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LETTER

Effects of lake warming on the seasonal risk of toxic cyanobacteria exposure

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Scientific Significance Statement

Large spatial studies have shown that human activities are leading to a global increase in the incidence of harmful cyanobacterial blooms. However, it is unclear how concentrations of a common cyanobacterial toxin (i.e., microcystin) are changing on an interannual and seasonal basis. This study provides evidence that while temporal patterns are site-specific within a large prairie lake region, warmer temperatures result in elevated microcystin concentrations, prolonged duration of elevated toxins levels, and increased probability of exceeding human health thresholds for exposure to microcystin.

Abstract

Incidence of elevated harmful algal blooms and concentrations of microcystin are increasing globally as a result of human-mediated changes in land use and climate. However, few studies document changes in the seasonal and interannual concentrations of microcystin in lakes. Here, we modeled 11 yr of biweekly microcystin data from six lakes to characterize the seasonal patterns in microcystin concentration and to ascertain if there were pronounced changes in the patterns of potential human exposure to microcystin in lakes of central North America. Bayesian time series analysis with generalized additive models found evidence for a regional increase in microcystin maxima and duration but recorded high variation among lakes. During the past decade, warmer temperatures, but not nutrient levels, led to a marked increase in the number of days when concentrations exceeded drinking and recreational water thresholds set by the World Health Organization and United States Environmental Protection Agency.

Growth of human populations and associated industrial and agricultural activities has altered global biogeochemical cycles and climate to the detriment of water quality and aquatic ecosystem services (Dodds et al. 2013; Glibert

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et al. 2014). Excess nitrogen and phosphorus, warmer water temperatures, and increased thermal stratification promote the expansion of cyanobacterial harmful algal blooms (cHABs), resulting in a wide range of water quality issues (Carey et al. 2012). Among these are the production of neuro- and hepatotoxins linked to acute and chronic health effects in humans, livestock, and wildlife (Chorus and Bartram 1999). Microcystin, a liver toxin produced by cyanobacteria, is a frequent cause of negative human health effects, such that the World Health Organization (WHO) and the United States Environmental Protection Agency (EPA) have set health advisories for microcystin concentrations in drinking and recreational waters (Chorus and Bartram 1999). Prediction of the timing and extent of toxic blooms and human health risks are a central concern for management agencies, but forecasts of the onset, duration, and magnitude of elevated microcystin concentrations are problematic due to multiple causal pathways (Beaulieu et al. 2013; Taranu et al. 2017).

cHABs are increasing in magnitude and spatial extent (O'Neil et al. 2012), particularly in areas with long histories of agriculture (Taranu et al. 2015). Total nitrogen and high phytoplankton biomass are two of many potential drivers of high toxin concentrations in lakes across North America (Orihel et al. 2012; Beaulieu et al. 2013) and the probability of intense outbreaks is elevated in agricultural landscapes (Taranu et al. 2017), although high forecast variability along local-to-continental scales remains a problem (Beaulieu et al. 2013; Yuan et al. 2014). At the local scale, basin-scale effects may account for high variability (Vogt et al. 2011), with more nutrients exerting a paramount effect on cyanobacteria in shallow polymictic sites, while temperature may control bloom formation in deep stratified lakes (Taranu et al. 2012), but further research is needed to identity how regulatory mechanisms vary among basins within individual lake districts (Maheaux et al. 2016).

Climatic effects on plankton phenology may influence the timing of cHAB outbreaks (Thackeray et al. 2016). Earlier onsets of spring phytoplankton blooms appear common (Winder and Schindler 2004; Peeters et al. 2007), while less is known of the effects of lake warming on late season taxa such as cyanobacteria. In some lakes, the onset of *Microcystis* spp. has advanced 5–7 d per decade over 30 yr (Deng et al. 2014), with the most intense blooms during years with warmer water temperatures and lower wind speeds (Zhang et al. 2012). While short-term seasonal studies of microcystin dynamics have identified strong seasonality in microcystin concentrations and high interannual variability in magnitude (Hotto et al. 2008), there are no decadal-scale studies of site-to-site variation in microcystin dynamics within lake districts.

Microcystin concentrations are expected to vary widely during the ice-free season because of variation in both cyanobacterial biomass and cell quota of toxins (Donald et al. 2011). Although microcystin is usually assumed to be absent from early year or cold water samples, the limit of detection for a commonly used technique (enzyme-linked immunosorbent assay [ELISA]) (0.16 μg L^{-1}) is similar to biologically relevant concentrations for infant drinking water (0.3 μg L^{-1}) (United States Environmental Protection Agency 2015). Statistical models are often used to address challenges associated with high detection limits and left-censored models characterize microcystin concentrations near and below the limit of detection by estimating the microcystin concentration of those data. Additionally, because biological responses are frequently nonlinear, approaches such as censored generalized additive models (GAMs), which better describe nonlinear patterns in environmental data, may provide an improved method of estimating likely toxin concentrations in situ.

