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Over the past two decades, western Lake Erie has experienced recurring summer cyanobacterial blooms that pose severe negative impacts on human, animal, and ecological health. Previous research has identified a strong correlation between annual cyanobacterial bloom intensity and preceding spring (March-July) phosphorus loading from the Maumee river, the largest tributary to western Lake Erie, which is used to predict upcoming summer bloom severity. Maumee river spring phosphorus load, however, does not explain all the variation of bloom severity between years. Considering additional environmental parameters may help to better capture the physical and biogeochemical processes that regulate bloom severity, eventually leading to improved cyanobacterial forecasts which serve as an early warning for Lake Erie stakeholders. We aggregated various environmental parameters that may influence western Lake Erie cyanobacterial blooms to examine these factors as potential predictors for annual bloom severity. These included nitrogen and phosphorus loading from the Maumee river, freshwater discharge from the primary rivers and tributaries (Detroit, Huron, Raisin, Maumee, and Portage rivers), seasonal lake surface water temperature (mean winter, spring, and summer temperature), and Lake Erie winter ice extent and duration from 2002-2022. Empirical model results show that spring phosphorus loading, as total bioavailable phosphorus, from the Maumee river remains the dominant environmental factor controlling cyanobacterial blooms. However, additional environmental factors, such as Maumee river winter phosphorus loads and Lake Erie winter ice extent and timing, are likely important in modulating bloom severity, particularly in years with moderate phosphorus loads. Finally, we suggest incorporating mechanistic or rule-based models, in addition to empirical models, to better understand and predict annual cyanobacterial bloom severity. The updated models not only improve seasonal forecast accuracy which provides advanced warning of bloom severity to Lake Erie stakeholders, but also helps identify which factors we can better manage to reduce the frequency of severe blooms.

Keywords: phosphorus, winter ice-cover, Great Lakes, harmful algal blooms, empirical modeling

Introduction

Western Lake Erie began experiencing intense cyanobacterial blooms in the 1960s and 1970s, which led, in part, to the passage of the Clean Water Act in 1972 (e.g. Kane et al., 2014). The point-source pollution reductions mandated by the act led to the recovery of the lake in the 1980s (Bridgeman

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et al., 2013). Since the early 2000s, however, annual cyanobacterial blooms have reappeared in the western basin, with up to a 1000 km^2 of bloom coverage during the most intense bloom years (Stumpf et al., 2012, 2016). One key factor in the resurgence of cyanobacterial blooms appeared to be the doubling of dissolved reactive phosphorus (DRP) concentrations, particularly in the Maumee river, starting in the mid-1990s through early-2000s (Baker et al., 2014). Almost all DRP is considered bioavailable and constitutes the largest fraction of total bioavailable phosphorus (TBP), the fraction of river phosphorus (P) loading that is directly available to phytoplankton (Baker et al., 2014). In addition, the Maumee river is the largest tributary to any Great Lake, dominating the river load in the southwestern part of Lake Erie's western basin (Figure S1; Bocaniov et al., 2023; Maccoux et al., 2016). Thus, there is a strong correlation between TBP loading from the Maumee river and annual cyanobacterial bloom severity (e.g. Kane et al., 2014; Stumpf et al., 2016).

Due to this relationship, multiple empirical models have been developed which demonstrate a strong, positive relationship between TBP loading from the Maumee river and annual summer cyanobacterial bloom intensity (Bertani et al., 2016; Ho and Michalak, 2017; Obenour et al., 2014; Scavia et al., 2023; Stumpf et al., 2012, 2016). This suite of empirical models has been used in the annual western Lake Erie Seasonal forecast, which provides an advanced warning of potential summer bloom severity to Lake Erie water treatment plant operators, coastal businesses reliant on tourism, and the broader management community. Overall, these empirical models have worked well in predicting upcoming annual bloom severity; however, not all the variation between years is completely explained by TBP loading (e.g. Ho and Michalak, 2017; Scavia et al., 2021, 2023; Stumpf et al., 2016). For example, Stumpf et al., (2016) hypothesized that early summer water temperatures may influence the overall bloom uptake of TBP, with cooler temperatures in June leading to reduced TBP uptake and bloom growth in subsequent months. Other studies have proposed that TBP loading from multiple previous years may be an additional factor in annual bloom severity (Ho and Michalak, 2017; Scavia et al., 2023), however, this would likely alter longer term trends in the base level of the blooms, rather than specific interannual bloom variability. In addition, with climate change, western Lake Erie is also seeing other changes in physical properties such as decreased winter ice cover (Ozersky et al., 2021; Wang et al., 2012).

In this study, we examined several environmental parameters that likely influence bloom severity, including nutrient loading from the Maumee river and various physical characteristics of the western Lake Erie basin, coupled with empirical modeling, to identify potential environmental factors that may influence interannual variability of cyanobacterial bloom severity. We hypothesized that spring TBP loading from the Maumee river would be the dominant driver of cyanobacterial bloom intensity, but that additional environmental variables would further modulate annual bloom severity. Ultimately, we seek to use these updated empirical models to better predict upcoming summer bloom severity (NOAA, 2022) and will be directly incorporated into the annual western Lake Erie Seasonal forecasts provided to lake managers.

