

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, S. Sharma, and P.R. Leavitt

Abstract: Aquatic ecosystems are subject to multiple interacting stressors that obscure regulatory mechanisms and reduce the effectiveness of management strategies. Here we estimate the unique and interactive effects of continental climate systems, regional meteorology, river hydrology, and internal lake characteristics on patterns of landscape-scale water quality in six productive lakes within a 52 000 km² catchment. We quantify variation in mean summer and monthly algal abundance, surface bloom intensity, water clarity, and density of potentially toxic cyanobacteria during 16 years on the Canadian Prairies. Internal lake characteristics best predicted overall water quality change, while climate systems, regional weather, and river hydrology characterized indirect pathways that influenced physicochemical environments. Scenario analysis of future environmental change predicted that atmospheric warming (3–5 °C) will have the strongest effect on water quality in these productive lakes, but unexpectedly predicted that even severe industrial water extraction (1% of inflow) will have negligible effects on transparency or algal abundance. Instead, nutrient management represents the only practical means to sustain water quality, although atmospheric and lake warming may override re-oligotrophication of eutrophied sites in future decades.

Résumé : Les écosystèmes aquatiques sont assujettis à de multiples facteurs de stress interagissant les uns avec les autres qui occultent les mécanismes de réglementation et réduisent l'efficacité des stratégies de gestion. Nous estimons les effets individuels et interactifs des systèmes climatiques continentaux, de la météorologie régionale, de l'hydrologie des rivières et des caractéristiques internes des lacs sur les motifs de qualité de l'eau à l'échelle du paysage dans six lacs producteurs dans un bassin versant de 52 000 km². Nous quantifions les variations des abondances estivale et mensuelle moyenne des algues, l'intensité des efflorescences en surface, la carte de l'eau et la densité de cyanobactéries potentiellement toxiques sur une période de 16 ans dans les Prairies canadiennes. Les caractéristiques internes des lacs prédisent le mieux les changements généraux de la qualité de l'eau, alors que les systèmes climatiques, la météo régionale et l'hydrologie des rivières caractérisent des voies indirectes qui influencent les environnements physicochimiques. L'analyse de scénarios de changements environnementaux futurs prédit que le réchauffement atmosphérique (3–5 °C) exercera l'effet le plus important sur la qualité de l'eau dans ces lacs producteurs, mais, contrairement aux attentes, prédit également que même une extraction industrielle d'eau intense (1 % de l'apport d'eau) aurait des effets négligeables sur la transparence ou l'abondance d'algues. La gestion des nutriments représente plutôt le seul moyen pratique pour maintenir la qualité de l'eau, bien que le réchauffement atmosphérique et des lacs pourrait contrer les effets de la réoligotrophisation de sites eutrophisés dans les décennies à venir. [Traduit par la Rédaction]

Introduction

Accurate prediction of the unique and interactive effects of climate and humans on aquatic ecosystems will require an improved mechanistic understanding of how ecosystems interact with and respond to environmental variability (Leavitt et al. 2009; Vogt et al. 2011). Among the many challenges associated with such ecological forecasting is the mounting evidence that threats to water quality (e.g., climate, nutrients, toxins, hydrologic flow, exotic species) vary in space and time and can interact through complex pathways (Christensen et al. 2006; Palmer and Yan 2013). Development of effective management strategies to protect aquatic ecosystems will require analytical frameworks suitable for large landscapes and that organize anthropogenic and climatic stressors into hierarchies of threat (Brown et al. 2011) by identifying the pathways by which environmental change degrades water qual-

ity. This need may be particularly pronounced for lakes in central North America and other continental interiors where dry conditions (Barrow 2009) combine with intensive agriculture (Hall et al. 1999; Bunting et al. 2016), urbanization (Leavitt et al. 2006; Waiser et al. 2010), and high climatic variability (Pham et al. 2009; Pomeroy et al. 2007) to create multifaceted controls of water quality (Schindler and 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

Received 7 December 2016. Accepted 16 February 2017.

R.J. Vogt* and P.R. Leavitt. Limnology Laboratory, Department of Biology, University of Regina, Regina, Sask., Canada.
S. Sharma. Department of Biology, York University, Toronto, Ont., Canada.

Corresponding author: R.J. Vogt (email: RichVogt@gmail.com).

*Present address: Groupe de recherche interuniversitaire en limnologie (GRIL), Département des sciences biologiques, Université du Québec à Montréal, Montréal, Que., Canada.

Copyright remains with the author(s) or their institution(s). Permission for reuse (free in most cases) can be obtained from RightsLink.

development is so pervasive in these regions (>75% of land area) that eutrophication has been favoured by increased tillage, crop fertilization, and industrial livestock activities (Hall et al. 1999; Bunting et al. 2016). Similarly, the low density and discharge of most regional rivers in dry interior regions (Bonsal and Shabbar 2008) can lead to disproportionate effects of nutrients and other contaminants from urban centres (Leavitt et al. 2006; Waiser et al. 2010). Pollution of these phosphorus (P)-rich lakes with nitrogen (N) has been shown to increase production and toxicity of cyanobacteria by up to 500% (Leavitt et al. 2006; Donald et al. 2011; Orihel et al. 2012), with unambiguous evidence that water quality has been degraded substantially by nutrients from agricultural and urban activities during the past century (Hall et al. 1999; Maheaux et al. 2016; Bunting et al. 2016).

Climate variability has pronounced effects on lakes within continental interiors (Barrow 2009; Schindler and Donahue 2006). In the Canadian Prairie region of the northern Great Plains, climate variability arises from the interaction of three major climate systems and three air masses (Arctic, Pacific, Gulf of Mexico) that supply moisture to the continental interior (Bonsal and Shabbar 2008). The Pacific Decadal Oscillation (PDO) (Mantua et al. 1997) and El Niño – Southern Oscillation (ENSO) (Trenberth and Hurrell 1994) both influence the influx of Pacific precipitation to the Prairies and runoff from western mountains (St. Jacques et al. 2010; Shabbar et al. 2011), with synergism among climate systems producing mild and arid conditions in winter and spring (Mantua et al. 1997; McCabe et al. 2004; Bonsal et al. 2006), 10-fold variation in spring runoff (Pomeroy et al. 2007), and up to 50-day variation in timing of plankton phenology (McGowan et al. 2005; Dröscher et al. 2009). Similarly, the North Atlantic Oscillation (NAO; computed using winter months) regulates annual cyclonic activity and winter breakouts of the 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). Such strong climatic forcing is forecast to intensify in the future, with a ~4 °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).

Lakes in continental interiors may be further subjected to intensive hydrologic management to regulate water supplies for urban, agricultural, and industrial applications (Saskatchewan Water Security Agency 2013). For example, low-elevation gradients (~0.4 m·km⁻¹) and high precipitation deficits (20–60 cm·year⁻¹) (Pham et al. 2009) combine with strongly seasonal precipitation (75% during summer) and runoff mainly (75% of annual discharge) within a 3-week interval during spring (Akinremi et al. 1999; Fang and Pomeroy 2007) to create low densities of small rivers through much of the northern Great Plains. In the central Canadian Prairies, potash solution mines also alter regional hydrology by each consuming up to 20 × 10⁶ m³·year⁻¹ of surface water at full production (J. Hovdebo, Director Licensing and Water Use, Saskatchewan Water Security Agency, personal communication). When combined with similar magnitudes of urban and agricultural uses, industrial applications could effectively eliminate flow in all but the largest regional rivers (Saskatchewan Water Security Agency 2013). Although compensatory increases in water conveyance alleviate shortfalls, perpetually augmented flows to offset

year-round industrial water extraction can favour vernal flooding and facilitate lotic transport of urban pollutants to downstream lakes (Leavitt et al. 2006; Wyn et al. 2007). Given that these rivers also supply most of the potable 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 Wheeler 2014).

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

Methods

Site description

The six productive study lakes are situated within the Qu'Appelle River catchment, a system that drains ~52 000 km² of mixed grassland in southern Saskatchewan, Canada (Fig. 1). This chain of lakes extends ~400 km eastward from mesotrophic (Lake Diefenbaker) and eutrophic reservoirs (Buffalo Pound) to hyper-eutrophic downstream lakes (Katepwa, Crooked), with subsaline Last Mountain Lake and hyper-eutrophic Wascana Lake reservoir draining into the Qu'Appelle River through small tributaries near the city of Regina. Regional climate is characterized as cool-summer humid continental (Köppen Dfb classification), 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. Mean annual precipitation is ~380 mm, with most rain falling between May and July and most runoff occurring 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; also refer to online Supplementary material, Table S1¹). Lakes are polymictic, although Katepwa and Diefenbaker can exhibit limited thermal stratification during some summers. Lakes share a common plankton composition distinguished by diverse summer assemblages of cyanobacteria and abundant cyclopoid copepods (Patoine et al. 2006; Vogt et al. 2011). Regional fish communities include walleye (*Sander vitreus*), northern pike (*Esox lucius*), yellow perch (*Perca flavescens*), cisco (*Coregonus artedii*), bigmouth buffalo (*Ictiobus cyprinellus*), and white sucker (*Catostomus commersonii*), although precise community composition and population densities are not known for most years.

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2016-0520>.

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 biweekly during the ice-free season (May–August) from 1995 to 2010. Four climate stations (indicated with crosses) provided weather data for the same interval (1995–2010).

