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

R. J. Vogt,^{a, b*} S. Sharma,^c and P. R. Leavitt^a

^aLimnology Laboratory, Department of Biology, University of Regina, Regina, Saskatchewan,
Canada

^bCurrent address: Groupe de recherche interuniversitaire en limnologie (GRIL), Département des
Sciences Biologiques, Université du Québec à Montréal, Montréal, Canada

^cDepartment of Biology, York University, Toronto, Ontario, Canada

*Corresponding author: RichVogt@gmail.com

Running head: Regulation of landscape-scale water quality

24 **Abstract**

25 Aquatic ecosystems are subject to multiple interacting stressors that obscure regulatory
26 mechanisms and reduce the effectiveness of management strategies. Here we estimate the unique
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
29 within a 52,000 km² catchment. We quantify variation in mean summer and monthly algal
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°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).

56 Decades of research have shown that cultural eutrophication remains among the greatest
57 threats to sustainable water quality (Carpenter et al. 1998; Schindler 2006). For example, lakes in
58 continental interiors often lie in large flat fertile agricultural catchments that deliver high nutrient
59 influx (Leavitt et al. 2006; Patoine et al. 2006) and characteristically exhibit high algal
60 productivity, low N:P ratios, and frequent blooms of nitrogen-fixing cyanobacteria (Haertel 1976;
61 Patoine et al. 2006; Orihel et al. 2012). Agricultural development is pervasive in these regions
62 (>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
84 development of the clear water phase during spring (McGowan et al. 2005; Dröscher et al. 2009).
85 Such strong climatic forcing is forecast to intensify in the future, with a ~4°C increase in mean

86 annual temperature of the Canadian Prairies by 2050 (Barrow 2009; Lapp et al. 2012; IPCC
87 2013), combining with lower snowfall and runoff (Cohen et al. 2015) to intensify both droughts
88 and extreme pluvial periods (van der Kamp et al. 2008; Lapp et al. 2013). Together, these events
89 increase the variability of water chemistry (Pham et al. 2009), regional hydrology (Schindler and
90 Donahue 2006; Pomeroy et al. 2007), and energy budgets (Dröscher et al. 2009) resulting in
91 altered planktonic production, community composition, and cyanobacterial abundance (Huisman
92 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
96 ($\sim 0.4 \text{ m km}^{-1}$) and high precipitation deficits ($20\text{-}60 \text{ cm yr}^{-1}$) (Pham et al. 2009), combine with
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
101 up to $20 \times 10^6 \text{ m}^3 \text{ yr}^{-1}$ of surface water at full production (J. Hovdebo, Director Licensing and
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

109 understanding of the effects of hydrologic regime on water quality is essential to developing
110 sustainable management strategies (Gober and Wheeler 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
125 River catchment, a system that drains ~52,000 km² of mixed grassland in southern Saskatchewan
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

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

139 Study lakes are all productive, but vary up to 10-fold in most morphometric and
140 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⁻¹) 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 (m³ 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

177 variations in water-column nutrient concentration (see below) can be used to approximate
178 historical 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- μm pore
185 membrane filter and analyzed at the University of Alberta Water Chemistry Laboratory for
186 concentrations of soluble reactive phosphorus (SRP, $\mu\text{g P L}^{-1}$) and total dissolved phosphorus
187 (TDP, $\mu\text{g P L}^{-1}$), as well as total dissolved nitrogen (TDN), ammonium (NH_4^+), and the sum of
188 NO_2^{2-} and NO_3^{2-} (all $\mu\text{g N L}^{-1}$). Total inorganic (TIC) and dissolved organic carbon (DOC)
189 concentrations (mg C L^{-1}) in filtered samples were quantified using a Shimadzu model 5000A
190 (Shimadzu, Kyoto, Japan) total carbon analyzer following Finlay et al. (2009). Water
191 temperature ($^{\circ}\text{C}$; T_{water}) and oxygen content ($\text{mg O}_2 \text{ L}^{-1}$) were computed as average values of
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).
197 Densities of individual species (ind. L^{-1}) were summed by month and for each year for a set of
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 (*Leptodiptomus siciloides*, *Diacyclops*
202 *thomasi*). 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
215 hepatotoxic microcystin (MC), and that toxin levels can exceed Canadian ($1.5 \mu\text{g L}^{-1}$) and World
216 Health Organization ($1.0 \mu\text{g L}^{-1}$) drinking water guidelines by 10-fold (Donald et al. 2011; Orihel
217 et al. 2012). Myxoxanthophyll concentration (nmoles L^{-1}) was measured using an Agilent model
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).