In this study, we modeled seasonal and interannual trends in microcystin concentrations using GAMs to test the hypothesis that both the magnitude and duration of detection of a common cyanobacterial toxin are increasing across six lakes in a 52,000 km^2 drainage area (Supporting Information Fig. S1). First, we predicted that elevated water temperatures and nutrient concentrations will coincide with high microcystin concentrations (Orihel et al. 2012). Second, we predicted that, despite site-specific differences in the rates of heating, stratification, and morphology (Dröscher et al. 2009), there will be a prolonged period during which microcystin is detectable in all lakes. Third, we quantified temporal changes in the risk of microcystin exposure by lake users at five different public health thresholds: (1) EPA infant drinking water health advisory limit (0.3 μg L^{-1}); (2) WHO drinking water limit (1.0 μg L^{-1}); (3) EPA adult drinking water health advisory limit (1.6 μg L^{-1}); (4) WHO moderate risk of health effects from recreation (> 10 μg L^{-1}), and; (5) WHO high risk of health effects from recreation (> 20 μg L^{-1}) (Chorus and Bartram 1999; United States Environmental Protection Agency 2015). Unexpectedly, variation in toxin levels mainly responded to interannual variation in water temperature, while nutrient concentrations had little effect on microcystin concentrations. Although the risk of exceeding human health thresholds varied by lake, microcystin levels above the WHO drinking water limit were highly probable in all lakes by midsummer, with only a low probability of exceeding high-risk concentrations.

Methods

Study sites

We tested our predictions in six lakes located along the 52,000 km^2 Qu'Appelle River drainage basin in southern Saskatchewan, Canada (Supporting Information Fig. S1; Table 1). Four of the lakes (Buffalo Pound, Pasqua, Katepwa, and Crooked) are naturally occurring basins with water control structures and are located along the main stem of the

Table 1 Average lake characteristics from 2006 to 2016. With the exception of mean depth and lake area, values presented are average values from the modeled period (DOY 130–240) [mean; (min, max)]. TDP and TDN are integrated water column samples and temperature and microcystin are from surface samples. ND = not detected (<0.16 μg L^{-1}).

	Buffalo Pound	Last Mountain	Wascana	Pasqua	Katepwa	Crooked
Mean depth (m)	3.0	7.9	1.5	6.0	14.3	7.9
Lake area (km^2)	29	227	0.5	20	16	15
Secchi depth (m)	1.1 (0.3, 3.1)	1.9 (0.8, 4.8)	0.7 (0.1, 3.5)	1.4 (0.1, 3.5)	1.4 (0.2, 3.5)	1.6 (0.1, 5.5)
TDP (μg L^{-1})	32.2 (9, 132)	54.3 (15, 164)	374 (33, 2150)	165 (5, 662)	173.8 (87, 348)	157.4 (35, 414)
TDN (μg L^{-1})	577.1 (327, 1160)	1036.7 (869, 1480)	1456.0 (769, 3750)	1653.0 (171, 3100)	1371.6 (888, 2180)	1081.0 (743, 2090)
Temperature (°C)	19.1 (6.8, 26.1)	16.9 (4.4, 22.3)	19.4 (10.1, 25.5)	18.8 (6.9, 25.5)	18.3 (6.3, 25.6)	18.7 (6.8, 26.1)
Microcystin (μg L^{-1})	1.5 (ND, 37.2)	0.7 (ND, 5.3)	0.4 (ND, 5.4)	1.7 (ND, 44.2)	1.1 (ND, 28.1)	0.5 (ND, 6.4)

Qu'Appelle River. Wascana Lake is a human-made impoundment of Wascana Creek, whereas Last Mountain Lake is a large subsaline naturally occurring lake. Both basins drain into the Qu'Appelle River mid-reach. Water storage times vary over 10-fold among lakes and years; however, low rates of summer precipitation lead to low flow conditions and extended residence times in summer months (Haig et al. 2020). Most lakes are eutrophic to hypereutrophic, except for mesotrophic Last Mountain Lake (Finlay et al. 2015). This region experiences a cool-summer humid continental climate (Köppen Dfb classification). While atmospheric warming has advanced the timing of spring conditions (Finlay et al. 2015), duration of ice cover is highly variable among years (130–170 d) and ice melt occurs between March and May (Finlay et al. 2015). Lakes are all polymictic, although Katepwa Lake occasionally exhibited thermal stratification by late summer in some years.