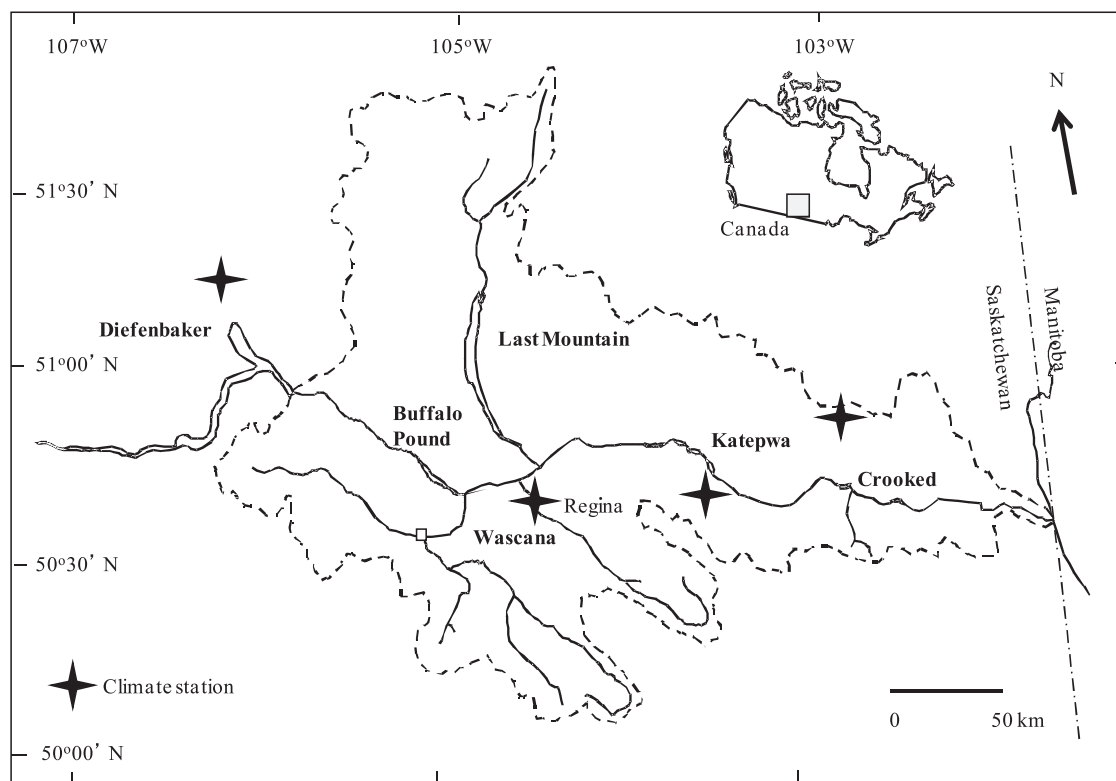


Table 1. Morphometric characteristics of study lakes are listed for the Qu'Appelle River catchment, Saskatchewan, Canada.

	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)	8.75×10 ⁷	1.21×10 ⁸	9.40×10 ⁹	2.33×10 ⁸	1.81×10 ⁹	7.00×10 ⁵
Water residence time (year)	0.70	0.50	1.30	1.34	12.60	0.05
Gross drainage area (km ²)	3.36×10 ³	5.32×10 ⁴	1.36×10 ⁵	4.86×10 ⁴	2.33×10 ⁴	2.68×10 ³
Effective drainage area (km ²)	1.28×10 ³	1.38×10 ⁴	8.69×10 ⁴	1.22×10 ⁴	2.90×10 ³	1.25×10 ³

Climate data

Time series of climate variables (1995–2010) were compiled from public archives, including the US National Oceanic and Atmospheric Administration (North Atlantic Oscillation index, NAO), the Australian National Climate Centre (Southern Oscillation Index, SOI), and the University of Washington Joint Institute for the Study of the Atmosphere and Ocean (PDO). Additionally, we estimated potential interactions between the PDO and ENSO (as SOI) as the product of the respective indices, because low-flow hydrological events are amplified by a synergistic interaction between El Niño phases of ENSO and positive phases of the PDO (Bonsal and Shabbar 2008; Shabbar and Yu 2012). The calendar day of year of spring ice melt 1995–2010 was obtained from Vogt et al. (2011).

Meteorology

Meteorological measurements (1995–2010) within the catchment were obtained from the Environment Canada National Climate Archives (<http://climate.weather.gc.ca>) for four weather stations that occupy the same latitudinal and longitudinal gradients as the

study lakes (Fig. 1). Mean monthly air temperature (°C), precipitation (mm), and daily wind speed (km·h⁻¹) were acquired for May–August and used to compute a mean summer value that overlapped with the limnological sampling regime (described below). Snow accumulation was estimated as the sum of monthly precipitation from January to March in each calendar year. Variation in solar irradiance was quantified by Environment Canada for each meteorological site (Vogt et al. 2011); however, because of discontinuous data availability, energy fluxes could not be estimated for all lakes and years, and irradiance data were not used in statistical models.

Hydrology

Hydrologic data were collected by the Saskatchewan Water Security Agency and were assessed as the total monthly or summer inflow to each lake (m³·day⁻¹). Inflows were estimated using flow gauges on streams, measurements of lake levels, and estimates of net evaporation. Inflow data and lake volume were used to compute residence time for each lake and year. In contrast, the nutrient content of river water was not available for most sites (c.f.

Donald et al. 2015), such that annual variation in allochthonous N and P influx could not be estimated for all lakes and years and thus were not included in statistical models. However, earlier mass balance studies comparing the outflow of upstream lakes with the inflow of basins immediately 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 approximate historical changes in nutrient influx during the ice-free period.

Internal lake variables

Study lakes were sampled biweekly using standard protocols from May to August during 1995–2010, except for Wascana Lake (1996–2010) (Patoine et al. 2006; Vogt et al. 2011). Depth-integrated samples were collected at midday at a standard geo-positioned station in each lake by pooling casts of a 2 L Van Dorn water bottle taken every metre to a maximum depth of 3 m (Buffalo Pound, Wascana), 6 m (Crooked), or 15 m (Diefenbaker, Last Mountain, Katapwa). These integrated samples were filtered through a membrane filter (0.45 μm pore) and analyzed at the University of Alberta Water Chemistry Laboratory for concentrations of soluble reactive P (SRP, $\mu\text{g P}\cdot\text{L}^{-1}$) and total dissolved P ($\mu\text{g P}\cdot\text{L}^{-1}$), as well as total dissolved N (TDN), ammonium (NH_4^+), and the sum of NO_2^{2-} and NO_3^{2-} (all $\mu\text{g N}\cdot\text{L}^{-1}$). Total inorganic carbon (TIC) and dissolved organic carbon (DOC) concentrations ($\text{mg C}\cdot\text{L}^{-1}$) in filtered samples were quantified using a Shimadzu model 5000A (Shimadzu, Kyoto, Japan) total carbon analyzer following Finlay et al. (2009). Water temperature ($^{\circ}\text{C}$; T_{water}) and oxygen content ($\text{mg O}_2\cdot\text{L}^{-1}$) were computed as mean values of depth profiles collected every 1 m using a YSI model 85 m (YSI, Yellow Springs, Ohio, USA), while pH was measured at the surface (0.5 m) using a calibrated handheld probe.

Zooplankton densities were estimated biweekly (May–August in 1995–2010) from vertical tows of a 20 cm diameter Wisconsin net (243 μm mesh) at the standard sampling station in each lake. Invertebrate samples were preserved and enumerated according to Patoine et al. (2006). Densities of individual species (individuals $\cdot\text{L}^{-1}$) were summed per month and per year for a set of taxonomic categories that included total zooplankton (all species), herbivorous or omnivorous taxa (carnivores excluded), large-bodied cladocerans (*Daphnia galeata mendotae*, *Daphnia magna*, *Daphnia pulex*, *Diaphanosoma birgei*), small-bodied cladocerans (*Daphnia retrocurva*, *Bosmina longirostris*, *Ceriodaphnia* sp., *Chydorus* sp.), and copepods (*Leptodiaptomus siciloides*, *Diacyclops thomasi*). We anticipated that landscape-scale changes in planktivory by fish and invertebrates (Vogt et al. 2013, 2015) would be evident as changes in the densities of large and small zooplankton due to size-selective trophic interactions (Carpenter and Kitchell 1993).

Water quality indices

Water clarity was measured using a 20 cm diameter Secchi disk lowered in shade at a standard sampling station. Total algal abundance (total algae) was estimated from depth-integrated water-column concentrations of chlorophyll *a* (Chl *a*), collected from pooled Van Dorn samples taken at 1 m intervals and quantified using standard trichromatic techniques (Vogt et al. 2011). Surface Chl *a* (surface bloom intensity) was measured similarly based on samples collected only in the uppermost 1 m of the water column. Concentrations of colonial cyanobacteria were assessed based on the depth-integrated concentrations of the taxonomically diagnostic carotenoid myxoxanthophyll, a biomarker for colonial and potentially toxic cyanobacteria. Microscopic analysis shows that *Microcystis* and *Anabaena* spp. are common phytoplankton in Qu'Appelle lakes, that these taxa produce hepatotoxic microcystin (MC), and that toxin levels can exceed Canadian ($1.5\ \mu\text{g}\cdot\text{L}^{-1}$) and World Health Organization ($1.0\ \mu\text{g}\cdot\text{L}^{-1}$) drinking water guidelines by 10-fold (Donald et al. 2011; Orihel et al. 2012). Myxoxanthophyll concentration ($\text{nmol}\cdot\text{L}^{-1}$) was measured using an Agilent model

1100 high-performance liquid chromatography system (Agilent, Palo Alto, California, 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.