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

223 incorporates considerations of both temporal and spatial autocorrelation, model selection, and
224 variation-partitioning procedures, and which estimates the relative influence of diverse potential
225 regulators on environmental quality. We apply this three-step framework to the lake ecosystems
226 described above, but anticipate that our approach will be suitable for other ecosystems with long
227 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).

237 In the second step, multiple regression models were developed independently for all water
238 quality indices using forward selection of predictors from the full suite of climatic,
239 meteorological, hydrological, and limnological variables (Sharma et al. 2013). As our goal was
240 to identify potential regulatory mechanisms, rather than develop the most parsimonious model,
241 final model composition was not based solely on Akaike's Information Criterion adjusted for
242 small sample sizes (AICc), although forward selection typically also produced the model with
243 lowest AICc (analysis not shown). Instead, we used a forward selection based on two-stopping
244 criteria to identify variables that would be included in the multiple regression model. Variables
245 were selected to be included in the model using significant alpha values less than 0.05, and

246 adjusted R^2 values (R^2_{adj}) that significantly increased explained variation (Blanchet et al. 2008).
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_{water} , 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
260 summarized using adjusted coefficient of determination (R^2_{adj}). The potential influence of
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
264 (analysis not shown). Similarly, time series were evaluated for the possibility of applying
265 regression tree analysis (Orihel et al. 2012), but this approach was not employed here because the
266 predictive power of such models was too low ($R^2 < 0.25$), *likely owing in part to the number of*
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⁻¹) 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**

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

292 colonial cyanobacteria in the shallowest lakes (Wascana, Buffalo Pound). When analyzed with
293 data collected in May, total algal abundance ($R^2_{\text{adj}} = 0.06, p=0.008$), surface bloom intensity (R^2_{adj}
294 $= 0.05, p=0.02$), and densities of colonial cyanobacteria ($R^2_{\text{adj}} = 0.04, p=0.04$) all increased
295 slightly through time, whereas water transparency did not exhibit significant change (analysis not
296 shown). There were no significant temporal trends for any water quality variable for analyses
297 restricted to data from June, July, or August.

298 Among internal lake characteristics, only mean summer pH increased significantly (R^2_{adj}
299 $= 0.28, p<0.0001$) during the 16-year sampling period (Finlay et al. 2009, 2015), although this
300 trend was statistically significant only during the months of May and July. Water temperature,
301 SRP, and TIC did not exhibit statistically significant trends in either summer or monthly mean
302 values. All limnological and environmental time series lacked significant temporal
303 autocorrelation over the period studied.

304 *Models of summer water quality* – Multiple regression models explained 26-75% of
305 variation (as R^2_{adj}) in mean summer water quality parameters (Fig. 3a). In general, intrinsic
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
314 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_{water} and concentrations of Chl *a* and SRP. Densities of colonial cyanobacteria
318 were correlated positively to T_{water} and negatively to wind speed and the ENSO (SI Table S2). In
319 all cases, model performance was equivalent when NH_4^+ 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_{water} , 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).
325 These new models explained 23-51% (R^2_{adj}) of mean summer variation in limnological drivers of
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_{water}
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.

335 *Monthly models of water quality* - Model performance varied substantially by month and
336 among water quality parameters (Fig. 4). For example, regression models based on data from
337 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_{adj}
341 = 0.65, $R^2_{\text{adj}} = 0.30$). Similar to models of mean summer conditions, internal lake characteristics
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_{water} , 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 ~75% with a 5°C increase in T_{water} , 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_{water}
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

384 to allow scientists and managers to develop effective and adaptive management strategies to
385 protect aquatic resources (Schindler 2001; Gober and Wheeler 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_{water} , solute content, and
388 inflow regimes, factors that were ultimately under climatic control (SI Table S2). Elevated T_{water}
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).