Methodology

Annual cyanobacterial bloom intensity

Western Lake Erie cyanobacterial bloom intensity was obtained from satellite imagery as described in Stumpf et al., (2016). The data sets were obtained from the Medium Resolution Imaging Spectrometer (MERIS, 2002-2011), the Moderate Resolution Imaging Spectroradiometer (MODIS, 2012-2018), and the Sentinel-3 Ocean and Land Colour Instrument (OLCI, 2019-2022), as the replacement for MERIS. Wynne et al., (2021) applied a multiplier to the MODIS data which allows for the direct comparison of MODIS to MERIS/OLCI images. Sequential 10-day composite images were generated following the methods of Stumpf et al., (2012) and Wynne and Stumpf (2015). The composites were created from the maximum cyanobacterial chlorophyll-related index (CI) value for each map pixel from individual scenes (Stumpf et al., 2012; Wynne and Stumpf, 2015; Figure S2). Generating 10-day composites provides several advantages over single-day images by removing interference from clouds and capturing maximum bloom extent during calm winds when cyanobacteria can be more easily seen by satellite. Finally, for each 10-day period, all the pixels in the western basin were summed to obtain the total biomass in CI units (Stumpf et al., 2016). The resulting annual CI max was used to estimate annual bloom severity. CI has units of dimensionless reflectance but can be equated to cyanobacterial concentration by: 1 CI=10^8 *Microcystis* cells ml^{-1} (Lunetta et al., 2015). In addition, a severity index (SI), which is used in annual bloom severity reporting (NOAA, 2022), was used to identify annual blooms with low and high biomass. The SI uses the average of the biomass in the three 10-day composites with the greatest biomass, normalized by log-scale with a value of 1 corresponding to the SI for 2005, and 10 corresponding to the SI in 2011 (Table S3).

Environmental and nutrient data

We aggregated a variety of environmental and nutrient loading data from openly available sources, which could be used as potential predictors of cyanobacterial bloom severity. Freshwater and nutrient loading from the Maumee river were obtained from Heidelberg University's National Center for Water Quality Research (NCWQR, 2022), including TBP and dissolved inorganic nitrogen (DIN) from 2002-2022. Spring monthly (March, April, May, June, July), spring (March-July), and winter (November-February) loads were summed from daily freshwater flow and nutrient concentrations (Richards et al., 2009). TBP was calculated from total P and DRP following Baker et al., (2014), where total bioavailable particulate P was calculated as the proportion (β=0.26) of total particulate P (total particulate P=total P - DRP). A settling term was also applied to the total bioavailable particulate P to account for settling of particulate P from the location of monitoring (Waterville, OH) to western Lake Erie (S=0.70). Finally, TBP is the sum of total bioavailable particulate P, scaled for settling, and DRP (Baker et al., 2014). DIN loads were calculated by summing nitrate (NO_3^-) and ammonium (NH_4^+) loads. NO_3^- loads were calculated as noted above, whereas monthly NH_4^+ loads were calculated by extrapolating weekly NH_4^+ concentrations using the monthly NH_4^+:NO_3^- ratio. TBP and DIN loads were used to calculate molar DIN:TBP (Figure S3).

In addition, we estimated the proportion of freshwater flow from the Maumee river as compared to other major tributaries entering the western basin including: the Huron, Raisin, and Portage rivers (Figure S1). Freshwater flows were obtained from the most downstream USGS gauging station (Table S1) and scaled to the ungauged watershed area. The proportion of Maumee river flow was calculated by dividing the Maumee river flow by the total tributary flow for the spring period. We estimated spring (March-July) Detroit river flow using monthly connecting channel flows provided by the U.S. Army Corps of Engineers-Detroit District (Figure S1, S4; D.C. Fielder, USACE-Detroit District, Detroit, MI, USA, pers. comm.). Flow from the Detroit river was not included in the proportion of Maumee river flow. Due to its low TBP concentration (~0.01 μg l^{-1} vs. 0.1 μg l^{-1} for the Maumee River), the Detroit river acts as a diluent in the western basin, rather than a source of TBP for summer cyanobacteria blooms (e.g. Bocaniov et al., 2023; Burniston et al., 2018; Downing et al., 2001).

Finally, we included several environmental parameters such as lake surface water temperature (SST), winter ice cover extent and duration, and the number of low wind speed days during the early bloom season. Lake SST was estimated via MODIS thermal data obtained from NASA Giovanni (NASA, 2023a, 2023b; Wynne et al., 2022). Night and day SST were averaged seasonally for winter (January-March), spring (April-June), and summer (July-September) from 2003-2022. Winter ice cover extent and duration from 2002-2022 for Lake Erie was obtained from NOAA's Great Lakes Environmental Research Laboratory and included the percent of maximum ice cover and day of maximum ice extent (GLERL, 2022). The day of maximum ice extent was then converted to day of year (DOY). While we acknowledge that the central and eastern basins likely play a role in controlling Lake Erie ice cover, we assume that patterns observed in all Lake Erie basins are representative of winter conditions in western Lake Erie. Finally, we used the number of low wind speed days during the early bloom season (July-August) as an estimate of internal nutrient loading due to potential periods of hypoxia/anoxia (Bridgeman et al., 2006). Briefly, hourly wind data were obtained from the Toledo Light weather station (NDBC, 2023) and averaged to daily values. Daily wind values <3 m s^{-1} were summed for the two-month period (July-August) for each year from 2005-2022 (Figure S5). We note that our identification of hypoxic/anoxic events is an over-simplification and does not explicitly account for other environmental conditions that might lead to these events, including entrainment of hypoxic bottom water from the central basin (Jabbari et al., 2019) and increased respiration due to elevated temperature (Bridgeman et al., 2006).