Limnological monitoring

Lakes were sampled fortnightly between May 1st and August 31st (~ 8 trips lake^{-1} yr^{-1}) from 2006 through 2016. Temperature was measured at 1 m depth intervals using an YSI-85 multiprobe meter (YSI, Yellow Springs, Ohio), while transparency was recorded with a 20 cm diameter Secchi disk. Depth-integrated samples consisted of pooled water samples from evenly spaced intervals throughout the water column. These samples were filtered through 0.45 μm pore membrane filters and stored at 4°C for nutrient analysis. Unscreened surface-water samples were frozen and stored for microcystin analysis.

Laboratory analyses

Depth-integrated water samples were analyzed for total dissolved phosphorus (TDP) and total dissolved nitrogen (TDN) using standard analytical procedures at the Biogeochemical Analytical Service Laboratory, University of Alberta, Edmonton, Alberta, Canada (Stainton et al. 1977).

Water for microcystin analysis was thawed and refrozen three times to lyse cells and release toxins, and filtered through 1.2 μm nominal pore-size glass-fiber filters. Microcystin concentrations were analyzed with EnviroLogix QuantiPlate ELISA kits as microcystin-LR equivalents following standard protocols. The limit of detection for this kit is 0.16 μg L^{-1}.

Modeling

Correlations between potential predictors and autocorrelations in time series make it difficult to disentangle the unique effects of predictors that regulate seasonal and interannual variation in microcystin concentrations. To detect and characterize any within- and between-year trends, we initially modeled the data using only sampling day of year (DOY) and year, respectively. After selecting the best-fit model with DOY and year as covariates, we then tested the additional predictive ability of variables previously shown to regulate