427 Interactions between river hydrology, nutrient status, and lake production revealed by
428 regression models (SI Tables S2, S3) are consistent with regulatory mechanisms identified by
429 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
452 of lakes (temperature, wind speed, ENSO), a combination of variables that is consistent with

453 other research showing that colonial cyanobacteria 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
465 clarity models were strong in May ($R^2_{\text{adj}} > 0.65$) when phytoplankton communities are composed
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

476 that the high thermal capacity of very large lakes can extend cooler waters and clear water phases
477 later into the summer (Dröscher et al. 2009). Instead, parameters related closely to elevated
478 temperatures played a more important role in regression models developed with data from August
479 (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 ~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).

493 Analysis of model forecasts suggests that resource managers in semi-arid agricultural
494 regions will have few options to improve regional water quality through regulation of energy and
495 water fluxes. For example, while water temperatures were the best predictor of algal production
496 (Table 2), direct reduction of energy influx to lakes is not possible. Similarly, the effectiveness
497 of indirect management of thermal properties by cold water runoff is likely to be limited to early
498 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 through 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^{-1})
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_4^+) 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 km² prairie
532 region, irrespective of basin hydrology (open or closed drainage). Although less well studied
533 than boreal regions, such continental interiors account for ~8,000,000 km² (Finlay et al. 2015)
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
540 eutrophication, but caution that improvements on the decadal scale may be offset by continued
541 climate warming (Table 2).

542

543

544

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724 phenology of cyanobacterial blooms: Implications for future climate change. *Water Res.* **46**:

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726 Table 1. Morphometric characteristics of study lakes are listed for the Qu'Appelle River catchment, Saskatchewan, Canada.
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	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 ²)	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 ³)	8.75x10 ⁷	1.21x10 ⁸	9.40x10 ⁹	2.33x10 ⁸	1.81x10 ⁹	7.00x10 ⁵
Water Residence Time (year)	0.70	0.50	1.30	1.34	12.60	0.05
Gross Drainage Area (km ²)	3.36x10 ³	5.32x10 ⁴	1.36x10 ⁵	4.86x10 ⁴	2.33x10 ⁴	2.68x10 ³
Effective Drainage Area (km ²)	1.28x10 ³	1.38x10 ⁴	8.69x10 ⁴	1.22x10 ⁴	2.90x10 ³	1.25x10 ³

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730 Table 2. Summary of scenario analysis depicting changes in total algae, surface bloom
 731 intensity, and water clarity under different hydrologic regimes, increases in water
 732 temperature, or water-column nutrient content. Changes are depicted with estimated
 733 values of total algae ($\mu\text{g Chl L}^{-1}$), surface blooms ($\mu\text{g Chl L}^{-1}$), and water clarity (depth,
 734 m) and percentage change in each response variable under each scenario. Further, values
 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.
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	Total Algae ($\mu\text{g L}^{-1}$)	% change	Surface Blooms ($\mu\text{g L}^{-1}$)	% change	Water 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

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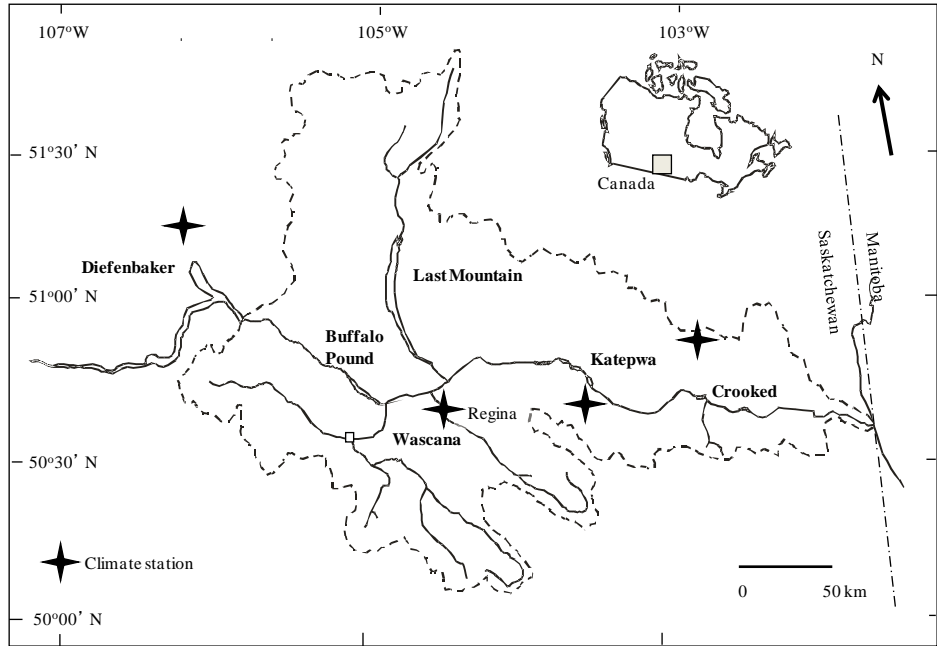


