Cyanobacterial Bloom Phenology in Saginaw Bay from MODIS and a comparative look with western Lake Erie

Timothy T. Wynne[1], Richard P. Stumpf[1], R. Wayne Litaker[2], Raleigh R. Hood[3]

[1] National Oceanic and Atmospheric Administration, National Ocean Service, National Centers for Coastal Ocean Science, 1305 East-West Highway, Silver Spring, MD 20910, USA

[2] CSS, Inc. Under contract with National Oceanic and Atmospheric Administration, National Ocean Service, National Centers for Coastal Ocean Science, 1305 East-West Highway, Silver Spring, MD 20910, USA

[3] Horn Point Laboratory, University of Maryland Center for Environmental Science, Cambridge, MD USA.

Keywords: Dissolved Reactive Phosphorus, DRP; Western Lake Erie basin, WLEB, Saginaw Bay, Cyanobacteria, Remote Sensing

ABSTRACT

Saginaw Bay and western Lake Erie basin (WLEB) are eutrophic catchments in the Laurentian Great Lakes that experience annual, summer-time cyanobacterial blooms. Both basins share many features including similar size, shallow depths, and equivalent-sized watersheds. They are geographically close and both basins derive a preponderance of their nutrient supply from a single river. Despite these similarities, the bloom phenology in each basin is quite different. The blooms in Saginaw Bay occur at the same time and place and at the same moderate severity level each year. The WLEB, in contrast, exhibits far greater interannual variability in the timing, location, and severity of the bloom than Saginaw Bay, consistent with greater and more variable phosphorus inputs. Saginaw Bay has bloom biomass that corresponds to relatively mild blooms in WLEB, and also has equivalent phosphorus loads. This result suggests that if inputs of P into the WLEB were reduced to similarly sized loads as Saginaw Bay the most severe blooms would be abated. Above 500 metric tons P input, which occur in WLEB, blooms increase non-linearly

indicating any reduction in P-input at the highest inputs levels currently occurring in the WLEB, would yield disproportionately large reductions in cyanobacterial bloom intensity. As the maximum phosphorus loads in Saginaw Bay lie just below this inflection point, shifts in the Saginaw Bay watershed toward greater agriculture uses and less wetlands may substantially increase the risk of more intense cyanobacterial blooms than presently occur.

1. Introduction

Harmful Algal Blooms (HABs) are increasing worldwide (Smayda, 1990; Hallegraeff, 1993; Paerl and Paul, 2012; Ho et al., 2019). In freshwater systems these blooms are dominated by cyanobacteria, which adversely affect public health, water quality, and the normal food webs found in healthy aquatic ecosystems (Brooks et al., 2016). In the Great Lakes, cyanobacteria frequently produce potent hepatotoxins, such as microcystins (Watson et al., 2008; Brooks et al., 2016). Additionally, they can make organic compounds, such as geosmin, that cause taste and odor issues in municipal water supplies, a potential problem for residents that rely on Lake Erie (USA) for drinking water. Since 2002, two drinking water advisories were issued due to cyanotoxins, the most notable of these occurred in 2014, when the metropolitan area of Toledo, Ohio went several days under a “Do not drink” order (Steffen et al., 2017). Cyanotoxins can also cause mortalities in domestic animals as well as wildlife, primarily through ingestion of cyanobacterial scums (Hilborn and Beasley, 2015). The cyanobacterial blooms in the western basin of Lake Erie (WLEB) have been the focus of many studies using remotely sensed imagery (Bosse et al., 2019; Gorham et al., 2017; Sayers et al., 2016; Stumpf et al., 2012; Stumpf et al. 2016; Wang et al., 2018; Wynne et al. 2008, 2010; Zhang et al., 2017). In contrast, relatively few remote sensing studies have focused on Saginaw Bay, Michigan, USA (Budd et al., 2001; Sayers et al., 2016).

Given this lack of information on bloom phenology in Saginaw Bay and the lower intensity blooms relative to the WLEB, whose watersheds share many morphological similarities, the current study was undertaken to address two primary objectives. The first was to describe the bloom phenology of Saginaw Bay using satellite data. The second was to compare the remotely sensed bloom phenology in Saginaw Bay with that of the more intensively studied WLEB to determine if the same or different environmental and anthropogenic factors govern the magnitude and timing of cyanobacterial bloom phenology in both systems. To accomplish these objectives, 20-year time series of satellite derived cyanobacterial bloom biomass estimates for both systems were calculated and used to produce bloom phenologies. The roles of phosphorus (P) load, land use practices, water residence times, and other environmental factors in regulating the observed cyanobacterial bloom phenologies were then evaluated. The input of phosphorus into WLEB has been identified as critical to bloom size (Stumpf et al., 2012; Kane et al., 2014; Obenour et al., 2014; Manning et al., 2019), while nitrogen (N) limitation has been identified as a key factor in bloom toxicity (Horst et al., 2014; Gobler et al., 2016; Chaffin et al., 2018) and in constraining the growth of late summer cyanobacterial blooms in Lake Erie (Chaffin et al., 2013, 2018). Saginaw Bay has not been as extensively studied as western Lake Erie. The Saginaw River has phosphorus load measurements, but lacks measurements on nitrogen loading and as such, the role of phosphorus on cyanobacterial biomass is the topic investigated here.

2. Materials and methods

A twenty-year time series of satellite derived cyanobacterial bloom estimates from the WLEB and Saginaw Bay was calculated and used to characterize bloom phenology in each system. The role of nutrient inputs, land use practices, water residence times, as well as other environmental factors in governing the observed variability, timing and intensity of the cyanobacterial blooms were examined. This comparison allowed assessment of whether the factors controlling bloom dynamics appeared similar or different between the two systems. The spatio-temporal dynamics of cyanobacterial blooms in Saginaw Bay were also examined in greater detail as these blooms have been previously less well characterized compared to the WLEB.