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

In the second step, multiple regression models were developed independently for all water quality 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 (AIC_c), although forward selection typically also produced the model with the lowest AIC_c (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 a significance level of $\alpha < 0.05$, and adjusted R^2 values (R_{adj}^2) that significantly increased explained variation (Blanchet et al. 2008). The relative contribution of each predictor was quantified using a type III sum-of-squares analysis of variance (ANOVA), in which variation explained by each predictor was summed into classes representing climate, meteorology, hydrology, and internal lake characteristics. In addition to the four water quality indices, regression models were developed for their most influential predictors (T_{water} , SRP, TIC, pH; see below) to assess indirect controls of water quality. Initial analyses focused on mean summer values, but data with monthly resolution were also used to quantify seasonal differences in potential regulatory mechanisms. Preliminary correlation analysis revealed that the only significant interaction between response variables was that of total algal abundance and water clarity; hence, this interaction alone was included in the final models.

In all models, variables were transformed (\log_{10}) as necessary to produce normal distributions, and multi-collinear parameters were excluded from final models ($\text{VIF} > 10$, $r > 0.7$). Significant ($p < 0.05$) model parameters were selected using a Monte Carlo forward selection procedure with 9999 permutations (Blanchet et al. 2008), and model explanatory power was summarized using adjusted coefficient of determination (R_{adj}^2). The potential influence of landscape position and site-specific, but unmeasured, limnological variables on regression models was estimated using a categorical lake identification code as a covariate; however, as lake 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 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 sites and length of time series. All data manipulation and statistical analyses were performed in the R language environment (R Core Team 2013).

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

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; Table S2¹). Similarly, time series showed no evidence of autocorrelation, despite an apparent 5-year cycle in colonial cyanobacteria in the shallowest lakes (Wascana, Buffalo Pound). When analyzed with data collected in May, total algal abundance ($R^2_{\text{adj}} = 0.06$, $p = 0.008$), surface bloom intensity ($R^2_{\text{adj}} = 0.05$, $p = 0.02$), and densities of colonial cyanobacteria ($R^2_{\text{adj}} = 0.04$, $p = 0.04$) 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 ($R^2_{\text{adj}} = 0.28$, $p < 0.0001$) 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.

Models of summer water quality

Multiple regression models explained 26%–75% of variation (as R^2_{adj}) in mean summer water quality parameters (Fig. 3a). In general, intrinsic limnological characteristics were the strongest predictors of total algae, surface blooms, water clarity, and abundance of colonial cyanobacteria, accounting for 53%–80% of explained variation. River hydrology played a secondary role in predictive models, accounting for an additional 9%–25% of explained variation, while

climate systems usually accounted for lower fractions of explained variation in models of total algae (~11%), water clarity (~7%), and colonial cyanobacteria (~15%). Regional meteorology was a substantial predictor for models of colonial cyanobacterial abundance (~33% of explained variation) (Fig. 3a).

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 (Table S2¹). In addition, total algal abundance was related inversely to the NAO index. In contrast, water clarity was correlated positively to lake inflow, TIC content, and PDO × ENSO interactions, and negatively to T_{water} and concentrations of Chl *a* and SRP. Densities of colonial cyanobacteria were correlated positively to T_{water} and negatively to wind speed and the ENSO (Table S2¹). In all cases, model performance was equivalent when NH_4^+ replaced SRP as a predictor (analysis not shown), suggesting that the effects of these dissolved nutrients could not be distinguished.

Given the relative importance of select physicochemical characteristics (T_{water} , dissolved nutrients, TIC, pH) as predictors of water quality, we built additional regression models to investigate how these limnological parameters responded to variation in the climate systems, regional meteorology, hydrological regimes, and other lake characteristics (Fig. 3b; Table S3¹). These new models explained 23%–51% (R^2_{adj}) of mean summer variation in limnological drivers of water quality, with river hydrology (~22%–83% of explained variation), climate (~20%–76%), and meteorological conditions (~10%–40%) making important model contributions. Specifically, T_{water} was correlated positively to air temperature, but negatively to volume of inflow, ice-off date, and snow accumulation, whereas SRP concentration was correlated negatively to river inflow and wind speed, and TIC content was correlated positively to ice-off date and inversely to inflow (Table S3¹). Only variation in mean summer pH was predicted by changes in other internal lake characteristics (~54% of explained variation) (Fig. 3b), with a positive correlation to water-column DOC content, and a negative relationship with TIC concentration, NAO index, summer precipitation, and date of ice melt.

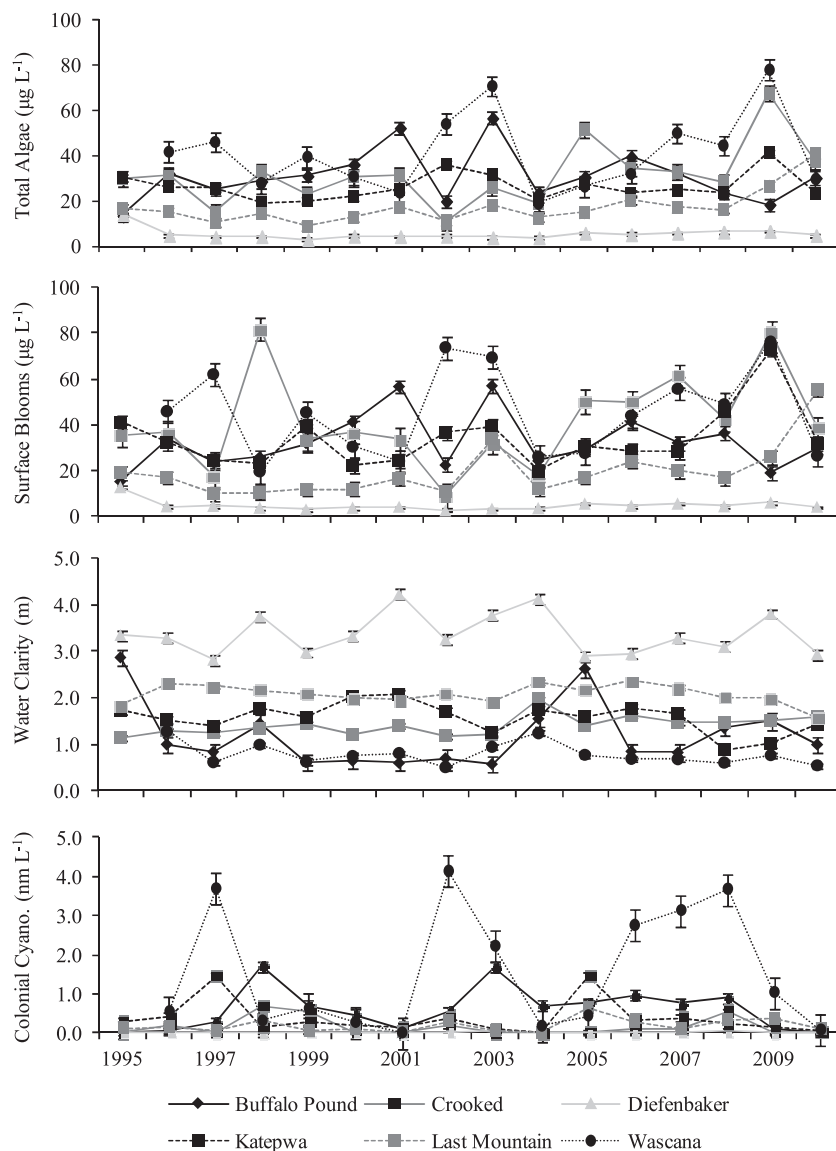
Monthly models of water quality

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

Forecasting future water quality

Scenario analysis with regression models suggested that increases in water temperature due to climate warming will have a greater effect on total algal abundance and surface bloom intensity in these productive lakes than will either regional management of nutrient sources or changes in hydrology resulting from industrial extraction or compensatory increases in river convey-

Fig. 2. Time series of four indices of water quality: total algae ($\mu\text{g}\cdot\text{L}^{-1}$), surface blooms ($\mu\text{g}\cdot\text{L}^{-1}$), water clarity (m), and colonial cyanobacteria (nmoles myxoxanthophyll- L^{-1}). Data are based on seasonal (May–August) means \pm 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).