Empirical modeling

We used several empirical models to identify important predictors of western Lake Erie annual bloom severity. First, we applied the standard least squares linear regression model developed by Stumpf et al., (2016) which identified a strong, positive relationship between $\log_{10}$(CI max) and spring Maumee river TBP loading. Specifically, we used the unweighted, March-July TBP model following:

$$\text{CI Max} = b * 10^{(a*\text{Mar-Jul TBP Loading})} \quad \text{(Eq. 1)}$$

where b=0.37 and a=3.26x10^3 (Stumpf et al., 2016). We then updated the standard least squares linear regression between $\log_{10}$(CI max) and spring TBP loading using available data from 2002-2022. We excluded 2003 and 2013 as anomalous years during model fitting (n=19; Stumpf et al., 2016).

Next, we categorized historical blooms based on their annual SI where low blooms were classified as SI<5 and high blooms were categorized as SI>5 (Table S3). We then applied a single logistic regression to the categorized data using Maumee river spring TBP loading as the predictor variable. We excluded 2003 as a year with an anomalously high spring TBP loading, but low overall bloom severity (Stumpf et al., 2016).

We also identified other environmental variables that could explain some of the additional variability in annual cyanobacterial bloom severity. To accomplish this, we conducted a series of multiple linear regressions. We first removed any collinear (Pearsons correlation coefficient, ρ>0.7) environmental variables (Table S2). We then developed an algorithm to randomly select up to two environmental variables to be used in forward, stepwise multiple linear regression. The developed models were then ranked by the Akaike Information Criteria (AIC) and the models within 2 AIC of the best fit model were selected for further analysis. For multiple linear regression, we used all years with available data for model fitting (2005-2007, 2009-2014, 2016-2019, 2021; n=14; Table S3). All data visualizations and empirical modeling were conducted in R v4.1.0 (R Core Team, 2021).

Results

Overall, the composited 10-day accumulated CI was highly variable (Figure 1). 2011 had the highest median 10-day CI (7.72), followed by 2015 (7.45), and 2013 (5.73). 2011 also had the highest CI max (29.9), followed by 2015 (29.2), then 2017 (15.5). 2019 had the highest CI max in the past five years (11.5) while 2022 had the highest median 10-day CI (3.3). The aggregated environmental predictors were also highly variable among years and between months and seasons (Figure 2, S3, S4, S5; Table S4). Total spring TBP loading ranged from 89 metric tons (mton) in 2012 to 722 mton in 2015 with a mean of 344±155 mton (Figure 2). For July, TBP loading ranged from 1.33-216 mton in 2012 and 2015 respectively, with a mean of 40.7±58.3 mton (Figure 2). Throughout the study period, the proportion of Maumee river flow to total tributary flow (i.e. from the Maumee, Huron, Raisin, and Portage rivers) into western Lake Erie remained >65% with a mean of 77±4.2% (Figure S4). Seasonal lake SST was relatively consistent among years (2004-2022; Figure 2; Table S4). Percent of maximum winter ice cover for Lake Erie was generally high with a few years of <50% ice cover (2002, 2006, 2012, 2017, 2020) and mean percent maximum winter ice cover of 75±32% (Figure 3). Finally, the day of year (DOY) of ice off ranged from 3 (2002) to 70 (2008) with a mean of 43±16 days (Figure 2).

Prior to empirical modeling, we removed environmental and nutrient parameters that were highly linearly correlated (ρ>0.70; Table S2). Monthly and seasonal TBP loading were highly correlated with freshwater discharge (Q) and DIN loading. Ultimately, we removed all monthly and seasonal Q and DIN loading. In addition, we removed all monthly TBP loading for March, April, May, and June; only retaining winter (November-February), spring (March-July), and July TBP loading for modeling.

Empirical model results

First, we updated the logarithmic relationship between CI max and Maumee river spring TBP loading following methods in Stumpf et al., (2016) and using the full dataset (2002-2022, excluding 2003, 2013; Figure 3). Similar to previous studies, we found a strong, positive correlation between $\log_{10}$(CI max) and Maumee river spring TBP loading (adjusted r^2=0.76; Table 1). Model residuals (modeled-observed) suggest the 2023 model (this study) was marginally better at predicting annual CI max, especially for high bloom years such as in 2015 (Figure 2). In both cases, 2022 had a relatively large error (Figure 3b). The two fits matched closely for TBP loading<400 mtons, and deviated as the load increased.

Logistic regression results suggest Maumee river spring TBP loading can be used to distinguish overall bloom severity (low vs. high blooms), for loads <273 mtons or >332 mtons. Between 273-332 mtons, the model was less able to predict bloom severity, which included three years with low blooms: 2007, 2018, 2020, and three with high blooms: 2009, 2021, and 2022. Finally, multiple linear regression identified three models that were within 2 AIC of the best-fit model (Table 1) and included a combination of: a positive relationship with Maumee river spring TBP loading and DOY of maximum ice extent, but a negative relationship with Maumee river winter TBP loading. Adjusted r^2 for the three identified models ranged from 0.65-0.66.