2.1. Western Lake Erie basin characteristics

The WLEB, west of Pelee Point to Avon Point (Fig. 1, lower panel), is located approximately 215 kilometers south of Saginaw Bay (Fig. 1, middle panel). It occupies the westernmost portion of the 25,740 km^2 surface area of Lake Erie and encompasses the area where cyanobacterial blooms in the region develop. The WLEB has a surface area of 3,375 km^2. It is relatively warm, shallow (mean depth of 7 m), and productive relative to the other Great Lakes. Approximately 12 million people, 1/3 of the population of the Great Lakes basin, reside within the Lake Erie watershed. In addition to supporting the largest fisheries stocks, it is the most anthropogenically-impacted portion of the Great Lakes (Steffen et al., 2014). The Maumee River watershed is the largest watershed in the Lake Erie region covering 21,538 km^2 with a population of 278,000 residents.

In the 1970s, the chlorophyll levels in the WLEB were often extremely high, exceeding the 50 $\mu g\ L^{-1}$ range (Rockwell et al., 2005). The Maumee River is the main supply of nutrient-enriched waters into the WLEB (Stumpf et al., 2012). The Detroit River, though having a much larger discharge (~35 times), has much lower phosphorus concentrations than the Maumee River. In addition to these low nutrient levels, the high dilution rates caused by the larger outflow precludes development of significant cyanobacterial blooms within the Detroit River plume itself (Wynne and Stumpf, 2015). As a result, the outflow of the Detroit River does not contribute significantly to cyanobacterial blooms in the WLEB other than by transporting a portion of the cyanobacterial population in Lake St. Clair to the WLEB via the Amherstburg Channel (Davis et al., 2014). The predominant land use in the watershed (78%) is agricultural, primarily row crops. Nearly the entirety of the WLEB watershed was once home to the approximately 4000 km^2, Great Black Swamp, which was drained for agriculture in the mid-19th century leaving the WLEB nearly devoid of wetlands (Mitsch, 2017).

The Maumee River plays a primary role in regulating cyanobacterial bloom intensity in WLEB through delivery of nutrients (Fig. 1; Stumpf et al., 2012; Kane et al., 2014; Obenour et al., 2014;). Some lacustrine systems are limited by nitrogen (N) or phosphorus (P) or a combination of both (Xu et al., 2009; Paerl and Otten, 2013; Paerl et al. 2016). In the case of western Lake Erie, the literature indicates that the development and overall magnitude of cyanobacterial blooms is primarily dependent on P-loading (Stumpf et al., 2012, 2016; Kane et al., 2014, Obenour et al. 2014; Bertani et al., 2016; Manning et al., 2019). While, neither Stumpf et al. (2012) nor Kane et al. (2014) found a relationship between N loads and cyanobacterial bloom size in the WLEB, this does not eliminate the importance of nitrogen. Newel et al. (2019 implicated an increase in the ratio of annual loads of reduced N (Total Kjeldahl nitrogen; TKN) to NO_3^- in the Maumee River to annual cyanobacterial bloom biomass, although they did not examine the nitrogen loads for either form, and this time period also corresponded to an increase in DRP load. However, other studies have examined the bloom response to nutrient enrichment and found that N limitation occurs in the developed bloom in WLEB, (Chaffin et al., 2013; Gobler et al., 2016; Chaffin et al., 2018). N-limitation also regulates bloom toxicity in WLEB, constrains the growth of late summer cyanobacterial blooms, and likely influences bloom duration and termination (Chaffin et al. 2013; Horst et al. 2014; Gobler et al. 2016; Chaffin et al. 2018; Boedecker et al. 2020). However, factors driving toxicity or duration are not part of this study. Also, as a practical matter, there are no data sets for nitrogen loads to Saginaw Bay, restricting us to examining phosphorus influence on bloom size or biomass. Given how close the Saginaw Bay and WLEB are to one another, and their similarities in geomorphologies, we can reasonably hypothesize that P-inputs play a similar role governing cyanobacterial bloom biomass in Saginaw Bay as in WLEB.

2.2. Saginaw Bay characteristics

Saginaw Bay (Fig. 1, upper panel) is a large catchment in the southwestern portion of Lake Huron in the Laurentian Great Lakes encompassing approximately 2,650 km^2. The Saginaw Bay watershed is primarily drained by the Saginaw River. This watershed is the largest in the U.S. state of Michigan and includes one of America's most extensive contiguous freshwater wetland systems. Fifteen percent of the land in Michigan lies within the Saginaw Bay watershed, and is home to approximately 1.5 million people. Most of these residents get their water from the northwest side of Saginaw Bay about 50 km southwest of Au Sable Point (Saginaw 2020). The land use within the watershed consists of 45% agriculture, 22% forest, 16% open water/wetland, 10% residential, 6% grassland, and 1% high density residential. Nearly the entire shoreline of the bay is lined with dense stands of three square bulrush, (*Schoenoplectus pungens*). The bathymetry of the bay is complicated (Fig. 1, upper panel), and makes for a complex circulation pattern. The water enters Saginaw Bay from Lake Huron on the western side of the basin and mixes with output from the Saginaw River before flowing along the eastern side of the bay and returning to Lake Huron. This predominant flow is reinforced by a small island located in the south central portion of the Bay that helps channel flow into and out of the Bay. The bottom substrate in Saginaw Bay consists primarily of limestone and dolomite bedrock and large cobble. The deeper outer portion of the bay, which mixes more completely with Lake Huron water, is more oligotrophic, clearer, and colder relative to the inner bay.