Fig. 1. The Qu'Appelle River catchment, Saskatchewan, Canada, originates at Lake Diefenbaker and flows eastward through Buffalo Pound, Katepwa, and Crooked lakes. Last Mountain Lake and Wascana Lake enter the river through tributary creeks. Limnological characteristics of study lakes were monitored bi-weekly 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).

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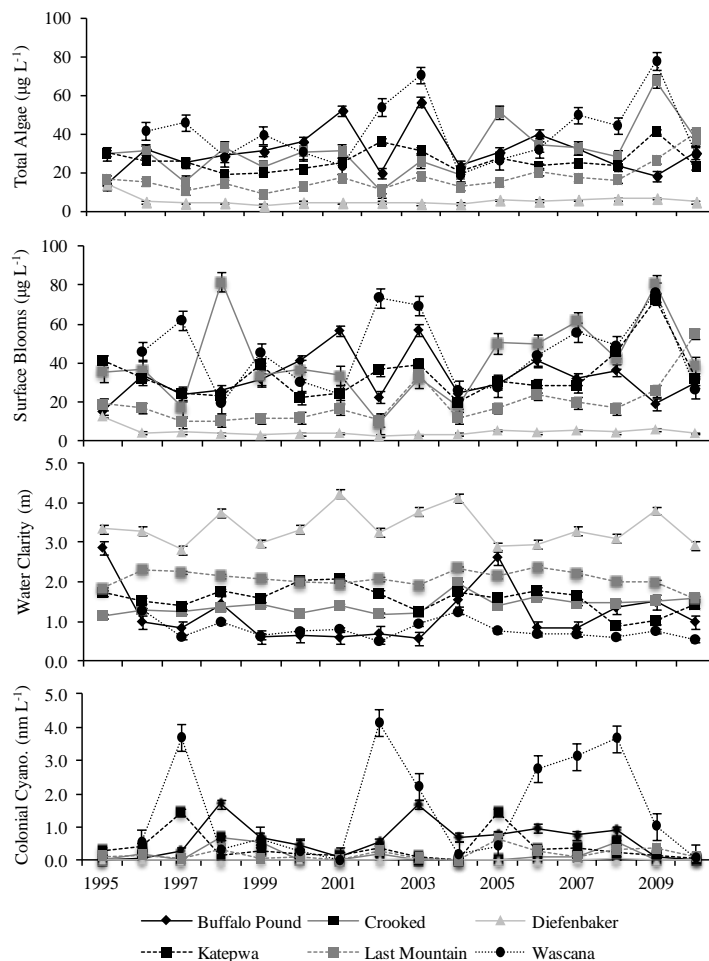
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776 **Fig. 2.** Time series of four indices of water quality: total algae ($\mu\text{g L}^{-1}$), surface blooms

777 ($\mu\text{g L}^{-1}$), water clarity (m), and colonial cyanobacteria (nmoles myxoxanthophyll L^{-1}).

778 Data are based on seasonal (May-August) means \pm standard error (SE) for the interval

779 1995-2010 and were collected from six study lakes; Buffalo Pound, Crooked,

780 Diefenbaker, Katepwa, Last Mountain, and Wascana. There were no statistically

781 significant trends in any time series (see Methods).

