0.51	< 0.00001	Inflow	0.00	19.8	38.8
•				Snow			Air Temp.	0.71	15.7	30.7
							Ice Out	-0.09	9.8	1929
							Snow	-0.08	5.7	11.23
							Intercept	16.20		
							Residual		49.0	
Soluble Reactive	0	0.74	0.01	- Inflow - Wind	0.29	< 0.00001	Inflow	0.00	24.2	83.4
Phosphorus (SRP)							Wind	-0.07	4.8	16.6
							Intercept	4.93		
							Residual		71.0	
Total Inorganic Carbon	0	0.74	0.09	Ice Out - Inflow	0.234	< 0.00001	Ice Out	0.49	18.2	77.6
(TIC)							Inflow	0.00	5.3	22.4
							Intercept	-8.30		
							Residual		76.5	
pН	0.28	< 0.00001	0.05	DOC - NAO - Summer Precipitation - Ice Out - TIC	0.38	< 0.00001	DOC	0.03	18.4	48.3
							NAO	-0.01	8.2	21.6
							Summer precip.	-0.01	6.3	16.5
							Ice Out	-0.01	2.8	7.4
							TIC	-0.01	2.4	6.23
							Intercept	10.28		
							Residual		61.9	