Beginning in the early 1990s, Saginaw Bay was invaded by both zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*) (Pillsbury et al., 2002; Vanderploeg et al., 2001). Both species became well established and were a fundamental component of the food web during this study period (Heath et al., 1995; Pillsbury et al., 2002). Their presence is important because these species likely promote cyanobacterial blooms by differentially consuming diatoms and other competing organisms (Vanderploeg et al., 2001). The cyanobacterial blooms, though favored by differential grazing, are generally reported to be less severe in Saginaw Bay (Fig. 1 upper panel, Sayers et al., 2016). The role of nutrients in controlling cyanobacterial biomass in this system cannot be addressed with the same accuracy as in the WLEB because only TP data are available for comparison (Cha et al., 2010; Stow et al., 2014).

2.3. Satellite data

Imagery from the Moderate-resolution imaging spectroradiometer (MODIS) used to assess cyanobacterial biomass was acquired from NASA. The MODIS sensor is onboard two separate spacecraft: Aqua and Terra. Imagery from both satellites was used in this study. The MODIS imagery was used to detect and quantify cyanobacteria blooms by applying the Cyanobacterial Index (CI). This algorithm was originally derived for the Medium Resolution Imaging Spectrometer (MERIS) (Wynne et al., 2008; Wynne et al., 2010; Wynne et al., 2013b), and is described in Equation 1.

(eq. 1) $CI = (- SS(678))*1.33$

Where SS is the spectral shape (or curvature; Stumpf and Werdell, 2010) and is determined as

$$SS(678) = Rho\_s(678) - Rho\_s(667) - \{Rho\_s(748) - Rho\_s(667)\} * \frac{(678 - 667)}{(748 - 667)}$$

(eq. 2)

Where *Rho_s* is the top of atmosphere reflectance corrected for Rayleigh radiance (NASA, 2019) and 1.33 in eq. 1 is a correction factor originating from Wynne et al. (2013b). *Rho_s* allows potential data retrieval in conditions where the atmospheric correction might fail, such as areas of high glint or aerosols (Gower and King, 2007). The standard cloud flagging procedure was used to mask clouds (L2 flags; NASA, 2019, Wynne et al., 2018). Wynne et al. (2013b) showed that the CI could be calculated from MODIS and that with proper corrections the MODIS CI is equivalent to the MERIS CI. A similar correction should be possible with the relatively newly launched Ocean Color Land Imager (OLCI). This will ensure data continuity to build a climatological time series of cyanobacteria blooms in the Great Lakes when MODIS, which is well beyond its mission life, fails. The CI algorithm has been used extensively in disparate water bodies, including the WLEB (Wynne et al., 2010; Wynne and Stumpf, 2015; Wynne et al., 2008), Saginaw Bay (Wynne et al., 2008); and various lakes in New England (Lunetta et al., 2015), Ohio, and Florida (Mishra et al., 2019). More recently the algorithm has been applied to lakes across the continental U.S. with successful results (Clark et al., 2017; Urquhart et al., 2017; Schaeffer et al., 2015, 2018).

The red bands used in this algorithm penetrate pure water to about two meters due to red light being strongly absorbed by water (Pope and Fry, 1997). The addition of material into the water column will lessen the depth penetration of the algorithm to under a meter (and shallower still in a cyanobacteria bloom). The spectral shape corrects for total albedo of shallow water, however, it may detect benthic cyanobacteria ("algal mats"). Bottom effects were problematic in the very shallow waters in areas of emergent land in eastern Saginaw Bay, near the Wildfowl Bay State Wildlife Area. Whether due to actual interference or benthic cyanobacteria in this region the wildlife area was included as part of the land mask to avoid potential interference due to benthic cyanobacteria (Fig. 1). Sediment does not typically cause false positives in the CI. Hawley et al. (2014) did an in-depth analysis on sediment resuspension in Saginaw Bay. A MODIS image with particularly high resuspension was used as an example in their manuscript. The same image showed no false positives with the algorithm employed in equation 1. The CI product has been used for years in Lake Erie without evidence of impact due to resuspended sediments (Wynne et al., 2012; Stumpf et al., 2016).

To analyze the data set, we partitioned the composites at 10-day intervals starting June 1 and extending through October 31 (Table 1). This follows the convention used by Stumpf et al. (2012) and Wynne and Stumpf (2015) and is based on the assumptions that the cyanobacteria are relatively slow growing (estimated at ~0.295 day^{-1}) and that during at least one day within the 10-day window, winds will be low and atmospheric conditions will be cloud free. This growth rate estimate is consistent with Wilson et al. (2006). They measured the maximal growth rates of numerous *Microcystis aeruginosa* isolates and found an average of 0.27 ± 0.02 day^{-1} (range 0.14 to 0.46 day^{-1}). Prevailing low winds allow cyanobacteria to accumulate at the surface, providing a better estimate of overall cyanobacteria concentrations within the water column. Wynne et al. (2010) showed that wind speeds where stress exceeds 0.1 Pascal (generated by winds > 7.7 m s^{-1}) were enough to mix the bloom through the water column so that the majority of the bloom material was out of the detection limit of satellite (roughly a depth of 0.5 meters in bloom conditions). Approximately 24 hours after the stress was removed cyanobacterial cells were able to redistribute to the surface of the water, where accurate bloom biomass estimations from satellite could be made. Because cyanobacteria prefer warm water temperatures, and Saginaw Bay often freezes in the winter, the CI values were calculated only from satellite images obtained during the warmer months.