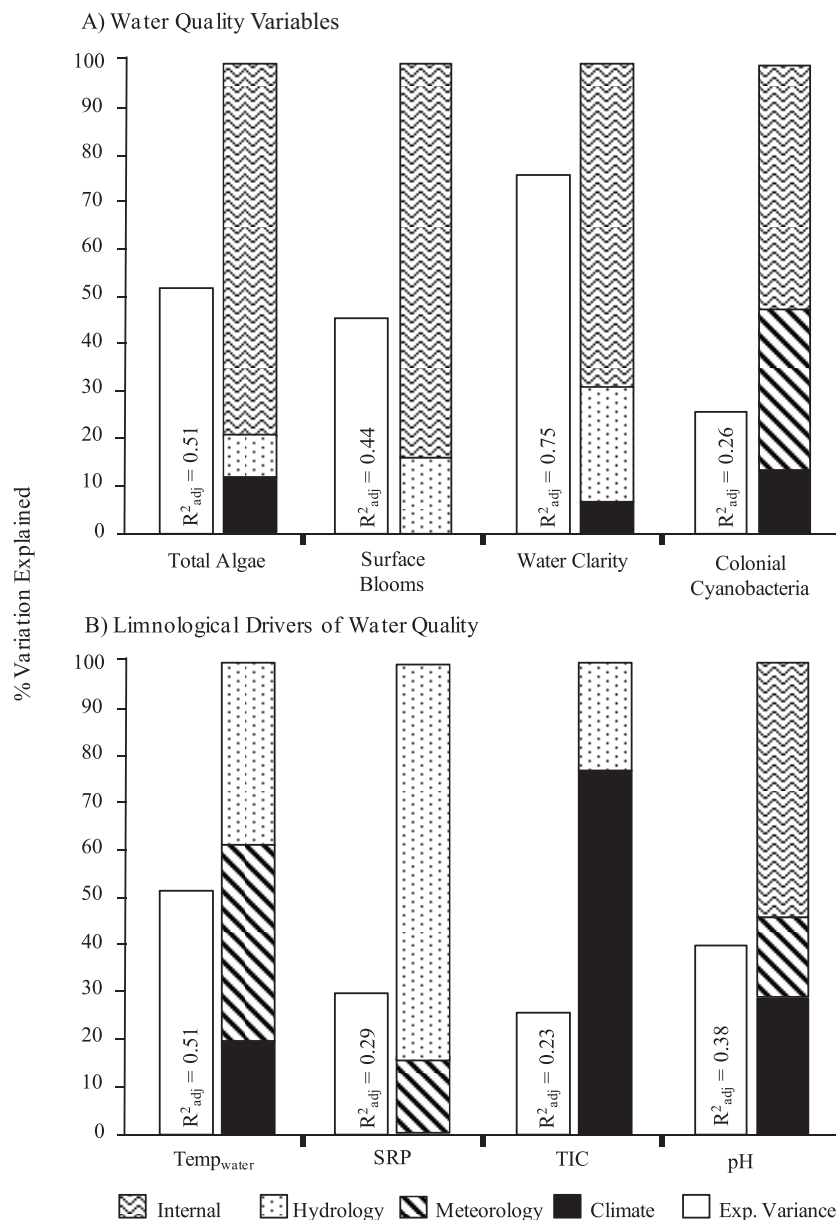
ance (Table 2). For example, models predicted that total algal abundance will increase by $\sim 75\%$ with a 5°C increase in T_{water} , whereas Chl *a* content is expected to vary little ($\pm 7\%$) if inflow is either doubled or declines to 1% of mean summer inflow. Instead, algal abundance only declined appreciably ($\sim 65\%$) when hydrologic input to lakes was increased 1000% over mean summer conditions, a value that exceeds the conveyance capacity of the Qu'Appelle River. Algal responses to changes in nutrient sources were of intermediate intensity, with models predicting a 64% increase with three-fold higher concentrations, and a 29% decline if nutrient content was reduced to 10% of current mean summer values. Similarly, the intensity of surface blooms increased progressively with T_{water} ($\sim 60\%$ for 5°C warming) and nutrients ($\sim 50\%$ for 300% increase), while a 200% change in mean river flow altered such blooms by $<10\%$. In contrast, water clarity is expected to change less than 3% with even extreme atmospheric warming, 10-fold variation in nutrient content, or a doubling of hydrologic inflow (Table 2). In all cases, interactions between temperature, nutrient, and river flow scenarios were purely additive, and there

was no evidence of either synergistic or antagonistic interactions when multiple parameters were manipulated.

Discussion

Analysis of 25 decadal time series demonstrated that water quality in eutrophic lakes of the Canadian Prairies is regulated mainly by variation in internal lake characteristics (water temperature, dissolved nutrients, pH; Fig. 3a), but that these limnological parameters are correlated in turn to variations in large-scale climate systems, regional meteorology, and river hydrology (Fig. 3b). Unexpectedly, the composition of predictive models varied substantially among closely related measures of phytoplankton communities (Table S2¹) and among months (Fig. 4), underscoring the need to explicitly evaluate both direct and indirect pathways for each ecological stressor and response parameter (Palmer and Yan 2013). Further, application of these models to realistic scenarios of future environmental change (Table 2) showed that potential regulatory mechanisms with the greatest effect on water quality

Fig. 3. Total explained variation (white) and proportion of nonresidual 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 9999 permutations and were classified into categories associated with variation in climate systems (black), regional meteorology (diagonal lines), river hydrology (dotted), and internal lake characteristics (waves).



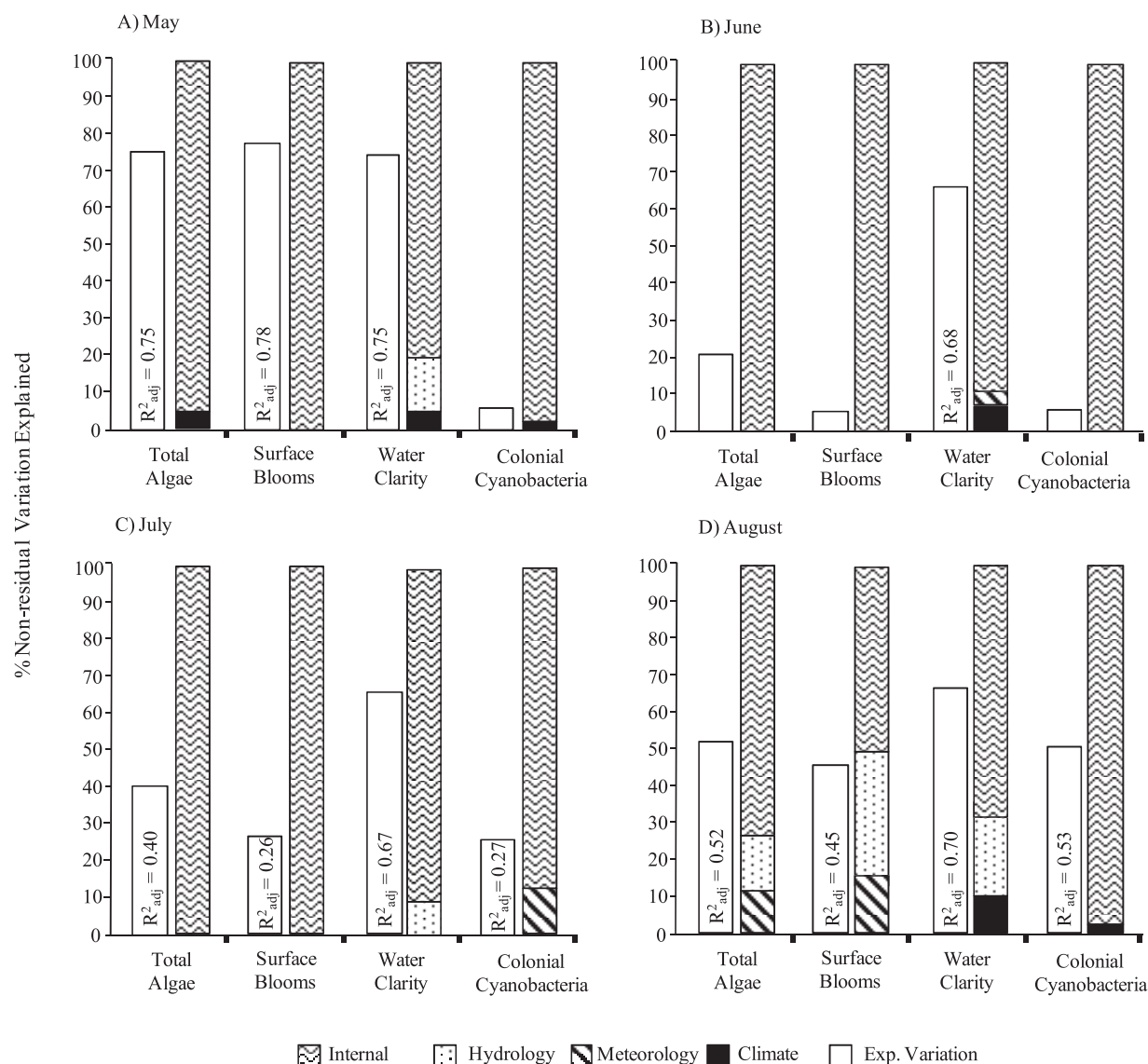
(temperature increase) or the greatest ease of management (1000% variation in river conveyance) did not represent the most effective means of sustaining regional water quality in the coming decades (nutrient diversion). Such quantitative assessment of the relative effects of multiple forcing mechanisms is important to allow scientists and managers to develop effective and adaptive management strategies to protect aquatic resources (Schindler 2001; Gober and Wheeler 2014).