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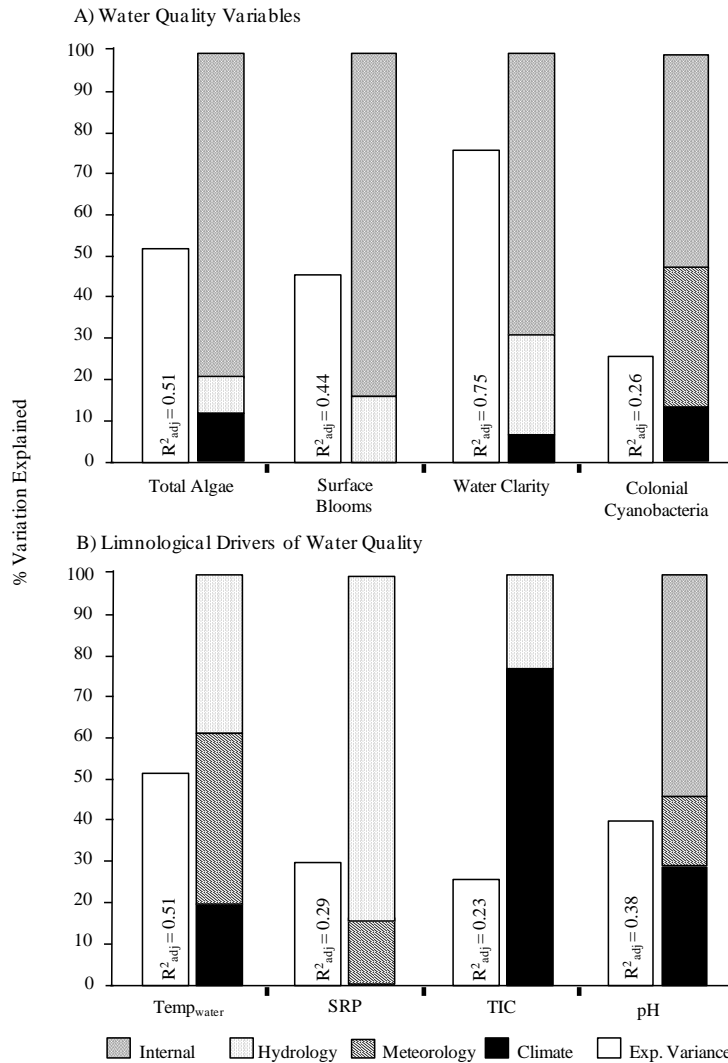


Fig. 3. Total explained variation (white) and proportion of non-residual variation explained (filled) by multiple regression models describing variation in mean summer (May-August) (A) water quality parameters, including total algae, surface blooms, water clarity, and potentially-toxic colonial cyanobacteria, or (B) key limnological characteristics, including water temperature (T_{water}), soluble reactive phosphorus concentration (SRP), total inorganic carbon content (TIC), and pH. Model performance was evaluated by adjusted coefficient of determination (R^2_{adj}). Significant ($p < 0.05$) 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).

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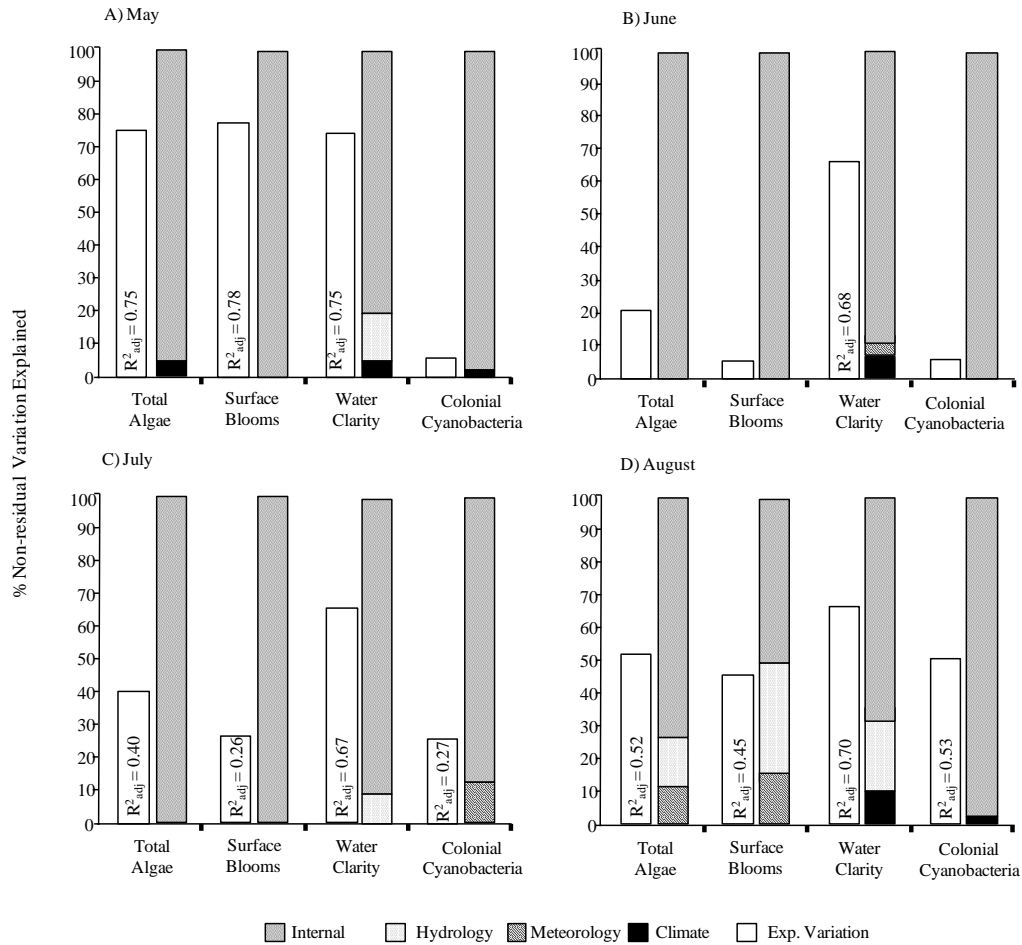