For each 10-day period the maximum CI value at each pixel observed in any of the satellite images for that time were retained to form a final "*composite*" image of maximum CI values at each pixel. All subsequent references to CI will indicate a composite image containing these pixel-specific maximum CI values for each 10-day period (Stumpf et al., 2012). CI values are useful for showing the spatial distribution of maximum CI values for a given 10-day composite. Each month contained three ten-day composites, so the third 10-day composite of a 31-day month was extended to encompass 11-days. For simplicity, these 11-day composites are also referred to as "10-day" composites (see Table 2 for details). In any CI data comparisons between Saginaw Bay and WLEB the same 10-day periods were used.

2.4. Interannual variability in bloom biomass

To address interannual variability of cyanobacteria biomass in Saginaw Bay the following steps were taken. Initially, for each available 10-day composite, the maximal CI values from every pixel were summed to provide an overall or "integrated" biomass estimate (Stumpf et al. 2012). This procedure produced 15 integrated CI estimates for each year between June 1 - October 31 (Table 1) from 2000 to 2019 in both Saginaw Bay and the WLEB. The largest of the 15 integrated CI biomass values each year was selected to represent the maximal annual biomass value (Stumpf et al., 2016). Cyanobacterial blooms in Saginaw Bay were retained within the Bay and only the pixels covering the 2,650 km^2 surface area were included in each scene. In contrast, blooms originating in the WLEB are sometimes transported into the central basin to the area near Avon Point (Fig. 1, lower panel). To capture this transport, satellite surveillance of blooms was extended beyond WLEB proper to include the areas west of a line between Pelee Point and Avon Point. This region has a surface area of 4,983 km^2. Hereafter, bloom in "the WLEB" will refer to cyanobacterial blooms that originated in the shallow basin proper plus biomass exported out of the basin captured in the satellite imagery. The goal was to encompass all the biomass originating within WLEB proper, but to exclude any blooms developing independently in the central basin of Lake Erie.

2.5. Bloom maxima in Saginaw Bay and western Lake Erie Basin

Given the similarities between Saginaw Bay and WLEB, a logical question to address is whether blooms in each develop and peak at the same or different times during the summer. To address this question, statistics (mean, standard deviation, mode, and median) describing the time period where the maximum CI value occurred were then determined for the integrated CI values for each 10-day period (e.g., June 1 to June 10) over all 20 years (Table 1).

2.6. Relationship of total phosphorus (TP) inputs and subsequent cyanobacterial bloom biomass in Saginaw Bay and the western Lake Erie basin

Total bioavailable phosphorus (TBP), which consists of DRP and the fraction of the particulate phosphorus that is bioavailable, is the primarily P-source used by cyanobacteria in the WLEB (Baker et al., 2014) and what regulates bloom biomass (Stumpf et al., 2016; Manning et al., 2019). Because TBP and TP are highly autocorrelated (Supplementary Fig. 1; r^2=0.91), both P measurements have been successfully used to predict P-loading and cyanobacterial bloom biomass in the WLEB (Stumpf et al., 2012; Obenour et al. 2014; Kane et al., 2014; Bertani et al., 2016). For Saginaw Bay TP, but no DRP, data are available. For this reason, TP was used as the comparable measurement of P-loading in both Saginaw Bay and the WLEB allowing the subsequent examination of the relationship between P-inputs and cyanobacterial biomass production. Total phosphorus is also generally used to set limits for eutrophication because it is the form most commonly and readily measured so the results can be directly related to existing water quality standards (GLWQANAS, 2019).

2.6.1. River discharges

The Saginaw River, and the Maumee River are the primary sources of nutrients driving cyanobacterial growth in both systems (Newell et al., 2019; Baker et al., 2014; Stumpf et al., 2012; Withers and Jarvie, 2008). Within the Saginaw Bay watershed, the Saginaw River is by far the largest source of water flowing into the bay contributing ~70% of the freshwater input (Stow et al., 2014) and ~90% of the nutrient load (Bierman et al., 1984). Likewise, the Maumee River is a key source of the nutrients entering WLEB, and along with the much smaller Cuyahoga and Sandusky Rivers contribute 50% of the P load into Lake Erie (Baker et al., 2014). Consequently, any differences in the magnitude in timing of water discharges from the Saginaw and Maumee Rivers can potentially affect timing and magnitude of cyanobacterial blooms. To document any differences in discharge patterns between the two rivers, Saginaw River flow measurements were obtained from the United States Geological Survey's (USGS) gage station 04157005 at Holland Avenue at Saginaw, MI, and those for the Maumee River from the USGS gage station 04193500 at Waterville, Ohio. The resulting data were utilized as described in the sections 2.6.2 and 2.6.3.

2.6.2. Estimating what period of river flow best correlated with the 10-day maximum CI value in Saginaw Bay

Research on cyanobacterial blooms in the WLEB demonstrated flow and TP inputs from March - June best predicted maximum cyanobacterial biomass later in the summer (Stumpf, 2012; Obenour et al. 2014). Stumpf et al. (2016) found that July loads also mattered when the mean water temperature in June was greater than 20 °C. It is not known which period of river flow best correlates with cyanobacterial biomass in Saginaw Bay. To address this question, we examined four different integrated periods of river discharge (m^3 x 10^9). These were: (1) The water year (October - September), (2) March - June, (3) March - July, and (4) January-April. The October - September time period reflects the TP input starting from the termination of cyanobacterial blooms by early October of the previous year through the bloom maximum the next summer as well as the termination of the bloom in September. Outflow for these various time periods each year were compared to the corresponding maximal integrated 10-day CI (maximal biomass) value for that year (section 2.4). This made it possible to perform regression analyses to determine if the volumetric out flow from the Saginaw River for any of the different time periods better correlated with maximal cyanobacterial biomass.