Discussion

Temporal variability of western Lake Erie cyanobacterial blooms

Overall, there was a high degree of inter- and intra-annual variability in the observed 10-day accumulated CI and CI max from 2002-2022, which likely reflects a range of competing external (i.e. nutrient loading, freshwater delivery) and internal (i.e. internal nutrient loading, light availability, water column mixing) environmental factors that modulate bloom severity. Several years had a wide range in 10-day accumulated CI values, including years with anonymously high 10-day periods (2003, 2008, 2009, 2010, 2011, 2017; Figure 1), that skewed the overall CI max. We note that the current method of assessing annual bloom severity (i.e. CI max) does not explicitly take into account temporal variability during the bloom. Thus, this may overestimate annual bloom severity by relying on a single 10-day period with abnormally high accumulated CI or it might underestimate bloom severity for years when there were multiple 10-day periods with similarly high accumulated CI. However, the CI max and CI average for the 30-day period are closely correlated (Stumpf et al., 2016). While updates to the CI max are likely needed to take into consideration both the maximum and the temporal intensity of the bloom over multiple 10-periods, the current CI max does reflect the maximum bloom severity, such that models of

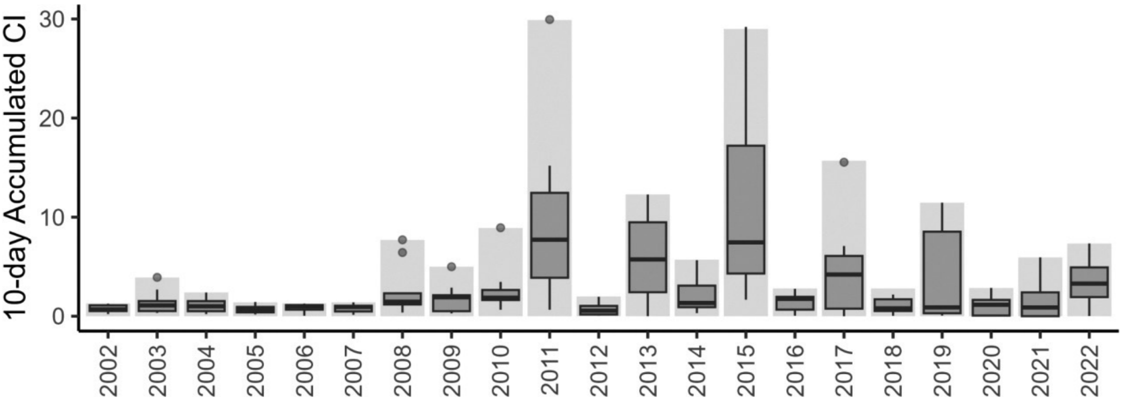

Figure 1. Boxplots of 10-day accumulated cyanobacterial index (CI) for the bloom season (July-October) along with a bar plot (gray bars) of maximum CI (CI max). For boxplots, the boxes represent the interquartile range (25th and 75th percentile), while the thick, horizontal line shows the median weekly accumulated CI. The vertical lines represent the minimum (25th percentile-1.5×Interquartile range) and maximum (75th percentile+1.5×Interquartile range). Points represent anomalous 10-day accumulated CI for that year (>1.5×Interquartile).

CI max can be used to reliably predict maximum annual bloom severity (Stumpf et al., 2012, 2016).

Spring phosphorus loading from the Maumee river is the dominant driver of annual bloom severity

Following Stumpf et al., (2016), Maumee river spring TBP loading was still a reliable predictor of annual maximum bloom severity (Table 1; Figure 3). The most apparent difference between the Stumpf et al., (2016) model and the model presented here (2023) was for high bloom years, primarily driven by 2015, but also due to intense blooms in 2017 and 2019. We do note that this regression results in a non-linear relationship between CI max and TBP loading (Figure 3), such that higher spring TBP loads lead to a proportionally larger annual bloom severity as compared to smaller TBP spring loads. A similar non-linearity has appeared in other models (e.g. Obenour et al., 2014; Scavia et al., 2023). This change with load suggests that either small blooms are less effective at using the available TBP, or less of the TBP is available to blooms during low load years.

Most relationships developed using TBP loading as a predictor of bloom severity, rely on TBP loads from the Maumee river, thus making the assumption that the majority of P originates from the Maumee watershed (e.g. Ho and Michalak, 2017; Scavia et al., 2023; Stumpf et al., 2016). To confirm this, we used the annual proportion of Maumee river flow to scale Maumee river TBP loading to total potential TBP loading for the entire western basin, as a predictor for annual bloom severity (Figure S6). While this resulted in a slight reduction in total model RMSE (4.66 to 3.91 CI max for un-scaled and scaled TBP loads, respectively), overall, the total TBP loading did not substantially improve model results. While not an exact representation of overall TBP loading to western Lake Erie, this supports the assumption that Maumee river loading is the dominant source of external P for summer cyanobacterial blooms,