Controls of summer water quality

Regression analysis suggested that water quality change during the past two decades was explained best by variation in T_{water} , solute content, and inflow regimes, factors that were ultimately

under climatic control (Table S2¹). Elevated T_{water} increases algal growth (Winder and Sommer 2012; Paerl and Otten 2013) and intensifies the thermal stratification that favours buoyancy-regulating, bloom-forming cyanobacteria in eutrophic lakes (Huisman et al. 2004; Cantin et al. 2011). Warmer surface waters arise from changes in the net energy budget of a lake (e.g., MacIntyre et al. 2014), which, for polymictic prairie lakes, is mainly due to altered transmission of solar irradiance (O'Reilley et al. 2015), variation in air mass and its temperature (Bonsal et al. 2006; Bonsal and Shabbar 2008), and influx of discrete water sources (Dröschner et al. 2009). Although direct irradiance measures were not available for all lakes and years as required for regression model analysis, previ-

Fig. 4. Total explained variation (white) and proportion of nonresidual 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).



ous analysis of data from six regional meteorological stations (Vogt et al. 2011) reveals a slow increase in regional receipt of solar energy and extremely low interannual variation (coefficient of variation = 6%), in contrast to stable but more annually variable lake parameters (Fig. 2). As well, earlier analysis of energy budgets for regional lakes reveals that interannual variation in the rate of summer heat accumulation in lakes (~50 days) is controlled by interactions between the mass of snow received the preceding winter, timing of spring ice melt, and the volume of cold-water runoff during the vernal freshet (Dröscher et al. 2009), all of which were identified as important predictors in our regression analysis (Table S3¹). Spring runoff also influences algal density by altering water renewal rates (dilution) in central North American lakes, as ~75% of regional river discharge occurs during a 3-week period in March–April, yet runoff volume varies by 10-fold among years (Fang and Pomeroy 2007; Pham et al. 2009). The importance of interannual variation in seasonal properties is underlined by the

fact that regression models explained up to 75% of interannual variation in water quality parameters, despite there being no linear or discontinuous changes in mean summer algal abundance, bloom characteristics, or water clarity (Fig. 2).

Identification of separate influences of climate systems and regional meteorology on water quality in eutrophic ecosystems is consistent with mechanisms known to regulate atmospheric conditions in central Canada. Regional warming occurs most commonly when El Niño and positive-phase PDO events interact to increase sea surface temperatures in the eastern North Pacific Ocean and force jet-stream position northward beyond the Prairies (Shabbar et al. 2011). Similarly, introduction of synoptic precipitation into central Canada is influenced by the position of continental jet streams that variously import water from the northern Pacific Ocean, the Gulf of California, and the Gulf of Mexico (Higgins et al. 1997; Liu and Stewart 2003). Finally, timing of ice melt is influenced strongly by atmospheric teleconnections,

Table 2. Summary of scenario analysis depicting changes in total algae, surface bloom intensity, and water clarity under different hydrologic regimes, increases in water temperature, or changes in water-column nutrient content.

	Total algae		Surface blooms		Water clarity	
	Concentration Chl <i>a</i> ($\mu\text{g}\cdot\text{L}^{-1}$)	% change	Concentration Chl <i>a</i> ($\mu\text{g}\cdot\text{L}^{-1}$)	% change	Depth (m)	% change
% of inflow						
1%	20.3	7.3	23.5	10.1	1.5	3.3
25%	19.9	5.6	22.9	7.7	1.6	2.5
50%	19.6	3.7	22.4	5.1	1.6	1.7
150%	18.2	-3.7	20.3	-5.1	1.6	-1.7
200%	17.5	-7.4	19.2	-10.2	1.7	-3.3
1000%	6.3	-66.7	1.7	-91.9	2.1	-29.9
Temperature increase						
1 °C	21.7	14.6	23.8	11.5	1.6	0.2
2 °C	24.4	29.3	26.3	22.9	1.6	0.4
3 °C	27.2	43.9	28.7	34.4	1.6	0.6
4 °C	29.9	58.6	31.2	45.9	1.6	0.8
5 °C	32.7	73.3	33.6	57.4	1.6	0.9
% increase of current nutrients						
10%	13.4	-29.0	16.2	-23.9	1.6	-0.6
25%	14.3	-24.2	17.1	-19.9	1.6	-0.5
50%	15.8	-16.1	18.5	-13.3	1.6	-0.3
200%	25.0	32.2	27.0	26.5	1.6	0.6
300%	31.1	64.5	32.7	53.1	1.6	1.2

Note: Changes are depicted with estimated values of total algae, surface blooms, and water clarity and percentage change in each response variable under each scenario. Further, values are given for each variable as estimates of current conditions from the model and as measured means of current conditions. Factor interactions were linear combinations of expected change and are not presented.

as warm spring conditions are common during synergistic interactions between El Niño events and the PDO (Bonsal et al. 2006), while winter extreme temperatures and ice cover are influenced by changes in atmospheric circulation in the Arctic (as NAO) (Dröschner et al. 2009). Thus, while regional air and water temperatures vary synchronously as a result of seasonal cycles of solar irradiance and direct water-column heating, interactions among climate systems provide additional indirect controls of lake warming through hydrologic variability (Dröschner et al. 2009).

Interactions between river hydrology, nutrient status, and lake production revealed by regression models (Tables S2 and S3¹) are consistent with regulatory mechanisms identified by decadal-scale macronutrient budgets (Patoine et al. 2006; Leavitt et al. 2006; Finlay et al. 2010). For example, regression models suggest that algal abundance is stimulated by nutrient content, but reduced by river inflow (Table 2), despite allochthonous nutrient influx being a ubiquitous predictor of lentic Chl *a* content (Schindler 2006). Analysis of mass-balance budgets reconciles these observations by demonstrating that lake sediments presently account for up to 85% of nutrient supply to the water column of these eutrophic lakes (Patoine et al. 2006). In addition, cold-region hydrological models (Pomeroy et al. 2007) and stable isotope analyses (Pham et al. 2009) both reveal that the brief snow melt in spring is the predominant source of water to regional rivers and lakes and that the volume of runoff is greatest when rapid snow melt occurs over frozen soils, conditions that favour water, but not necessarily nutrient, mobilization. As well, we note that flow in the Qu'Appelle River is subject to engineered conveyance from upstream lakes, and that such channelized flow can decouple the relationships between climate, runoff, and lotic nutrient concentrations seen elsewhere (McCullough et al. 2012; Bunting et al. 2016). Thus, while it remains necessary to be cautious about inference of regulatory mechanisms from a regression-based analysis, the strong support of our models by whole-lake mass balance budgets, catchment-scale nutrient transport studies, and centennial-

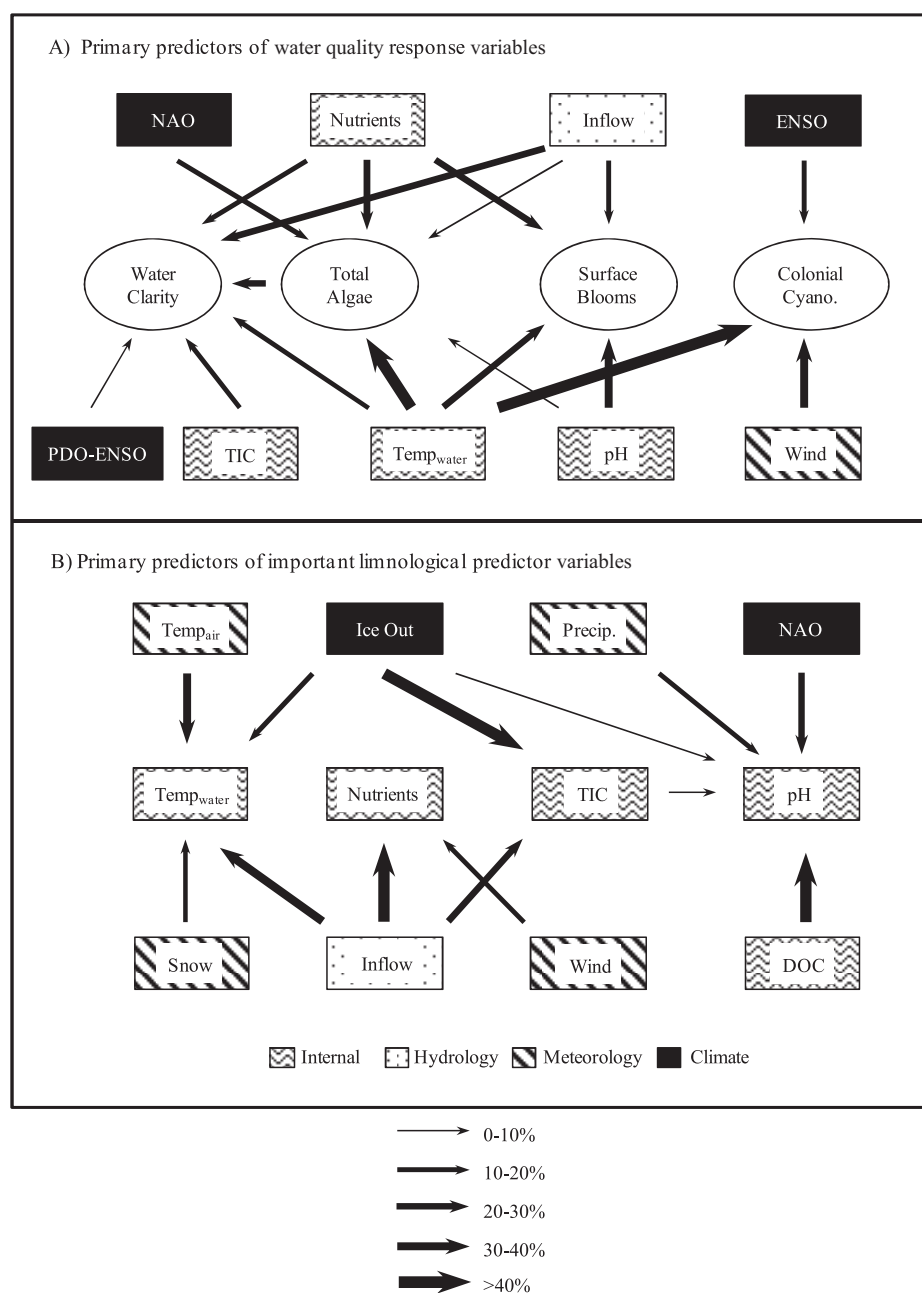
scale paleoecological research provides a solid mechanistic basis for our findings and their application to eutrophic lakes.