Additionally, a direct comparison of the average river discharge patterns in Saginaw Bay and the WLEB was also undertaken to establish how similar or different the pattern of monthly discharge was in the two water bodies. This was accomplished by determining the mean monthly water discharge volume for both rivers from 2000-2019. The data were analyzed from October to September which corresponds with the annual bloom progression observed in Saginaw Bay and Lake Erie.

2.6.3. TP loading in Saginaw Bay and Western Lake Erie Basin

TP loads for the Maumee River are available from Heidelberg University's National Center for Water Quality Research (NCWQR) (Heidelberg University, 2019) from 1975 to the present. For Saginaw Bay, the only TP-loading data available are from the study by Cha et al. (2010), which modeled the TP from 2000-2008. That study utilized known phosphorus concentrations, river flow rates, and loading estimates directly measured by Michigan Department of Environmental Quality or obtained from other sources from 1974 - 1991 and 2001 - 2005 (MDEQWB, 2010). Those data allowed development of a Bayesian model predicting the TP loads from flow rates. This model, along with flow rates from the USGS allowed continuous estimation of loading from 1968-2008, despite the lack of measured nutrient concentration data in some years. The last 9 years of the Cha et al. (2010) data set overlap with the first 9 years of this study. As a result, it was only possible to obtain estimates of TP concentrations for the period between 2000-2008. How P-loading drives cyanobacterial blooms in both Saginaw Bay and the WLEB was therefore limited to this nine year time period.

The cumulative TP loading for each year for the Saginaw from 2000-2008 was calculated from the Cha et al. (2010) data using the following equation:

(eq. 3) $$TP = \sum_{i=March}^{n=June\ 30} (TP_T \times q_i/Q_T)$$

Where TP is the total phosphorus input from March to June, TP_T is the TP load for the year in metric tons, q_i is the discharge for the month i, and Q_T is the total discharge for the year for the Saginaw River calculated from sources described in section *2.4.1*, and i is month (Sigleo and Frick, 2003).

2.7 Changes in TP concentrations in the Saginaw River over time

Baker et al. (2014) showed a decrease in TP loads from the Maumee River over time from the 1970s to 1990s as abatement measures were put into effect. The degree to which P-loading in Saginaw Bay has declined over the same time, if any, has been less well studied. To determine if a corresponding decline in TP inputs also occurred in Saginaw Bay, two studies done almost a decade apart were analyzed. Specifically, the regression equation for the relationship between annual volumetric discharge from the Saginaw River and annual TP loading for the periods 1974 - 1991 and 2001 - 2005, respectively, were analyzed. The data used in the analysis were collated from different sources by the Michigan Department of Environmental Quality Water Board

(MDEQWB, 2010; Supplementary Fig. 2). The slope of each regression line corresponded to the average flow weighted mean concentration (FWMC) for each period. Changes in the FWMC were indicative of how loading has changed in response to abatement efforts. The relationship of annual output from the Saginaw River versus TP loading from 1974 - 1991 shows an average FWMC of 0.27 mg L^{-1} (from the slope) versus 0.17 mg L^{-1} for the 2001 - 2005 period (MDEQWB, 2010) (Supplementary Fig. 2). This difference indicates a 37% drop in average FWMC of TP in response to efforts to reduce loading as of 2005, which shows the efficacy of P-reduction efforts in the Saginaw Basin. It also indicates the relationship between TP load and discharge (FWMC) changed such that the same models may not be applicable to both current and historical conditions.

2.8. Modeled maximum, cumulative 10-day CI predicted from total phosphorus (TP) loading

To assess the similarity or differences in response to P-inputs in Saginaw Bay and WLEB, we used a modified version of the model previously developed for western Lake Erie by Stumpf et al. (2016). That model predicts cyanobacterial biomass based on a given March to June TP input. Using the model and annual March to June TP loading values for 2000-2008, it is possible to calculate expected maximal cyanobacterial biomass for each year of the study. A comparison of the modeled versus actual maximal biomass estimates can be used to evaluate if equivalent TP loading in Saginaw Bay produces the same amount of cyanobacterial biomass as occurs in the WLEB and if the modeled results agree well with the measured maximal cyanobacterial biomass estimated from satellite imagery. The modeling procedure is given below.

The model developed by Stumpf et al. (2016) equating phosphorus load to total cyanobacterial biomass in CI “units” (CI_{MERIS}) using the existing MERIS and adjusted MODIS data is:

(eq. 4) $$CI_{MERIS\,model} = B \times 10^{a \times X}$$

Where $CI_{Meris\ model}$ = modeled CI value, a = 7.48x10^{-4}, B = 0.57 and X = total phosphorus load in metric tons for March-June estimated in section 2.6.3. As the MERIS sensor failed it was replaced by the MODIS sensor. This transition required recalibration of the MERIS algorithm from Stumpf et al. (2016) to fit the MODIS data used in this study because the MERIS composited imagery had CI_{max} values slightly lower than the MODIS CI_{max} values for overlapping scenes. This was particularly true of the 2011 bloom in which MODIS experienced saturation of the sensor in scum areas (Wynne et al., 2013b). The algorithm that was used to estimate the CI in the scum areas most likely overestimated the CI relative to MERIS, which does not have a saturation issue (Wynne et al., 2018). Equation 4 needed to be recalibrated to account for these differences. The CI MERIS from Stumpf et al. (2016) was plotted against with the CI_{MODIS} in this study (Supplementary Fig. 3) and the resultant equation was

(eq. 5) $$CI_{MODIS} = 0.81 \times CI_{MERIS} - 1.3$$

Combining equations 4 and 5 yields the following equation for $CI_{MODIS\ model}$

(eq. 6) $$CI_{MODIS\ model} = B_{MODIS} \times 10^{a \times X} + 1.6$$

where a remains = 7.48×10^{-4}, $B_{MODIS} = 0.70$, with X = total phosphorus load in metric tons. For Saginaw Bay and WLEB, the March-June TP loading values previously determined in section *2.4.3* were inserted into eq. 6 to calculate maximal 10-day $CI_{modeled}$ values for both Saginaw Bay and WLEB from 2000 - 2008.