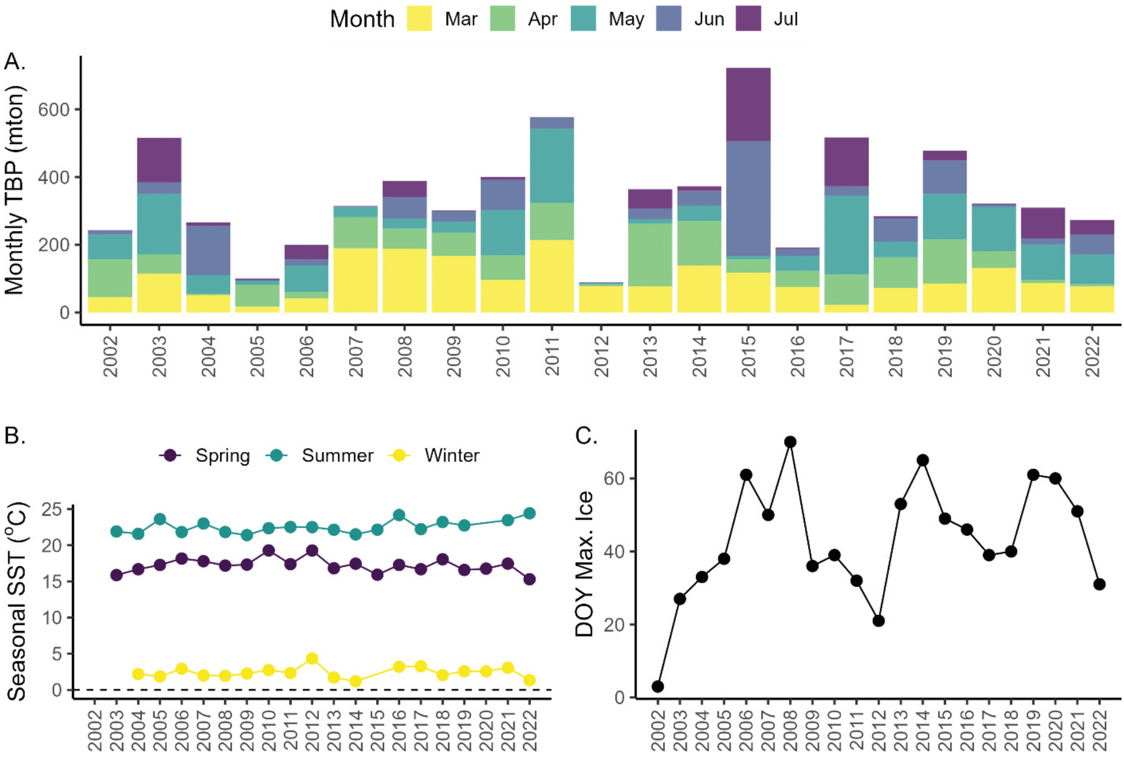

Figure 2. Selected environmental parameters plotted from 2002-2022 and used as potential predictors for annual cyanobacterial bloom intensity including: A) Monthly total bioavailable phosphorus (TBP) loading from March-July (mton); B) western Lake Erie seasonal sea surface temperature (SST, °C) as estimated using NASA Giovanni data for winter, spring, and summer; and C) Day of year (DOY) of maximum ice extent for the entirety of Lake Erie.

and is suitable for empirical models used to estimate overall bloom severity. Future studies and mechanistic modeling efforts should, however, consider loads from additional river sources.

Following studies which have found the Detroit river to be a substantial source of river P load to Lake Erie, we also included spring Detroit river load as a potential environmental predictor. While the Detroit river is a substantial freshwater and nutrient source to Lake Erie (Bocaniov et al., 2023; Burniston et al., 2018; Scavia and Calappi, 2023), our results show it was not a factor in determining summer cyanobacterial bloom severity. As compared to the Maumee, the Detroit river has about an order of magnitude lower bioavailable P concentrations (~0.01 µg l^{-1} total P, with about half being DRP vs. ~0.1 µg l^{-1} for Maumee TBP flow weighted mean concentration; Bocaniov et al., 2023; Burniston et al., 2018; Scavia and Calappi, 2023). The Detroit river also tends to have relatively little interannual variability in P load, with more variation occurring in long term trends associated