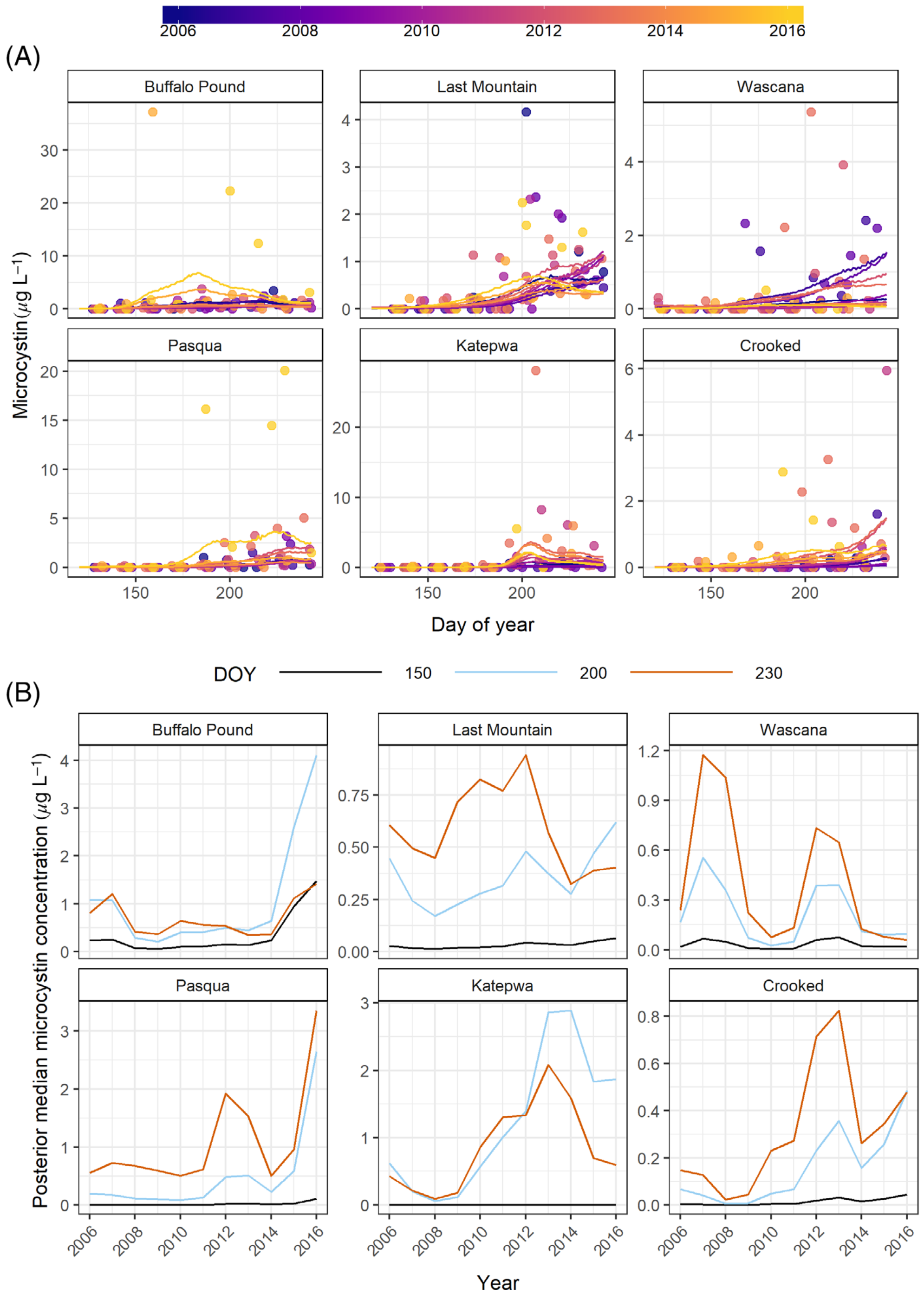

Fig. 1. (**A**) Measured microcystin concentrations (points) and median microcystin concentration predicted from the posterior distribution of the GAM (lines) for each lake, DOY, and year. Note the differences in scale on the y-axis. (**B**) Median microcystin concentration predicted from the posterior distribution of the GAM (lines) each lake, year, and three days of year (DOY): Late spring (DOY 150), early summer (DOY 200), and late summer (DOY 230). Panels are organized in order of flow; outflow from the lakes in the top row (Buffalo Pound, Last Mountain, and Wascana) converge and flow into Pasqua which is upstream of Katepwa, and Crooked. Panels are organized in the same way for all multilake figures.

cyanobacterial abundance in these lakes (Vogt et al. 2018) including surface-water temperature, TDN, and TDP.

We modeled microcystin conditionally upon covariates as a left-censored gamma distributed random variable. We applied this approach because microcystin concentrations are left censored; for a concentration x_i that is less than or equal to the level of detection (LoD) of our laboratory method c ($c = 0.16\ \mu$g L^{-1}), we only know that the concentration lies in the interval $0 \leq x_i \leq c$.

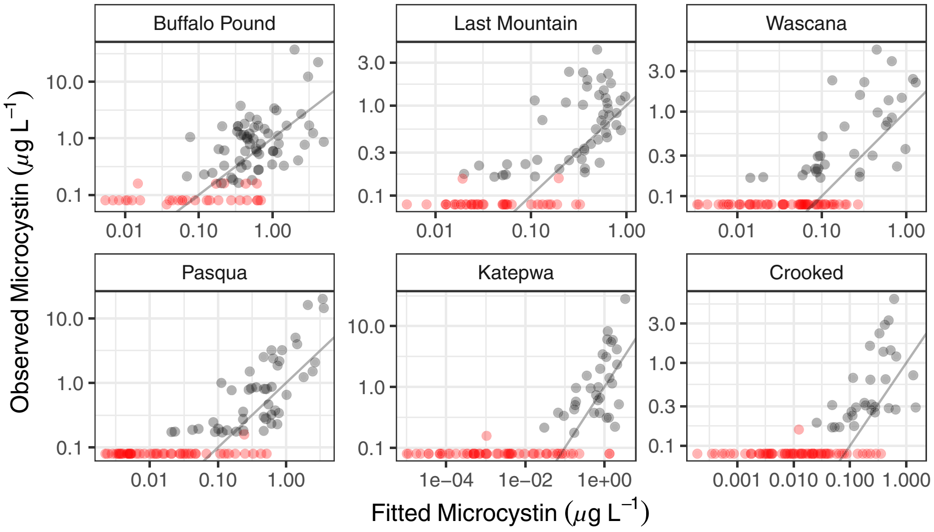

Fig. 2. Observed vs. fitted microcystin concentrations from the complex model. Fitted values are the median value from 8000 samples drawn from the posterior distribution. Observed concentrations below the limit of detection of the ELISA kit are indicated in red.

Exploratory data analysis suggested that the within- and between-year trends varied between lakes. The most complex model fitted a separate tensor product of DOY and year for each lake via a factor-smooth interaction:

$$\mu_i = \exp\left(\alpha_j + f_1(\mathrm{DoY}_i, \mathrm{Year}_i)_j\right),$$

where the expected microcystin concentration, μ_i, is modeled as a smooth interaction of DOY and year for the j^{th} lake via a tensor product smooth.