2.9. Effects of other forcing functions on bloom dynamics in Saginaw Bay

Other environmental factors besides P-input can modulate cyanobacterial bloom intensity in the two systems. The factors that were considered in this study included cloud cover, incoming shortwave irradiance (proxy for incoming photosynthetically active radiation), water temperature, and wind stress (intensity and direction). Differences in average light availability are associated with latitude and cloud cover, both of which may affect the growth of cyanobacteria that often prefer high light. Water temperature was chosen because cyanobacteria growth is strongly influenced by temperature (Paerl and Huisman, 2008). Wind stress was chosen because it can affect the vertical distribution of cells and vertical migration directly affecting CI values that only come from the top meter or so of the water column (Reynolds et al., 1987; Wynne et al., 2010).

To examine how well these environmental factors correlated with bloom biomass, the June-October data for the factors listed above were downloaded as climatological monthly means from NASA's Giovanni reanalysis dataset (Giovanni, 2020) for the years 2000 to 2019. These included products from the AIRS 1-degree cloud fraction, the MERRA-2 model (incoming shortwave flux, surface wind stress), and the water temperature from the MODIS nighttime 11-micron 4 km data. The corresponding CI scenes were binned to create monthly composites instead of the 10-day integrated CI composites used elsewhere in this study. Once the June-October monthly values were calculated, single parameter correlations were then performed using the monthly CI and environmental data.

2.10. Bloom phenology in Saginaw Bay

The following analyses were performed to provide a more detailed resolution regarding the temporal and spatial distribution of Saginaw Bay cyanobacterial blooms, which have been less well investigated than those in western Lake Erie. The analyses were begun by first segregating all the scenes from 2000-2019 into 15 datasets each containing the scenes for the same 10-day period each year (Table 1). Each of the 15 datasets was then analyzed separately. CI values from each corresponding pixel from all 20 scenes (2000-2019) in each data set were identified, averaged and plotted as a single composite image showing the average CI distribution across Saginaw Bay for that 10-day period. The resulting 15 composite plots of average CI values across Saginaw Bay for each 10-day period were then presented in chronological order to show the seasonal bloom progression from the summertime initiation to the final demise in the fall. This analysis included any bloom where the CI is above the detection limit, i.e. > 0, which is estimated to be ~10,000 - 20,000 cells mL^{-1} (Davis et al., 2018).

In addition, two frequency analyses previously used to investigate bloom severity in WLEB were performed (Wynne and Stumpf, 2015). The 2000-2019 MODIS imagery were used to illustrate the bloom phenology described above and were partitioned into the same 15 datasets containing the scenes for specific 10-day composite images from the first 17 years of the study. However, instead of using the data to calculate an average composite pixel CI value, the data for each year was examined to determine how many years during the time series the CI value for each pixel exceeded a defined threshold value. The number of years where the threshold exceeded the prescribed threshold value was then divided by 17 and multiplied by 100 to provide a frequency estimate ranging from 0 to 100 percent. In the first frequency analysis, the threshold value was CI = 0 as defined above. The resulting 15 frequency plots for each 10-day period were presented in chronological order to show how frequently a bloom with CI>0 was present in each section from spring (June 1) to fall (Oct 31). The second analysis was performed in exactly the same manner, but used a threshold value CI ≥ 0.001, equivalent to a concentration of ~10^5 cells mL^{-1} (Stumpf et al., 2012). This is the concentration recommended by the World Health Organization as the upper limit for recreational exposure to cyanobacteria (Chorus and Bartram, 1999) and represents the frequency of severe blooms throughout Saginaw Bay on average over the bloom season. By analyzing the frequency of severe blooms only, the noise in the data is reduced.

2.11. Spatial distribution of blooms in Saginaw Bay relative to the prevailing circulation pattern

Another understudied aspect of the cyanobacterial blooms in Saginaw Bay is their spatial distribution. The predominant flow in Saginaw Bay consists of water entering from Lake Huron along the western side of the Bay and exiting along the eastern shore. This flow is reinforced by an island located in the approximate center of the Bay that helps channel flow into and out of the Bay. To determine how this flow pattern might influence spatial differences in the bloom intensity, Saginaw Bay was divided into five different subregions. These included: (1) the area closest to the river mouth at the southern end of the Bay, (2) the inner and (3) outer regions on the eastern side of the Bay and (4) the inner and (5) outer regions along the western side. Previous studies have similarly partitioned the Bay into these same subregions as a means of documenting spatial differences in various biological measurements associated with differences in depth and circulation patterns (Bierman et al., 1984; Fishman et al., 2010). The integrated CI for each subregion for each 10-day composite period (Table 1) were then determined from the MODIS data and shown as a separate time series from 2000-2019.

To further quantify interannual variability in bloom intensity among the different subregions of Saginaw Bay, an integrated CI value for each year between 2000-2019 for each subregion was determined. The annual subregional, integrated CI values were then normalized to the surface area of each corresponding subregion (integrated CI km^{-2}).