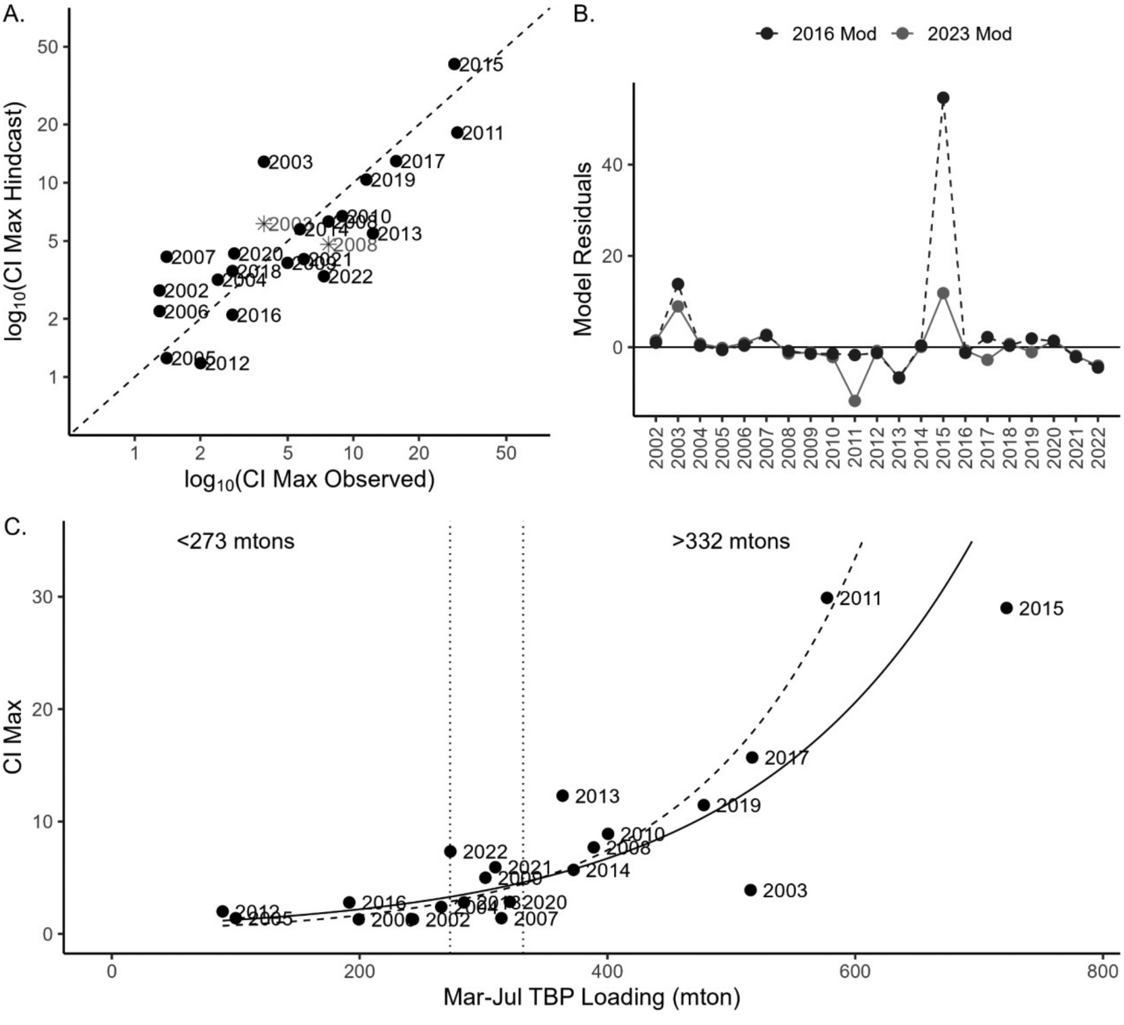

Figure 3. Regression results for the updated total bioavailable phosphorus (TBP) model. A) Comparison of observed and calculated cyanobacterial index (CI) max. Gray asterisks indicate cool June years (2003, 2008) when March-June loading was used, following Stumpf et al., (2016). The dashed line represents the 1:1 line. Results are plotted as $\log_{10}$ values for visualization. B) Model residuals (modeled-observed) plotted for the Stumpf et al., (2016) model and the updated TBP model (2023) from this study. C) Logarithmic relationship between annual CI max and spring (March-July) TBP loading. The dashed line is the relationship observed in Stumpf et al., (2016) while the solid line is the relationship identified in this study (2023). The vertical dashed lines indicate 273 mtons TBP loading and 332 mtons TBP loading, respectively, as it corresponds to the logistic regression below.

Table 1. Linear regression (TBP model) and multiple linear regression results for the top three identified models (Model 1-3). Multiple linear regression models were included if they were within 2 Akaike Information Criteria (AIC) of the best-fit model. Columns include the model intercept, spring (March-July) total bioavailable phosphorus (TBP) loading, day of year (DOY) of maximum ice extent, and winter (November-February) TBP loading. The AIC adjusted r^2 (Adj. r^2), and root mean square error (RMSE) are reported. The mean and standard error (mean ± standard error) are reported for each variable.

	Intercept	Spring TBP	DOY	Winter TBP	AIC	Adj. r^2	RMSE
TBP Model	-0.146 ± 0.117	$2.4\text{x}10^{3} \pm 3.2\text{x}10^{4}$				0.76	4.66
Model 1	-0.095 ± 0.134	$2.3\text{x}10^{3} \pm 3.6\text{x}10^{4}$			-41.47	0.66	4.31
Model 2	-0.153 ± 0.187	$2.2\text{x}10^{3} \pm 3.7\text{x}10^{4}$	$1.6\text{x}10^{3} \pm 2.5\text{x}10^{3}$		-41.81	0.65	4.37
Model 3	-0.0720 ± 0.208	$2.4\text{x}10^{3} \pm 4.0\text{x}10^{4}$		$-4.9\text{x}10^{5} \pm 3.3\text{x}10^{4}$	-42.64	0.65	4.32

with Great Lakes water levels (Scavia and Calappi, 2023). In addition, blooms were shown to develop in Maumee Bay during the early bloom season (July-August) where TBP concentrations from the Maumee river are high, and are rarely observed in the Detroit river plume (Wynne and Stump, 2015). While we cannot discount the Detroit river flow as an important contributor to background TP concentrations in the western and central basins of Lake Erie, our results suggest it is not the driving factor of western basin cyanobacterial bloom intensity.

Finally, we identified a relationship with spring TBP loading to separate low and high blooms, based on bloom SI, where low blooms were identified with >75% certainty at TBP loads <273 mton and high blooms were identified with >75% certainty at TBP loads >332 mton (Figure 4). This suggests there are TBP thresholds at which we can reliably predict a low versus high bloom which may help to guide early season predictions for upcoming bloom severity. Conversely, this also implies there is a range of TBP loads (273-332 mton) where we are unable to use spring TBP loading to reliably predict bloom size, suggesting additional environmental parameters may be necessary to fully separate blooms by size.

While Maumee river spring TBP loading was identified as the primary environmental variable constraining annual CI max in all regression models, one multiple linear regression model also identified a negative relationship with Maumee river winter TBP loading. The negative relationship was surprising, given the strong correlation between spring TBP loading and annual bloom severity, as well as studies that have identified western Lake Erie as primarily P-limited (Chaffin et al., 2014; Steffen et al., 2014). We hypothesize the negative relationship with winter TBP loading is a proxy for winter temperature and precipitation conditions that influence both watershed and in-lake processes. First, higher winter TBP loading implies a warmer winter, which could decrease spring runoff due to drier soil antecedent conditions. Second, differences in winter TBP loading may influence winter under-ice (Beall et al., 2016) and/or spring diatom blooms that occur nearly annually in western Lake Erie (Reavie et al., 2014). Specifically, higher winter TBP loading may fuel larger winter or spring phytoplankton growth, altering the timing, duration, and intensity of these blooms which may influence the availability of P into summer.