Fig. 4. Total explained variation (white) and proportion of non-residual variation explained (filled) by multiple regression models describing variation in mean monthly estimates of total algal abundance, surface bloom intensity, water clarity, and density of colonial cyanobacteria for data from (A)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

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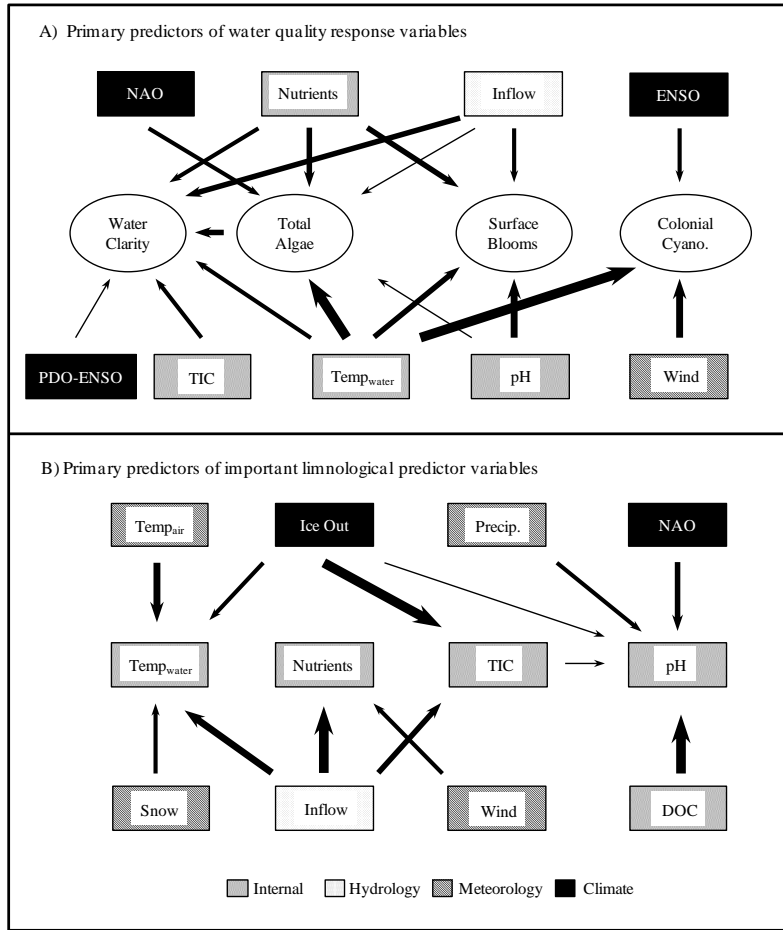


Fig. 5. A schematic representation of the predictive relationships between explanatory and response variables for (A) water quality and (B) important internal lake characteristics. Water quality response variables are depicted with open ovals. All predictor variables are depicted with shaded rectangles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