A simpler model used a single tensor product of DOY and year for all lakes, but allowed for lake-specific within- and between-year marginal effects via additional difference smooths for both temporal components:

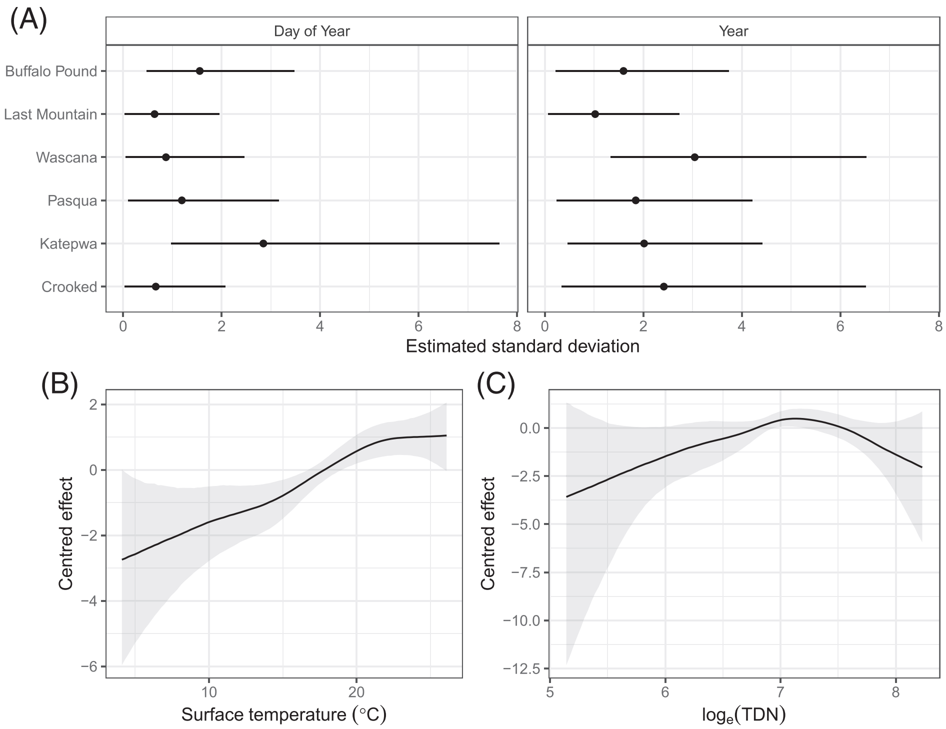

Fig. 3. (**A**) Standard deviation associated with individual lakes in the DOY and year model terms for the best fit model. Global splines for the effect of temperature (B) and nutrient (C) nitrogen spline presented although phosphorus spline showed a similar nonsignificant trend.

$$\mu_i = \exp\left(\alpha_j + f_1(\mathrm{DoY}_i, \mathrm{Year}_i) + f_2(\mathrm{DoY}_i)_j + f_3(\mathrm{Year}_i)_j\right),$$

where the tensor product smooth (f_1) is applied to all lakes, and f_2 and f_3 are the lake-specific smooths, indicated by the subscripts j.

Difference smooths were implemented using thin plate spline basis expansions with first-order penalties, which penalize departure from a flat function representing zero departure from the common within- and between-year trend. The simpler model estimated the same common within- and between-year trends for all sites as the more complex model, while simultaneously allowing for lake-specific deviations from the common trend.

To test whether water temperature or nutrient concentrations explained variation beyond the seasonal pattern in microcystin, we modified the models described above to include smooth functions of these additional covariates. As temperature and nutrients are seasonally structured, they would normally appear to be important predictors of microcystin concentration, even if there were no causal relation—a phenomenon known as "spurious correlation." By including the covariates in a model that already contains a seasonal smooth of DOY, we required temperature or nutrients to explain variation over and above the seasonal variation in order to be identified as having a regulatory effect on microcystin concentration. With this approach, we are estimating