Comparison of regression model composition (Table S2¹) suggests that regulatory pathways may differ substantially among even highly correlated water quality parameters or limnological characteristics (Fig. 5). For example, models of total algal abundance and water clarity were complex, of similar predictive power, and influenced by a combination of climate systems, hydrologic characteristics, and limnological properties, as described above. In contrast, 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 other research showing that colonial cyanobacteria are most abundant in eutrophic sites during years when waters are warm, wind speed is low, and lakes exhibit stronger thermal stratification (Huisman et al. 2004; Zhang et al. 2012; Paerl and Otten 2013). All these conditions are enhanced during El Niño events, and, accordingly, we note that both shallow lakes (Wascana, Buffalo Pound) exhibited ~5-year cycles of colonial cyanobacteria abundance (Fig. 2), which, while not statistically significant, peaked during known El Niño events (e.g., 1997). Such marked differences among predictive models are important to document, as they suggest that eutrophic lake management strategies will vary according to the precise regulatory goal (e.g., increased transparency, reduced cyanobacteria).

Seasonal variation in predictive models

Pronounced variation in the predictive power of water quality models developed with monthly data (Fig. 4) is consistent with known patterns of plankton phenology in the Qu'Appelle catchment. For example, algal abundance and water clarity models were strong in May ($R^2_{\text{adj}} > 0.65$), when phytoplankton communities are composed of diatoms and flagellates and complete water-column mixing eliminates vertical zonation of phytoplankton (McGowan et al. 2005; Vogt et al. 2011). In contrast, colonial cyanobacteria are rare in Qu'Appelle lakes during spring (Patoine et al.

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 (waves). Arrow thickness increases with percentage of nonresidual variation explained for each model. Interactions among water quality variables were not measured except for that between total algal abundance and water clarity.



2006), consistent with the nonsignificant model for their characteristic biomarker, myxoxanthophyll, during May. Overall, statistical models suggested a role of herbivory in regulating water quality in early summer (but not all summer), with the inclusion of large-bodied herbivores as predictors of water clarity in May and June, the months in which intense grazing by large-bodied *Daphnia* spp. reduces algal biomass and increases Secchi depth by up to 10-fold (Dröscher et al. 2009). In addition, while all water quality models were significant when developed with data from either July or August, the latter 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).

Landscape management of lakes

The analytical framework employed here allows us to differentiate among global climate systems, regional meteorology, river hydrology, and site-specific limnological features as potential controls of water quality in productive lakes at the landscape scale. Although our models were based solely on linear regression analysis, this simple approach was warranted by the data structure, and more complicated analytical approaches were unnecessary (e.g., detrending, regression trees, multivariate autoregressive

models, spectral analysis) (Hampton et al. 2013). Regardless, our analysis explained on average ~50% of observed interannual variation in algal abundance (Table S2¹), despite the absence of any progressive trend in lake production during the past two decades (Fig. 2). Instead, application of these models allowed us to develop a roadmap for adaptive management of continental lakes in the face of future warming of 1.5–5 °C (IPCC 2013), nutrient pollution from farms and cities (Leavitt et al. 2006; Bunting et al. 2016), and industrial extraction of water by agriculture or solute mines (Saskatchewan Water Security Agency 2013).

Analysis of model forecasts suggests that resource managers in semiarid 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 (Dröschner et al. 2009) owing to high seasonality of discharge (Pomeroy et al. 2007; Fang and Pomeroy 2007) and long hydrological transit times among lakes (Fig. 1). In addition, although water conveyance through the Qu'Appelle River has been managed for over a century via reservoirs (Diefenbaker, Buffalo Pound, Wascana) and outlet dams on natural lakes (Hall et al. 1999; Saskatchewan Water Security Agency 2013), the limited channel capacity and low topographic relief (0.4 m·km⁻¹) greatly constrains river discharge unless accompanied by re-channelization of the river. Even so, our analysis shows that more than a doubling of lotic conveyance will have negligible effects (<5%) on water quality (Table 2), a pattern that may generalize well to other dry continental regions. In fact, even unrealistically diminished river flow (1% of mean summer values) appears to have only relatively minor effects (<10% reduction) on water quality (Table 2). Further analysis of the independent influx of nutrients and water from discrete sources (livestock operations, cities, crop production) will help refine this observation (Bunting et al. 2016).

Application of regression models to realistic scenarios suggests that reductions in nutrient influx may be the most practical means of preserving regional water quality in the immediate future. Consistent with this prediction, previous research shows that algal abundance in eutrophic Qu'Appelle lakes has increased up to 300%, and cyanobacteria by >500%, as a linear function ($r^2 > 0.70$, $p < 0.05$) of the influx of dissolved N (mainly NH₄⁺) from urban centres during 1900–1980 (Hall et al. 1999; Leavitt et al. 2006, 2009). Presently, urban point sources represent ~70% of total ecosystem N in downstream lakes (Leavitt et al. 2006); however, wastewater treatment plants are mandated by federal legislation to reduce NH₄⁺ pollution to ~15% of current discharge by 2017, and are already operational in the city of Regina. Because fertilization with NH₄⁺ increases algal bloom density and toxicity by up to 400% in these SRP-rich lakes (reviewed in Donald et al. 2011), substantial diversion of N is expected to improve water quality. Interestingly, our models forecast less improvement in water quality (Table 2) than would be expected on the basis of paleolimnological, mass-balance, and experimental studies (Hall et al. 1999; Leavitt et al. 2006; Donald et al. 2011), possibly because our regression-based approach cannot estimate centennial-scale changes in nutrient regimes, sedimentary sources may reduce lake sensitivity to allochthonous nutrient influx (Jeppesen et al. 2005; Patoine et al. 2006), or because some Qu'Appelle lakes are not impacted by urban wastewater (Leavitt et al. 2006).

Regulatory mechanisms and management strategies identified here should generalize well to continental landscapes with similar climatic, edaphic, and limnological characteristics. Long-term changes in carbon fluxes (Finlay et al. 2010, 2015), nitrogen biogeochemistry (Bogard et al. 2012), water sources (Pham et al. 2009), and climatic forcing (Pham et al. 2009, Vogt et al. 2011) are highly synchronous among Qu'Appelle and other lakes within a 235 000 km² prairie

region, irrespective of basin hydrology (open or closed drainage). Although less well studied than boreal regions, such continental interiors account for ~8 × 10⁶ km² (Finlay et al. 2015), and their fresh waters are critical resources for social and economic development (Barica 1987; Schindler 2001) as well as regulation of climatic processes (Finlay et al. 2015). The models presented here represent an important first step in establishing a predictive understanding of the relative importance of environmental and human mechanisms threatening lakes in these districts (Brown et al. 2011). Collectively, the analyses presented here suggest that regional management 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 climate warming (Table 2).

Acknowledgements

We thank members of the Limnology Laboratory for assistance with data collection since 1994; Curtis Halborg and Bart Oegema at the Saskatchewan Water Security Agency for estimates of river flow; and Daniel Schindler, Kerri Finlay, James Rusak, Gavin Simpson, Björn Wissel, Matthew Bogard, and Heather Haig for insightful comments that improved the manuscript. This paper was also improved by critiques from G.W. Kling and two anonymous reviewers. This work was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grants, the Canada Research Chair Program, Canada Foundation for Innovation, the Province of Saskatchewan, the University of Regina, Nature Regina, York University, and Université du Québec à Montréal.