859 **Supporting Information Table S1.** Variables initially included in regression models. Categories include large-scale climate systems, regional
860 meteorology, river hydrology, and internal lake characteristics. Mean values were computed at seasonal resolution (May-August), from 1995-2010 ±
861 standard deviation (SD). Ranges are presented as the maximum and minimum seasonal values from 1995-2010. PDO = Pacific decadal Oscillation
862 index, ENSO = El Niño-Southern Oscillation index, NAO = winter North Atlantic Oscillation index, SRP = soluble reactive phosphorus, TDP = total
863 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 ± 6.40	114.02 ± 5.05	120.69 ± 8.76	114.06 ± 7.36	112.94 ± 6.59	105.97 ± 3.09	
		Range	95-120	107-123	108-121	103-128	105-128	100-110	
	Climate Teleconnections		PDO	ENSO	NAO				
		Mean ± SD	0.03 ± 0.74	0.54 ± 6.24	-4.82 ± 12.79				
		Range	-1.29-1.46	-11.76-10.17	-41.74-0.39				
Meteorology	Summer Temperature (°C)	Mean ± SD	15.62 ± 1.06	15.17 ± 1.03	15.89 ± 0.97	14.72 ± 1.11	15.62 ± 1.06	15.62 ± 1.06	
		Range	13.20-17.08	12.60-16.83	14.08-17.33	12.20 - 16.25	13.20 - 17.08	13.20 - 17.08	
	Precipitation (May-August) (mm)	Mean ± SD	56.95 ± 14.49	64.85 ± 20.48	50.50 ± 16.53	56.34 ± 23.07	56.95 ± 14.49	56.95 ± 14.49	
		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 ± SD	32.32 ± 6.43	36.87 ± 8.91	29.46 ± 8.55	33.62 ± 10.16	32.32 ± 6.43	32.32 ± 6.43	
		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 ± SD	14.91 ± 4.71	15.25 ± 8.00	13.29 ± 5.48	17.03 ± 6.89	14.91 ± 4.71	14.91 ± 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 ⁻¹)	Mean ± SD	14.98 ± 2.64	14.16 ± 5.24	11.90 ± 3.67	12.06 ± 3.09	15.50 ± 3.38	9.28 ± 3.67	
		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 ³)	Mean ± SD	1.3E5 ± 2.2E4	2.8E5 ± 1.7E5	7.0E6 ± 2.6E6	2.4E5 ± 1.5E5	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 ± SD	0.73 ± 0.09	0.62 ± 0.46	1.60 ± 0.72	1.39 ± 1.04	11.62 ± 4.20	0.08 ± 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 (µg L ⁻¹)	Mean ± SD	30.70 ± 63.27	82.89 ± 42.84	10.52 ± 12.28	108.88 ± 54.57	24.25 ± 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 ($\mu\text{g L}^{-1}$)	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 \pm 27.32	301.49 \pm 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 ($\mu\text{g L}^{-1}$)	Mean \pm SD	76.87 \pm 80.30	93.85 \pm 99.44	167.22 \pm 93.67	204.83 \pm 183.96	61.14 \pm 57.06	153.78 \pm 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 ($\mu\text{g L}^{-1}$)	Mean \pm SD	32.86 \pm 44.87	30.49 \pm 28.03	18.55 \pm 20.94	75.32 \pm 84.19	28.40 \pm 23.99	81.42 \pm 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 \pm 3.30	13.28 \pm 5.95	6.76 \pm 3.16	13.70 \pm 5.10	16.44 \pm 7.59	17.90 \pm 6.67
	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 \pm 6.17	49.82 \pm 7.90	33.56 \pm 4.93	48.60 \pm 7.55	57.86 \pm 7.85	40.16 \pm 7.81
	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
pH	Mean \pm SD	8.72 \pm 0.43	8.82 \pm 0.41	8.66 \pm 0.45	8.97 \pm 0.44	8.82 \pm 0.38	9.04 \pm 0.33
	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 \pm 0.96	16.72 \pm 1.18	13.16 \pm 0.97	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 ($\mu\text{S cm}^{-1}$)	Mean \pm SD	468.7 \pm 80.5	1210.7 \pm 148.7	411.0 \pm 134.7	1135.5 \pm 159.3	1776.2 \pm 177.6	900.3 \pm 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 ⁻¹)	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 (ind L ⁻¹)	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 \pm 13.53	48.42 \pm 32.47
	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 ⁻¹)	Mean \pm 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 \pm 9.84
	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 ⁻¹)	Mean \pm SD	23.36 \pm 45.19	1.42 \pm 1.83	2.61 \pm 1.61	2.22 \pm 3.07	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 ⁻¹)	Mean \pm SD	31.31 \pm 26.23	43.29 \pm 17.04	11.88 \pm 9.56	46.79 \pm 21.62	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 ($\mu\text{g L}^{-1}$)	Mean \pm SD	30.86 \pm 11.40	31.24 \pm 13.54	5.38 \pm 2.53	26.24 \pm 5.97	17.04 \pm 7.61	40.89 \pm 16.99