While external TBP loading was shown to be a dominant driver of annual bloom severity, we note that we did not explicitly include a term for internal P loading, which may be a potentially important source of P for western Lake Erie cyanobacterial blooms (Bocaniov et al., 2023; Matisoff et al., 2016). The overall magnitude of internal P-load would be influenced by both sediment disturbance and by the development of near-bottom hypoxia, which varies annually (Matisoff et al., 2016). However, determining the exact role of hypoxia-driven internal P-loading, requires additional modeling efforts to account for temporary water column stratification and subsequent hypoxic events. Additional internal loading during high biomass years, when hypoxia might be more likely, may be an additional source of P during high bloom years, contributing to the non-linear relationship observed between CI max and spring TBP.

Other environmental variables modulate annual bloom severity

While Maumee river spring TBP loading was identified as a reliable predictor of cyanobacterial bloom intensity, there was still variability in our ability to accurately estimate annual blooms. The TBP model assumes that all TBP loading from the Maumee river is used by the cyanobacterial bloom; however, in some years, this relationship led to an overestimation of bloom severity (i.e. 2003, 2007) while in others, it led to an under-estimation (i.e. 2013, 2022; Figure 3). In addition, the logistic relationship used to identify low versus high blooms under-estimated blooms in 2009, 2021, and 2022, but over-estimated blooms in 2007, 2018, and 2020, which corresponded to years with TBP loads between 273-332 mton. Below, we discuss other environmental variables that may further constrain annual bloom severity.

For example, Stumpf et al., (2016) identified June water temperature as a modulator for the spring TBP versus CI max relationship. Specifically, they hypothesized that a cool June (water temperature <20°C) resulted in lower uptake of TBP during the early bloom, negating the influence of the July TBP load. Instead, they used March-June TBP loading to estimate bloom severity for years with June water temperatures <20°C, which helped to adjust the predicted CI max (Figure 3). In 2007, an anomalously high flow event occurred in late August (Figure S7; Baker et al., 2014; Bridgeman et al., 2013), which likely disrupted the bloom by either introducing turbidity or flushing the bloom into the lake. Wynne and Stumpf (2015) found that blooms begin rapid expansion during the last 10 days of August; thus, it is possible that this elevated discharge event in August 2007 led to a smaller bloom than was predicted by spring TBP loading.

We also hypothesize that July TBP loading may further modulate bloom severity. For example, low bloom years in the mid-TBP loading range (273-332 mton; i.e. 2007, 2018, 2010; Figure 4) had July TBP loads <5.75 mtons which is substantially lower than both the mean (40.7 mton) and median (9.7 mton; Table S4) loads. In contrast, both 2021 and 2022, which were high blooms under this same TBP range, had substantially higher July loads (90.3 and 42.5 mton, respectively). The 2009 bloom had a low July TBP load (2.2 mton), but had no load feature that distinguished it from the low bloom years within this TBP range. The complexity of bloom variability is evident, but the result for five out of six years suggests that the timing of TBP loads, as lower or higher July loads may modulate

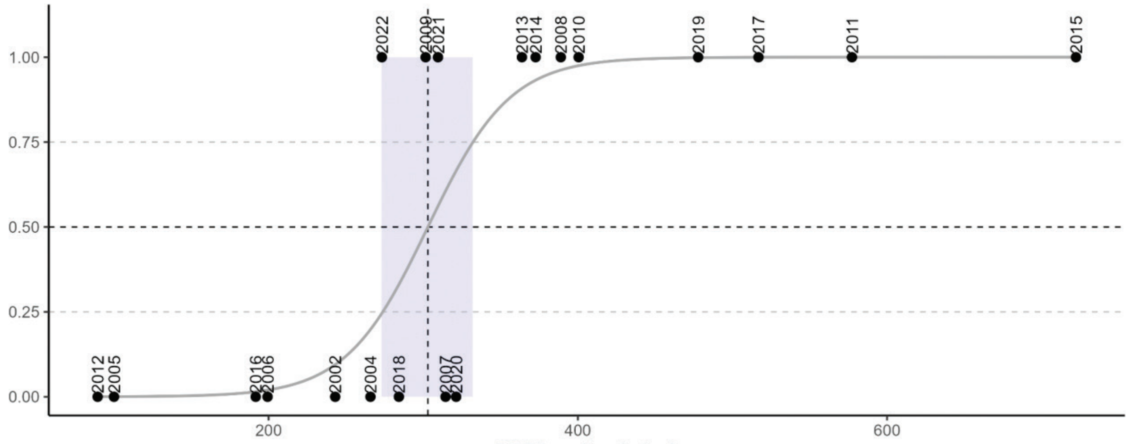

Figure 4. Results from the logistic regression used to identify low (0) and high (1) bloom years based on total bioavailable phosphorus (TBP) loading as measured from March-July. The horizontal dashed lines indicate 25% (273 mton TBP loading), 50% (303 mton TBP loading), and 75% (332 mton TBP loading) certainty, respectively. The vertical dashed line corresponds to the TBP loading at 50% certainty. The blue box represents TBP loading from 25-75% certainty.

the overall spring TBP loading relationship. The relative influence of July loads will likely become clearer over the next few years, given that 7 of the last 10 years had July loads exceeding the 20-year median (Table S3, S4).

Finally, we speculate that winter ice cover might also influence annual bloom severity. We found that the DOY of maximum ice extent was identified as having a weak, positive relationship with bloom severity (Table 1). Similarly, extensive Lake Erie ice cover was more common in winters prior to high bloom years, where 9 out of 10 years had ≥84% maximum ice cover, while in low bloom years, 4 out of 10 years had ≤22% cover. As noted earlier, we hypothesize that cooler winter and spring temperatures alter the delivery of spring nutrient loading as well as the duration and intensity of under-ice winter (Beall et al., 2016) and spring diatom blooms (Reavie et al., 2016), which could influence summer blooms.