References

- Akinremi, O.O., McGinn, S.M., and Cutforth, H.W. 1999. Precipitation trends on the Canadian Prairies. *J. Clim.* 12: 2996–3003. doi:10.1175/1520-0442(1999)012<2996:PTOTCP>2.0.CO;2.
- Barica, J. 1987. Water quality problems associated with productivity of prairie lakes in Canada: a review. *Water Qual. Bull.* 12: 107–115.
- Barrow, E. 2009. Climate scenarios for Saskatchewan. Prairie Adaptation Research Collaborative Report. University of Regina, Regina, Saskatchewan, Canada.
- Blanchet, F.G., Legendre, P., and Bocard, D. 2008. Forward selection of explanatory variables. *Ecology*, 89: 2623–2632. doi:10.1890/07-0986.1. PMID:18831183.
- Bogard, M.J., Donald, D.B., Finlay, K., and Leavitt, P.R. 2012. Distribution and regulation of urea in lakes of central North America. *Freshw. Biol.* 57: 1277–1292. doi:10.1111/j.1365-2427.2012.02775.x.
- Bonsal, B., and Shabbar, A. 2008. Impacts of large-scale circulation variability on low streamflows over Canada: a review. *Can. Water Res. J.* 33: 137–154. doi:10.4296/cwrj3302137.
- Bonsal, B.R., Prowse, T.D., Duguay, C.R., and Lacroix, M.P. 2006. Impacts of large-scale teleconnections on freshwater-ice break/freeze-up dates over Canada. *J. Hydrol.* 330: 340–353. doi:10.1016/j.jhydrol.2006.03.022.
- Brown, C.J., Schoeman, D.S., Sydeman, W.J., Brander, K., Buckley, L.B., Burrows, M., Duarte, C.M., Moore, P.J., Pandolfi, J.M., Poloczanska, E., Venables, W., and Richardson, A.J. 2011. Quantitative approaches in climate change ecology. *Global Change Biol.* 17: 3697–3713. doi:10.1111/j.1365-2486.2011.02531.x.
- Bunting, L., Leavitt, P.R., Simpson, G.L., Wissel, B., Laird, K.R., Cumming, B.F., St. Amand, A., and Engstrom, D.R. 2016. Increased variability and sudden ecosystem state change in Lake Winnipeg, Canada, caused by 20th century agriculture. *Limnol. Oceanogr.* 61: 2090–2107. doi:10.1002/lno.10355.
- Cantin, A., Beisner, B.E., Gunn, J.M., Prairie, Y.T., and Winter, J.G. 2011. Effects of thermocline deepening on lake plankton communities. *Can. J. Fish. Aquat. Sci.* 68(2): 260–276. doi:10.1139/F10-138.
- Carpenter, S.R. 1993. Statistical analysis of the ecosystem experiments. In *The trophic cascade in lakes*. Edited by S.R. Carpenter and J.F. Kitchell. Cambridge, pp. 26–42.
- Carpenter, S.R., and Kitchell, J.F. 1993. *The trophic cascade in lakes*. Cambridge University Press.
- Carpenter, S.R., Caraco, N.F., Correll, D.L., Howarth, R.W., Sharpley, A.N., and Smith, V.H. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecol. Appl.* 8: 559–568. doi:10.1890/1051-0761(1998)008[0559:NPOSWW]2.0.CO;2.
- Christensen, M.R., Graham, M.D., Vinebrooke, R.D., Findlay, D.L., Paterson, M.J., and Turner, M.A. 2006. Multiple anthropogenic stressors cause ecological surprises in boreal lakes. *Global Change Biol.* 12: 2316–2322. doi:10.1111/j.1365-2486.2006.01257.x.
- Cohen, S., Koshida, G., and Mortsch, L. 2015. Climate and water availability indicators in Canada: challenges and a way forward. Part III — Future scenarios. *Can. Water Resour. J.* 40: 160–172. doi:10.1080/07011784.2015.1006021.