	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
Clarity (Secchi depth m)	Mean \pm SD	1.18 \pm 0.70	1.41 \pm 0.21	3.36 \pm 0.44	1.57 \pm 0.32	2.08 \pm 0.21	0.79 \pm 0.23
	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
Cyanobacteria density	Mean \pm SD	0.62 \pm 0.53	0.16 \pm 0.23	0.02 \pm 0.02	0.38 \pm 0.43	0.19 \pm 0.17	1.54 \pm 1.54
(nmoles myxo. L ⁻¹)	Range	0.01 - 1.71	0 - 0.68	0 - 0.06	0 - 1.44	0 - 0.64	0 - 4.13

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866 **Supporting Information Table S2.** Summary of regression models predicting four indices of water quality; concentrations of total algae, surface
867 blooms, water clarity, and concentrations of colonial cyanobacteria. Models are based on 16 years of monitoring in six study lakes (May-August,
868 1995-2010). Model performance is summarized using an adjusted coefficient of determination (R^2_{adj}), and models were significant with a probability
869 level of p . Multiple regression models include predictor variables for each water quality index selected using a Monte Carlo forward selection. SRP
870 = soluble reactive phosphorus concentration, NAO = winter North Atlantic Oscillation index, TIC = total inorganic carbon concentration, wind =
871 mean wind speed, ENSO = El Niño-Southern Oscillation index, and temp. = temperature.

Water Quality Variable	Linear Regression			Multiple Regression			Predictor	Coefficient	% Total Variation Explained	% Explained Variation
	R^2_{adj}	p	slope		R^2_{adj}	p				
Total algae	0.02	0.09	0.60	Water Temperature + SRP - NAO - Inflow + pH	0.51	<0.00001	Water Temp.	2.77	23.5	45.6
							SRP	3.88	13.1	25.6
							NAO	-0.22	6.0	11.7
							Inflow	0.00	4.5	8.7
							pH	5.70	4.3	8.4
							Residual		48.6	
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 ₁₀ 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 + ENSO*PDO	0.75	<0.00001	Chl a	-0.01	18.7	24.9
							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	
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
874 P content, TIC, and pH. Models are based on 16 years of monitoring in six study lakes (May-August, 1995-2010). Model performance is
875 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
877 of year of ice melt, DOC = dissolved organic carbon concentration, NAO = winter North Atlantic Oscillation index, and precip. = precipitation.
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Water Quality Variable	Linear Regression			Multiple Regression				% Total Variation Explained	% Explained Variation	
	R^2_{adj}	p	slope	R^2_{adj}	p	Predictor	Coefficient			
Water Temperature	0	0.97	0.00	- Inflow + Summer Air Temperature - Ice Out - Snow	0.51	<0.00001	Inflow	0.00	19.8	38.8
							Air Temp.	0.71	15.7	30.7
							Ice Out	-0.09	9.8	19.29
							Snow	-0.08	5.7	11.23
							Intercept	16.20		
							Residual		49.0	
Soluble Reactive Phosphorus (SRP)	0	0.74	0.01	- Inflow - Wind	0.29	<0.00001	Inflow	0.00	24.2	83.4
							Wind	-0.07	4.8	16.6
							Intercept	4.93		
							Residual		71.0	
Total Inorganic Carbon (TIC)	0	0.74	0.09	Ice Out - Inflow	0.234	<0.00001	Ice Out	0.49	18.2	77.6
							Inflow	0.00	5.3	22.4
							Intercept	-8.30		
							Residual		76.5	
pH	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	