3. Results

3.1. Satellite-derived interannual variability

Every year during the 2000-2019 study period Saginaw Bay experienced a cyanobacterial bloom (Figs. 1 and 2A). The magnitude of these blooms, as indicated by the largest integrated CI value (biomass) during a 10-day period, showed relatively little interannual variation. The largest 10-day integrated biomass estimate for the entire Bay occurred from 1-10 September, 2017. The smallest bloom maximum occurred between 1-10 August, 2016. These maximum and minimum bloom biomasses indicated blooms varied by no more than 4.25-fold interannually. If the 2017 maximum biomass value is excluded, the interannual variation drops to a 1.6-fold difference. In contrast, blooms in the WLEB exhibited a much higher degree of interannual variability during the same period. Maximal 10-day biomass estimates in this system ranged from an integrated CI of 1.5 in 2005 to CI of 40 in 2011, corresponding with a 27-fold interannual difference in bloom concentrations. If 2011 (which was the largest annual bloom, according to the methods described here) is excluded, the interannual variation was still 15-fold. Figure 2B shows the maximum integrated CI values for the same 10-day composites in Saginaw Bay superimposed over the WLEB integrated CI. Blooms in WLEB during "minor bloom years" (2000-2002; 2005-2007) were of similar magnitude to those in Saginaw Bay. Starting in 2008, the magnitude of the cyanobacterial blooms in the two systems diverged. While the magnitude of blooms remained relatively stable in Saginaw Bay, much larger blooms began to develop in WLEB during the years 2008-2009, 2011, 2013-2015 and 2017. This divergence corresponded to a shift from drier, more low flow years on average (2000-2008) to wetter years with generally higher flow rates (2009-20017, 2019; Figs. 2B, 3).

3.2. Timing of bloom maxima in Saginaw Bay and western Lake Erie Basin

The mean, median, and mode of integrated CI values for each of the 10-day periods (Table 1) over the course of the times series were determined, as was the 10-day period having the highest mean, median, and mode values over the time series (Table 2). The mean, median, and mode results all showed that the blooms peaked in Saginaw Bay about 20 days before those in WLEB. Corresponding mean monthly water temperature estimates for 2002-2019 from the USGS discharge stations from the Maumee River and the Saginaw River indicate the warmest 10-day period in both rivers occurred from 21 July - 31 July. The maximal temperatures, however, were slightly different between the two systems. Mean monthly water temperatures for WLEB were 24.0 °C in July, 24.2 °C in August and 21.6 °C in September, compared to 21.7 °C in July, 22.0 °C in August and 19.4 °C in September for Saginaw Bay. Supplementary Fig. 4 shows the tight correlation and a slope near unity of the mean monthly surface water temperatures between WLEB and Saginaw Bay.

3.3. Flow period that best corresponds with maximum 10-day integrated CI value

The Saginaw River was weakly correlated with the Saginaw Bay annual cumulative CI among the time periods of March - June, March-July, January - April, and the water year (Fig. 3; R^2 ~0.2). Consequently, flow rate and associated nutrient loading estimates for Saginaw Bay were integrated from March - June. This timeframe is as good as any other for predicting cyanobacterial biomass in Saginaw Bay and is the period where river flow and TP loading best correlate with maximal cyanobacterial biomass in the WLEB from 2000-2009 (Stumpf et al., 2012). Integrating loading and flow over the same March - June period also simplified comparisons of the mechanisms driving cyanobacterial blooms in both systems.

The average annual discharge pattern for the Saginaw and Maumee Rivers were similar with peak flow occurring in April in the Saginaw River and March in the Maumee River (Fig. 3). Though the pattern was similar, average discharge volumes from the Maumee River in March were substantially higher than from the Saginaw River. April and May discharges from both rivers were equivalent while those in June were again substantially higher from the Maumee River. As a result, on average the overall discharge volume from the Maumee River is higher than that from the Saginaw River. Another major difference between the two rivers was the larger interannual variation relative to mean flow in the Maumee River, particularly between March and July (Fig. 4).

3.4. Relationship between the estimated March-June TP loading versus subsequent maximal 10-day composite CI values

The relationship between TP loading from the Saginaw and Maumee Rivers versus resultant maximal cyanobacterial biomass was calculated as detailed in section *2.5*. The volumetric discharge of the Saginaw and Maumee Rivers during the drier period from 2000-2008, for which TP data for the Saginaw River are available, were similar. In contrast, the amount of cyanobacterial biomass produced for the same amount of river discharge was not equivalent. As March - June outflow increased in the Saginaw Bay, the cyanobacterial biomass rose in a linear fashion. In contrast, as discharge exceeded about 2×10^9 m^3, cyanobacterial biomass in WLEB increased in a non-linear fashion with the linear increases in flow producing progressively and disproportionately more intense blooms compared to Saginaw Bay (Fig. 5A).

The plot of March - June TP inputs versus maximal cyanobacterial biomass showed a different pattern than observed for river discharges (Fig. 5B). TP inputs between 110 to 400 metric tons caused similar, linear increases in maximal bloom intensity in both Saginaw Bay and WLEB. TP input into Saginaw Bay for 8 of the 9 years examined fell below this cut off point. The remaining year received TP inputs of only 450 metric tons. TP inputs into WLEB exceeded 400 metric tons for 7 of the 9 years with maximal loading exceeding 1,050 metric tons. As loading levels exceeded 450 metric tons of TP in the WLEB, linear increases in TP produced a non-linear response of progressively more intense cyanobacterial blooms (Fig. 5B).