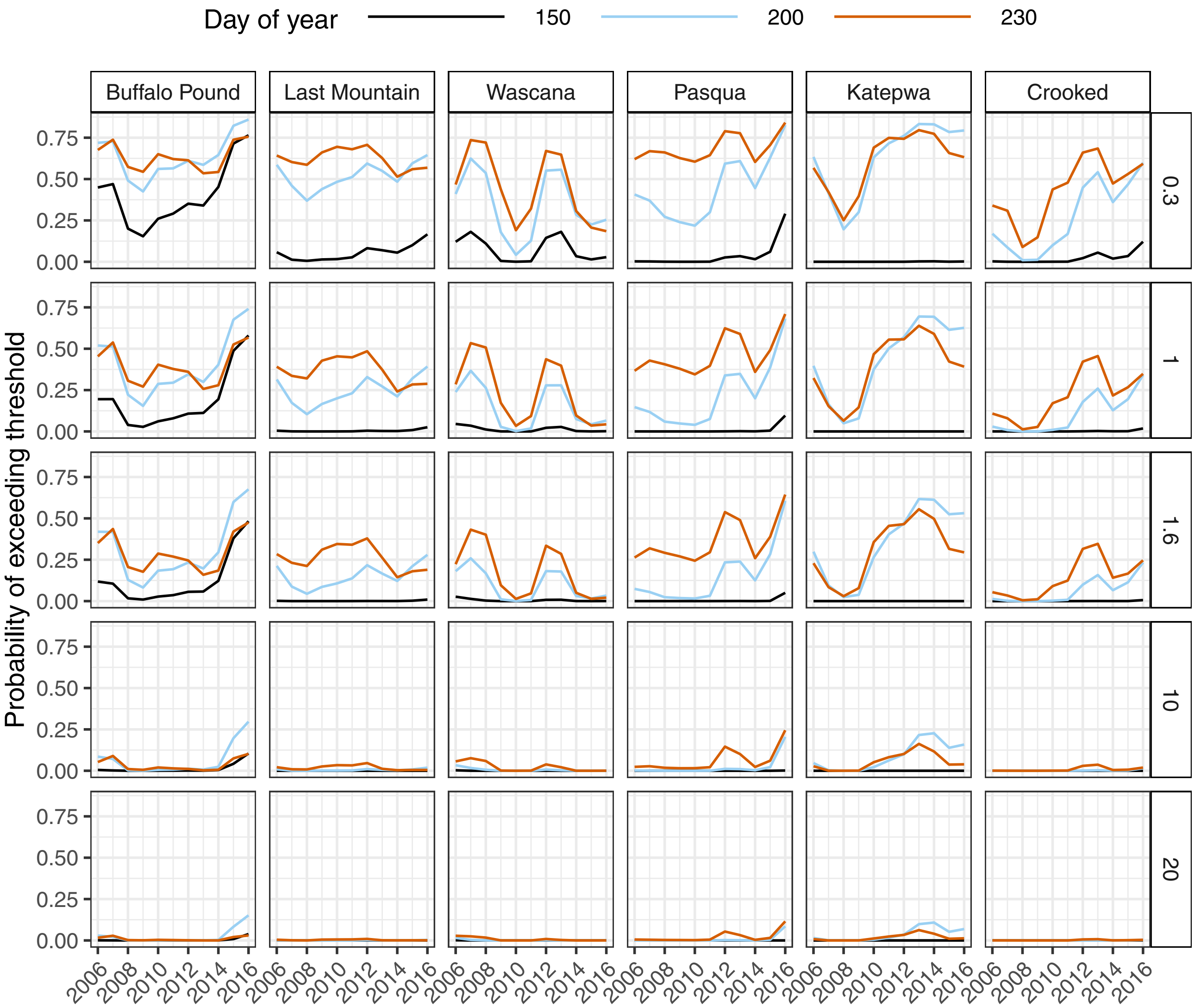

Fig. 4. Probability of microcystin exceeding five WHO and US EPA drinking—and recreational—waters thresholds (EPA infant drinking water limit—0.3 μg L^{-1}; WHO drinking water limit—1.0 μg L^{-1}; EPA adult drinking water limit—1.6 μg L^{-1}; EPA moderate risk of causing acute health effects—> 10 μg L^{-1}; and EPA high risk of causing acute health effects—> 20 μg L^{-1}). Probabilities of exceedance are shown for 3 d of the year for all 11-yr. The days of year represent a spring sample (DOY = 150), an early summer sample (DOY = 200), and a late summer sample (DOY = 230).

the additive effects of temperature and nutrients independent of their already accounted for seasonal effects.

Models were estimated in a Bayesian framework using the brms package (version 1.10.2; Bürkner 2017) for R (version 3.6.3; R Core Team 2019), using the probabilistic programming language Stan (Carpenter et al. 2017) and Hamiltonian Monte Carlo with the No U-Turn sampler (NUTS; Hoffman and Gelman 2014). Each model was estimated using four parallel chains with a burnin of 1000 iterations, followed by sampling 2000 observations from the posterior distribution. We used *k*-fold cross-validation of the log-predictive density (Vehtari et al. 2017) to select between candidate models. Following best practice, we performed a number of posterior predictive checks to assess the fit of the model to the observed data (Supporting Information Fig. S2). Subsequent inference was based upon 8000 samples from the model posterior for each combination of DOY and year; results are presented using the median and uncertainty via the 0.025 and 0.975 probability quantiles, of the posterior samples. The probability of exceeding a particular threshold was determined by counting, for each DOY in each year, the number of posterior predictive samples that exceeded the threshold divided by the number of samples.