- Donald, D.B., Parker, B.R., Davies, J.-M., and Leavitt, P.R. 2015. Nutrient sequestration in the Lake Winnipeg watershed. *J. Great Lakes Res.* **41**: 630–642. doi:10.1016/j.jglr.2015.03.007.
- Donald, D.B., Bogard, M.J., Finlay, K., and Leavitt, P.R. 2011. Comparative effects of urea, ammonium, and nitrate on phytoplankton abundance, community composition, and toxicity in hypereutrophic freshwaters. *Limnol. Oceanogr.* **56**: 2161–2175. doi:10.4319/lo.2011.56.6.2161.
- Dröscher, I., Patoine, A., Finlay, K., and Leavitt, P.R. 2009. Climate control of the spring clear-water phase through the transfer of energy and mass to lakes. *Limnol. Oceanogr.* **54**: 2469–2480. doi:10.4319/lo.2009.54.6.2469.
- Fang, X., and Pomeroy, J.W. 2007. Snowmelt runoff sensitivity analysis to drought on the Canadian prairies. *Hydrol. Process.* **21**: 2594–2609. doi:10.1002/hyp.6796.
- Finlay, K., Vogt, R.J., Bogard, M.J., Wissel, B., Tutolo, B.M., Simpson, G.L., and Leavitt, P.R. 2015. Decrease in CO₂ efflux from northern hardwater lakes with increasing atmospheric warming. *Nature*, **519**: 215–218. doi:10.1038/nature14172. PMID:25731167.
- Finlay, K., Leavitt, P.R., Wissel, B., and Prairie, Y.T. 2009. Regulation of spatial and temporal variability of carbon flux in six hard-water lakes of the northern Great Plains. *Limnol. Oceanogr.* **54**: 2553–2564. doi:10.4319/lo.2009.54.6.2553.
- Finlay, K., Leavitt, P.R., Patoine, A., and Wissel, B. 2010. Magnitudes and controls of organic and inorganic carbon flux through a chain of hard-water lakes on the northern Great Plains. *Limnol. Oceanogr.* **55**: 1551–1564. doi:10.4319/lo.2010.55.4.1551.
- Gober, P., and Wheatley, H.S. 2014. Socio-hydrology and the science-policy interface: a case study of the Saskatchewan River basin. *Hydrol. Earth Syst. Sci.* **18**: 1413–1422. doi:10.5194/hess-18-1413-2014.
- Haertel, L. 1976. Nutrient limitation of algal standing crops in shallow prairie lakes. *Ecology*, **57**: 664–678. doi:10.2307/1936181.
- Hall, R.I., Leavitt, P.R., Quinlan, R., Dixit, A.S., and Smol, J.P. 1999. Effects of agriculture, urbanization, and climate on water quality in the northern Great Plains. *Limnol. Oceanogr.* **44**: 739–756. doi:10.4319/lo.1999.44.3.739.
- Hampton, S.E., Holmes, E.E., Scheef, L.P., Scheuerell, M.D., Katz, S.L., Pendleton, D.E., and Ward, E.J. 2013. Quantifying effects of abiotic and biotic drivers on community dynamics with multivariate autoregressive (MAR) models. *Ecology*, **94**: 2663–2669. doi:10.1890/13-0996.1. PMID:24597213.
- Higgins, R.W., Yao, Y., Yarosh, E.S., Janowiak, J.E., and Mo, K.C. 1997. Influence of the Great Plains Low-Level Jet on summertime precipitation and moisture transport over the Central United States. *J. Clim.* **10**: 481–507. doi:10.1175/1520-0442(1997)010<0481:IOTGPI>2.0.CO;2.
- Huisman, J., Sharples, J., Stroom, J.M., Visser, P.M., Kardinaal, W.E.A., Verspagen, J.M.H., and Sommeijer, B. 2004. Changes in turbulent mixing shift competition for light between phytoplankton species. *Ecology*, **85**: 2960–2970. doi:10.1890/03-0763.
- Hurrell, J.W. 1995. Decadal trends in the North Atlantic Oscillation — regional temperatures and precipitation. *Science*, **269**: 676–679. doi:10.1126/science.269.5224.676. PMID:17758812.
- IPCC. 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Edited by T.F. Stocker and others. Cambridge University Press.
- Jeppesen, E., Sondergaard, M., Jensen, J.P., Havens, K.E., Anneville, O., Carvalho, L., Coveney, M.F., Deneke, R., Dokulil, M.T., Foy, B., Gerdeaux, D., Hampton, S.E., Hilt, S., Kangur, K., Kohler, J., Lammens, E.H.H.R., Lauridsen, T.L., Manca, M., Miracle, M.R., Moss, B., Nøges, P., Persson, G., Phillips, G., Portielje, R., Romo, S., Schelske, C.L., Stråle, D., Tatrai, I., Willen, E., and Winder, M. 2005. Lake responses to reduced nutrient loading — an analysis of contemporary long-term data from 35 case studies. *Freshw. Biol.* **50**: 1747–1771. doi:10.1111/j.1365-2427.2005.01415.x.
- Lapp, S.L., St. Jacques, J.M., Barrow, E., and Sauchyn, D.J. 2012. GCM projections for the Pacific Decadal Oscillation under greenhouse forcing for the early 21st century. *Int. J. Climatol.* **32**: 1423–1442. doi:10.1002/joc.2364.
- Lapp, S.L., St. Jacques, J.M., Sauchyn, D.J., and Vanstone, J.R. 2013. Forcing of hydrologic variability in the northwestern Great Plains since AD1406. *Quat. Int.* **310**: 47–61. doi:10.1016/j.quaint.2012.09.011.
- Leavitt, P.R., Fritz, S.C., Anderson, N.J., Baker, P.A., Blenckner, T., Bunting, L., Catalan, J., Conley, D.J., Hobbs, W.O., Jeppesen, E., Korhola, A., McGowan, S., Rühland, K., Rusak, J.A., Simpson, G.L., Solovieva, N., and Werne, J. 2009. Paleolimnological evidence of the effects on lakes of energy and mass transfer from climate and humans. *Limnol. Oceanogr.* **54**: 2330–2348. doi:10.4319/lo.2009.54.6.2330.
- Leavitt, P.R., Brock, C.S., Ebel, C., and Patoine, A. 2006. Landscape-scale effects of urban nitrogen on a chain of freshwater lakes in central North America. *Limnol. Oceanogr.* **51**: 2262–2277. doi:10.4319/lo.2006.51.5.2262.
- Liu, J., and Stewart, R.E. 2003. Water vapor fluxes over the Saskatchewan River Basin. *J. Hydrometeorol.* **4**: 944–959. doi:10.1175/1525-7541(2003)004<0944:WVFTS>2.0.CO;2.
- MacIntyre, S., Romero, J.R., Silsbe, G.M., and Emery, B.M. 2014. Stratification and horizontal exchange in Lake Victoria, East Africa. *Limnol. Oceanogr.* **59**: 1805–1838. doi:10.4319/lo.2014.59.6.1805.
- Maheux, H., Leavitt, P.R., and Jackson, L.J. 2016. Asynchronous onset of eutrophication among shallow prairie lakes of the northern Great Plains, Alberta, Canada. *Global Change Biol.* **22**: 271–283. doi:10.1111/gcb.13076.
- Mantua, M.J., Hare, S., Zhang, Y., Wallace, J.M., and Francis, R.C. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* **78**: 1069–1080. doi:10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2.
- McCabe, G.J., Palecki, M.A., and Betancourt, J.L. 2004. Pacific and Atlantic Ocean influences on multidecadal drought frequency in the United States. *Proc. Natl. Acad. Sci. U.S.A.* **101**: 4136–4141. doi:10.1073/pnas.0306738101. PMID:15016919.
- McCullough, G.K., Page, S.J., Hesslein, R.H., Stainton, M.P., Kling, H.J., Salki, A.G., and Barber, D.G. 2012. Hydrological forcing of a recent trophic surge in Lake Winnipeg. *J. Great Lakes Res.* **38**(S3): 95–105. doi:10.1016/j.jglr.2011.12.012.
- McGowan, S., Patoine, A., Graham, M.D., and Leavitt, P.R. 2005. Intrinsic and extrinsic controls of lake phytoplankton synchrony. *Verh. Int. Verein Limnol.* **29**: 794–798.
- O'Reilly, C.M., Sharma, S., Gray, D.K., Hampton, S.E., Read, J.S., Rowley, R.J., Schneider, P., et al. 2015. Rapid and highly variable warming of lake surface waters around the globe. *Geophys. Res. Lett.* **42**: 10773–10781. doi:10.1002/2015GL066235.
- Orihel, D.M., Bird, D., Brylinsky, M., Chen, H., Donald, D., Huang, D., Giani, A., Kinniburgh, D., Kling, H., Kotak, B., Leavitt, P., Nielsen, C., Reedyk, S., Rooney, R., Watson, S., Zurawell, R., Vinebrooke, R., and Smith, R.H. 2012. High microcystin concentrations occur only at low nitrogen-to-phosphorus ratios in nutrient-rich Canadian lakes. *Can. J. Fish. Aquat. Sci.* **69**: 1457–1462. doi:10.1139/f2012-088.
- Paerl, H.W., and Otten, T.G. 2013. Harmful cyanobacterial blooms: Causes, consequences, and controls. *Microb. Ecol.* **65**: 995–1010. doi:10.1007/s00248-012-0159-y. PMID:23314096.
- Palmer, M.E., and Yan, N.D. 2013. Decadal-scale regional changes in Canadian freshwater zooplankton: the likely consequence of complex interactions among multiple anthropogenic stressors. *Freshw. Biol.* **58**: 1366–1378. doi:10.1111/fwb.12133.
- Patoine, A., Graham, M.D., and Leavitt, P.R. 2006. Spatial variation of nitrogen fixation in lakes of the northern Great Plains. *Limnol. Oceanogr.* **51**: 1665–1677. doi:10.4319/lo.2006.51.4.1665.
- Pham, S.V., Leavitt, P.R., McGowan, S., Wissel, B., and Wassenaar, L. 2009. Spatial and temporal variability of prairie lake hydrology as revealed using stable isotopes of hydrogen and oxygen. *Limnol. Oceanogr.* **54**: 101–118. doi:10.4319/lo.2009.54.1.0101.
- Pomeroy, J.W., Gray, D.M., Brown, T., Hedstrom, N.R., Quinton, W.L., Granger, R.J., and Carey, S.K. 2007. The cold regions hydrological model: A platform for basing process representation and model structure on physical evidence. *Hydrol. Process.* **21**: 2650–2667. doi:10.1002/hyp.6787.
- R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Austria.
- Saskatchewan Water Security Agency. 2013. 25 Saskatchewan Year Water Security Plan [online]. Saskatchewan Water Security Agency, Moose Jaw, Saskatchewan. Available from https://www.wsask.ca/Global/About%20WSA/25%20Year%20Water%20Security%20Plan/WSA_25YearReportweb.pdf.
- Schindler, D.W. 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. *Can. J. Fish. Aquat. Sci.* **58**(1): 18–29. doi:10.1139/f00-179.
- Schindler, D.W. 2006. Recent advances in the understanding and management of eutrophication. *Limnol. Oceanogr.* **51**: 356–363. doi:10.4319/lo.2006.51.1.356.
- Schindler, D.W., and Donahue, W.F. 2006. An impending water crisis in Canada's western prairie provinces. *Proc. Natl. Acad. Sci. U.S.A.* **103**: 7210–7216. doi:10.1073/pnas.0601568103. PMID:16606829.
- Shabbar, A., Bonsal, B.R., and Szeto, K. 2011. Atmospheric and oceanic variability associated with growing season droughts and pluvials on the Canadian Prairies. *Atmosph.-Ocean*, **49**: 339–355. doi:10.1080/07055900.2011.564908.
- Shabbar, A., and Yu, B. 2012. Intraseasonal Canadian winter temperature responses to interannual and interdecadal Pacific SST modulations. *Atmosph.-Ocean*, **50**: 109–121. doi:10.1080/07055900.2012.657154.
- Sharma, S., Walker, S., and Jackson, D.A. 2008. Empirical modelling of lake water relationships: a comparison of predictive modelling approaches. *Freshw. Biol.* **53**: 897–911. doi:10.1111/j.1365-2427.2008.01943.x.
- Sharma, S., Magnuson, J.J., Mendoza, G., and Carpenter, S.R. 2013. Influences of local weather, large-scale climatic drivers, and the ca. 11 year solar cycle on lake ice breakup dates; 1905–2004. *Clim. Change*, **118**: 857–870.
- St. Jacques, J.M., Sauchyn, D.J., and Zhao, Y. 2010. Northern Rocky Mountain streamflow records: global warming trends, human impacts or natural variability? *Geophys. Res. Lett.* **37**: L06407. doi:10.1029/2009GL042045.
- Trenberth, K.E., and Hurrell, J.W. 1994. Decadal atmospheric-ocean variations in the Pacific. *Clim. Dyn.* **9**: 303–319. doi:10.1007/BF00204745.
- Van der Kamp, G., Keir, D., and Evans, M. 2008. Long-term water level changes in closed-basin lakes of the Canadian Prairies. *Can. Wat. Res. J.* **33**: 23–38. doi:10.4296/cwrj3301023.
- Vogt, R.J., Sharma, S., and Leavitt, P.R. 2015. Decadal regulation of phytoplankton abundance and water clarity in a large continental reservoir by climatic, hydrologic and trophic processes. *J. Great Lakes Res.* **41**: 81–90. doi:10.1016/j.jglr.2014.11.007.

- Vogt, R.J., Rusak, J.A., Patoine, A., and Leavitt, P.R. 2011. Differential effects of energy and mass influx on the landscape synchrony of lake ecosystems. *Ecology*, **92**: 1104–1114. doi:[10.1890/10-1846.1](https://doi.org/10.1890/10-1846.1). PMID:[21661571](https://pubmed.ncbi.nlm.nih.gov/21661571/).
- Vogt, R.J., Matthews, B., Cobb, T.P., Graham, M.D., and Leavitt, P.R. 2013. Food web consequences of size-based predation and vertical migration of an invertebrate predator (*Leptodora kindtii*). *Limnol. Oceanogr.* **58**: 1790–1801. doi:[10.4319/lno.2013.58.5.1790](https://doi.org/10.4319/lno.2013.58.5.1790).
- Waiser, M.J., Tumber, V., and Holm, J. 2010. Effluence-dominated streams. Part 1. Presence and effects of excess nitrogen and phosphorus in Wascana Creek, Saskatchewan, Canada. *Environ. Toxicol. Chem.* **30**: 496–507. PMID:[21072844](https://pubmed.ncbi.nlm.nih.gov/21072844/).
- Wang, X.L., Wan, H., and Swail, V.R. 2006. Observed changes in cyclone activity in Canada and their relationships to major circulation regimes. *J. Clim.* **19**: 896–915. doi:[10.1175/JCLI3664.1](https://doi.org/10.1175/JCLI3664.1).
- Winder, M., and Sommer, U. 2012. Phytoplankton response to a changing climate. *Hydrobiologia*, **698**: 5–16. doi:[10.1007/s10750-012-1149-2](https://doi.org/10.1007/s10750-012-1149-2).
- Wyn, B., Sweetman, J.N., Leavitt, P.R., and Donald, D.B. 2007. Historical metal concentrations in lacustrine food webs revealed using fossil ephippia from *Daphnia*. *Ecol. Appl.* **17**: 754–764. doi:[10.1890/06-0868](https://doi.org/10.1890/06-0868).
- Zhang, M., Duan, H., Shi, X., Yu, Y., and Kong, F. 2012. Contributions of meteorology to the phenology of cyanobacterial blooms: Implications for future climate change. *Water Res.* **46**: 442–452. doi:[10.1016/j.watres.2011.11.013](https://doi.org/10.1016/j.watres.2011.11.013). PMID:[22123520](https://pubmed.ncbi.nlm.nih.gov/22123520/).