Study limitations and future directions

While this study represents an increase in the amount of data used to identify environmental predictors of western Lake Erie cyanobacterial bloom intensity, we still acknowledge some study limitations. First, we focused on TBP due to the extensive literature which has identified Maumee river TBP loading as the dominant factor driving cyanobacterial blooms (Bertani et al., 2016; Ho and Michalak, 2017; Obenour et al., 2014; Scavia et al., 2023; Stumpf et al., 2012, 2016). While there is an inherent autocorrelation among Q, DIN, and TBP loading (Table S2), spring DIN:TBP in the Maumee river suggests substantially more N than P in incoming loads (mean molar DIN:TBP=118±33; Figure S3; Table S4). Similarly, Stow et al., (2022) found that TBP loads from the Maumee river have almost doubled over the past 30+ years while DIN loads have remained relatively constant, all while summer cyanobacterial bloom intensity has increased. Finally, the western basin is largely P-limited, especially during the early and peak bloom season, and does not become N-limited until after the bloom is established (Chaffin et al., 2014; Steffen et al., 2014). These lines of evidence suggest that TBP is still the dominant driver of annual cyanobacterial bloom intensity, though N-limitation is likely a factor during the late bloom season (Chaffin et al., 2013; Jankowiak et al., 2019).

Second, the majority of annual bloom prediction models rely on statistical relationships between Maumee river TBP loading and cyanobacterial bloom severity. While TBP loads are the dominant driving factor of bloom intensity, this study suggests other environmental factors modulate this relationship. With the relatively small number of study years (~20 years) and the large number of environmental variables (>20) identified, statistical models cannot accurately represent how additional environmental variables may work to modulate bloom severity. While they can guide hypotheses, additional years of data are needed to elucidate these relationships more clearly.

These limitations suggest additional modeling strategies are likely needed. The information gleaned from the broad range of statistical models (e.g. Ho and Michalak, 2017; Scavia et al., 2023; Stumpf et al., 2016), along with experimental and modeling studies, can be used to develop mechanistic models which may help to fill some of the gaps left by empirical models, including dynamic, process-based, numerical models like the Western Lake Erie Ecosystem Model (WLEEM; e.g. Verhamme et al., 2016). Empirical models are also unable to account for any fundamental ecosystem changes that may have occurred which influence annual bloom severity, limiting the ability of these relationships to predict future ecosystem changes. Finally, in a predictive framework, we are limited to environmental parameters that can be appropriately forecasted, such as river discharge forecasts produced for the Maumee river (OHRFC, 2023) or previously observed winter or spring temperature. Thus, while empirical models are useful in predicting upcoming bloom severity, we argue that additional, mechanistic or rule-based models, will help to better identify other environmental processes modulating bloom severity and enhance our ability to predict upcoming bloom severity.

Providing advanced warning for the Lake Erie management community

Recurring summer cyanobacterial HABs pose severe negative impacts on human, animal, and ecological health, which impact drinking water resources, lead to beach closures, and may discourage or prevent people from fishing, swimming, boating, or visiting the shoreline. Since 2016, the annual western Lake Erie seasonal forecast has provided advanced warning to lake managers, drinking water treatment plant operators, and the general public on the potential bloom severity for the upcoming summer. The updated and new empirical models developed in this study will be directly incorporated into these annual forecasts, improving our ability to provide advanced warning of potential bloom severity to the Lake Erie management community. In addition, previous relationships between Maumee river TBP loading and annual bloom severity were used to identify the necessary 40% reduction in watershed TBP loading needed to reduce overall cyanobacterial bloom severity (Annex 4 Objectives and Targets Task Team, 2015). Additional analysis from this study could help to identify additional environmental factors to better manage the frequency of severe blooms in the future.

Conclusions

Overall, results from this study show that Maumee river spring TBP loading is still the dominant factor controlling annual western Lake Erie cyanobacterial bloom severity and can be reliably used to predict upcoming bloom severity (Bertani et al., 2016; Ho and Michalak, 2017; Obenour et al., 2014; Scavia et al., 2023; Stumpf et al., 2012, 2016). Thus, we recommend continuing to use established relationships between Maumee river spring TBP loading and annual bloom severity for seasonal cyanobacterial bloom predictions. However, our results suggest additional models should be considered to distinguish the threshold between a low or high blooms, especially during the early spring season when predictions of annual spring TBP loading may be more variable. Results also suggest we are likely missing key environmental factors that further modulate bloom severity, particularly in the mid-TBP loading range (273-332 mton). Under these mid-range conditions, additional environmental parameters may be needed to better predict bloom severity. Due to the limited years of data, these additional relationships are still under consideration, though winter TBP loading, as well as winter ice dynamics, along with July TBP loading, may be important. We suggest that alternative, mechanistic or rule-based models which can explicitly incorporate known mechanisms, are an important future direction for annual bloom severity predictions, which would also allow for future climate predictions to be incorporated into models. Importantly, these and future model updates will be incorporated into the NOAA western Lake Erie Seasonal Forecasts to provide advanced warning of upcoming summer bloom severity to the Lake Erie management community and can help identify additional environmental factors to better manage the frequency of severe blooms.

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Disclaimer

The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the author(s) and do not necessarily reflect those of NOAA or the Department of Commerce.

Supplementary material

Supplementary material is available for this paper and can be accessed on-line at the publiher's website.

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