Results

Although microcystin was detectable in all lakes in most years (60 out of 65 of the sampling years across all lakes), toxin concentrations varied by orders of magnitude between lakes, years, and seasons (Fig. 1A). Measured microcystin concentrations varied from $< 0.16\ \mu\mathrm{g\ L}^{-1}$ (below LoD) to $44.3\ \mu\mathrm{g\ L}^{-1}$, with detectable microcystin concentrations in 49.1% of samples (255 out of 519 sampling dates).

Model fit

The complex model, which allowed for the seasonal pattern of median microcystin to vary by year and lake, was the best-fit model (Fig. 2). The complex model was conservative at low microcystin concentrations; the model predicted a greater number of samples below the LoD and a greater number of detectable samples at microcystin concentrations less than $0.3\ \mu\mathrm{g\ L}^{-1}$ than were observed (Fig. 2; Supporting Information Fig. S2). There was strong coherence between observed and fitted values in the detectable range (Fig. 2), although lake-specific differences in coherence remained even after accounting for the effects of lake identity in the model. For example, in Last Mountain and Crooked lakes observed values were consistently elevated relative to fitted values.

Patterns and regulation of toxin concentration

The seasonal and interannual patterns of microcystin content varied by lake, with the standard deviation (random effect variance parameters) of all lakes excluding zero for both the DOY and year splines (Fig. 3) indicating that seasonal patterns of microcystin were lake and yearspecific. Despite lake-specific seasonal patterns, microcystin concentrations were lowest in spring (DOY = 150) and elevated for mid- and late-summer sample dates (DOY 200 and 230) when considered across all lakes (Fig. 1B). However, in some years and lakes, spring microcystin concentrations were elevated (e.g., Buffalo Pound in 2015 and 2016), while in other cases summer concentrations were depressed relative to the lake mean (e.g., Wascana Lake in 2009–2011; Crooked Lake in 2008–2009).

Model performance was improved by including a global spline for the effect of temperature, even after accounting for seasonal variation (Fig. 3B); warmer surface-water temperatures led to higher microcystin concentrations. Conversely, the effect size for nutrient concentration was small and effectively removed from the model fit via shrinkage indicating that any effect of nutrients on microcystin was largely seasonal (Fig. 3).

Probabilities of exceedance

From 2006 to 2016, the probability that the microcystin concentration exceeded WHO and EPA drinking and recreational water limits increased in four out of six lakes (Fig. 4; Supporting Information Fig. S3). There was a $> 50\%$ probability of exceeding the two lowest thresholds (0.3 and $1\ \mu\mathrm{g\ L}^{-1}$) for part of the growing season in all 11-yr in four lakes. All lakes had a nonzero probability of reaching concentrations that confer a moderate risk of acute health effects ($10\ \mu\mathrm{g\ L}^{-1}$) in at least 1 yr. The probability of exceeding recreation limits (10 and $20\ \mu\mathrm{g\ L}^{-1}$) increased in the last 2 yr in three lakes that provide numerous ecosystem services, including in Buffalo Pound Lake, an urban drinking water reservoir, Pasqua Lake, a lake bordering Pasqua First Nations, and Katepwa Lake, a basin with abundant cottages.

Discussion

Analysis of a decade-long, highlyresolved monitoring program provided novel insights into the temporal evolution of cyanobacterial toxins and cHABs. While previous research has identified a global increase in the magnitude and spatial extent of cHABs (Taranu et al. 2015), we found high variability and nonlinear patterns in microcystin concentrations at decadal scales in a series of eutrophic lakes representative of the Canadian Prairies (Orihel et al. 2012; Donald et al. 2015). Despite the direct hydrological connection of several of the lakes (Haig et al. 2020), the seasonal and interannual patterns were site-specific, with local factors modifying regional signals of climate change. While there is a low probability of exceeding recreational health limits in spring, models revealed that microcystin was likely present throughout the ice-free season, with an increasing probability of exceeding higher risk thresholds by midsummer. Despite strong effects of seasonal changes in temperature, interannual differences in water-column warming also exerted unique effects on toxin levels between years and among lakes.

Microcystin concentrations were frequently below the limit of detections (337 of 604 samples), reflecting seasonal patterns in cyanobacteria abundance (Vogt et al. 2018; Hayes et al. 2019), variable cell quotas of microcystin (Donald et al. 2011), and detection techniques with high LoD relative to biologicallyrelevant concentrations. A variety of statistical approaches have been used to account for the high frequency of samples below the LoD in microcystin studies including: (1) using logistic models to describe samples when samples are above the limit of detection (Yuan et al. 2014; Taranu et al. 2017); and (2) assigning samples below the LoD an alternative value (e.g., zero or one half the limit of detection). The left-censored approach used herein leads to unbiased and consistent estimators (converge on the true value with finite sampling), and provides estimated values for the censored observations instead of a probability of detection (cf. hurdle gamma model of Taranu et al. 2017).

Contrary to our hypothesis, temperature but not nutrients had a positive effect on microcystin concentration beyond the seasonal pattern. In fact, there was no effect of nutrient concentrations on microcystin concentrations (confidence intervals for the global spline included zero). This finding contrasts with prior research demonstrating that nitrogen supply is a key predictor of microcystin content in Canadian Prairie lakes (Orihel et al. 2012) and primary production in Qu'Appelle lakes (Leavitt et al. 2006), but is consistent with recent research suggesting that temperature has exhibited a paramount effect on cHABs densities in grassland lakes during the past 25 yr (Vogt et al. 2018). Although speculative, we suggest that four factors may interact to obscure the effects of nutrients, particularly N, on microcystin content. First, nutrient budgets demonstrate that sediments are the main source of nitrogen to surface waters in our study lakes, but that the importance of legacy nutrients varies substantially among lakes (Leavitt et al. 2006; Donald et al. 2015). Second, while nitrogen fixation is sporadically important in some lakes, the importance of atmospheric sources of N varies asynchronously among Qu'Appelle lakes (Hayes et al. 2019). Third, aqueous N pools are composed largely of dissolved organic N compounds of uncertain availability to cHABs (Hayes et al. 2019). Fourth, recent evidence suggests that phytoplankton response to N supply may be nonlinear over a wide range of fluxes (Bogard et al. 2020). In contrast to these multiple sources of variability, cHABs, especially *Microcystis*, are known to respond predictably to increased temperatures (Paerl and Huisman 2008), potentially increasing the likelihood of detecting thermal effects.

Consistent with previous efforts to model spatial variation in microcystin levels (Taranu et al. 2017), we note a high variability in water-column concentrations of microcystin (range: LoD to 43.3 μg L^{-1}). Overall microcystin concentrations seen in this study are comparable to those in other agricultural areas (Taranu et al. 2017), as well as other regional prairie lakes (Orihel et al. 2012). For example, while microcystin concentrations in the moderate- to high-risk categories (> 10 and > 20 μg L^{-1}) were rare in the Qu'Appelle lakes (1.7% of samples), extremely high microcystin concentrations were common in a contemporaneous survey of small prairie lakes (Supporting Information Fig. S4). Fortunately, maximum microcystin concentrations in both the Qu'Appelle (August range: 0.16–6.9 μg L^{-1}; median of detects: 0.71 μg L^{-1}) and regional lakes during 2016 (range: 0.16–43.3 μg L^{-1}; median of detects: 2.0 μg L^{-1}) were well below those observed in lakes in the U.S. Great Plains (range: 0.16–13,000 μg L^{-1}; median of detects: 3 μg L^{-1}; Graham et al. 2010). Given that the northern Great Plains are expected to experience greater than average regional warming (Dibike et al. 2017), we caution that human health threats posed by cyanobacteria are likely to increase in coming decades.

The frequency and spatial extent of cHABs are increasing at the global scale as a result of nutrient pollution (Glibert et al. 2014), climate change (Carey et al. 2012), and their interaction (Rigosi et al. 2014). Here, we demonstrate that microcystin concentrations were highly variable at the seasonal and interannual scale and that these patterns were lake-specific, even within a single catchment. However, because lakes are warming and the growing season is extending throughout the northern Great Plains (Finlay et al. 2015; Dibike et al. 2017), we anticipate regional advances in the onset of cHABs leading to greater risk of exposure earlier in the year. Our data show that there is high probability of chronic exposure at low-concentrations in these important waterbodies and that the likelihood of chronic exposure is likely increasing in lakes anywhere the ice-free season is expanding. Finally, we suggest that future research focus on collecting multidecadal, seasonallyresolved data to identify more fully the factors regulating increasing microcystin concentrations.

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Conflict of Interest

None declared.

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