3.5. Modeled CI as a function of TP

The modeled cyanobacterial biomass based in March - June TP input fell along a 1:1 line for both Saginaw Bay and WLEB (Fig. 6). This is consistent with the model having been developed for WLEB, which takes into account the non-linear response with increased TP loading. Because the Saginaw Bay loading values were low, they fell in the more linear portion of the model consistent with the observations in Fig. 5B. The tight clustering of points in Saginaw Bay are also consistent with the low interannual variation in bloom intensity compared to the much larger dynamic range for the WLEB. When interpreting these data, it should be noted that the Maumee

River Basin entered a wet phase in 2008 (Fig. 2B) and that is the only wet year included in this analysis. As a result of this wet phase, TP loading for 2009 - 2019 for the Maumee River was much greater, however, the corresponding TP measurements were not available for the Saginaw River (Stumpf et al., 2016).

3.6. Additional forcing functions effects on bloom dynamics in Saginaw Bay

The single regression analyses of cloud cover, incoming shortwave irradiance, mean water temperature and wind stress (intensity and direction) versus CI were conducted. Results revealed that no single input parameter had a correlation above 0.05 to the integrated CI value.

3.7. Bloom phenology and intensity in Saginaw Bay

The average CI patterns from each 10-day composite for the entire 20-year time series is shown in Fig. 7 for Saginaw Bay. The blooms peak in August, and subside relatively quickly in early September. This differs from the WLEB, where a similar analysis showed peak concentrations in mid-September (Wynne and Stumpf, 2015). Blooms are primarily distributed along the shoreline every year forming a halo that does not fully extend into the center of the bay. Nguyen et al. (2014) showed the prevailing current field in Saginaw Bay has strong divergent currents in the center portion of the bay that move water away from the center of the bay towards the shore, which prevents the cyanobacterial cells from accumulating there. These currents are particularly strong in July and August, when the blooms are at their peak. The frequency of all blooms (CI > 0) per 10-day composite are shown in Fig. 8A, and the severe blooms (CI > 0.001) are shown in Fig. 8B. These analyses also show the same pattern as observed in Fig. 7 with nearshore areas clearly experiencing more blooms on average. In combination these results show blooms reliably initiating in July, reaching peak in mid-August, fully dissipated by October and disproportionately impacting areas adjacent to shore.

3.8. Quantifying magnitude of cyanobacterial blooms in subsections of Saginaw Bay

To examine differences in bloom intensity along various segments of the shoreline in Saginaw Bay, the integrated CI values were calculated for 5 different subregions of Saginaw Bay for the entire 20-year time series (Fig. 9B). The time series again revealed the same relatively invariant pattern of annual blooms across the entire study period (Fig. 9A). The subsection where the Saginaw River enters Saginaw Bay exhibited the highest composite CI values and the inner Bay had generally higher CI values than the outer Bay. There was also an across Bay gradient in CI values with Regions 2 (inner Bay) and 4 (outer Bay) along the western shore exhibiting lower CI values than the corresponding subregions 3 (inner) and 5 (outer) along the eastern shore (Fig. 9C). This general pattern in cyanobacterial bloom intensity again corresponds with inflowing oligotrophic waters from Lake Huron preferentially diluting the cyanobacteria bloom along the western shore and outflowing currents differentially transporting bloom populations from near the mouth of the Saginaw River along the eastern shore. A minor portion of the observed CI differences may also be partially due to regions on the western side of the Bay having a lower percentage of coastal adjacent pixels relative to the two regions on the eastern part of the bay. Pixels immediately along the shoreline can sometimes have bottom reflectance or other adjacency issues that cause overestimated CI values.

4. Discussion

4.1. *Factors governing severity and variability of cyanobacterial blooms in Saginaw Bay and the western Lake Erie Basin (WLEB).*

The interannual differences in the variability and intensity of cyanobacterial blooms observed in the WLEB relative to Saginaw Bay were extreme given both watersheds are similarly sized and have a close geographic proximity. Saginaw Bay experienced relatively moderate, similarly sized, cyanobacterial blooms each year between 2000-2019. In contrast, blooms in the WLEB ranged from the intensities observed in Saginaw Bay to an order of magnitude higher (Figs. 1, 2). Many of the larger WLEB blooms caused significant adverse impacts (Michalak et al., 2012; Stumpf et al. 2016). The differences in bloom intensity were largely driven by two factors: the greater flow weighted mean concentrations (FWMC) of TP in the Maumee River and the higher and more variable volumetric discharge from the Maumee River (Figs. 3-5). The estimated FWMC for TP in the Maumee is 0.36 mg L^{-1} from 2000-2008 based on Stumpf et al. (2016) and only 0.17 mg L^{-1} for Saginaw Bay (Supplementary Fig. 2B). The impact of the differences in

FWMC of TP on cyanobacterial bloom formation was evident in comparing the influence of discharge and TP on the maximal summertime biomasses in Saginaw Bay and the WLEB (Fig. 4). During this relatively dry 9-year period, the range in annual discharge volumes was equivalent for these two similarly sized watersheds. Yet the same volumetric discharge from the Maumee River produced more intense cyanobacterial blooms than equivalent discharges by the Saginaw River (Fig. 5A). In contrast, when maximal biomasses in Saginaw Bay and the WLEB were plotted versus the total March-June TP loading for both the Saginaw and Maumee Rivers, comparable loading produced equivalent cyanobacterial biomass in both systems (Figs. 4B, 5A). Blooms in Saginaw Bay clustered at the low end of the TP input range and were tightly grouped reflecting the small interannual variation in TP inputs and resulting blooms. The largest variation in cyanobacterial biomass occurred in the WLEB during the wetter period from 2009-2019, and was again driven by much greater variations in May-June phosphorus loads from the P-enriched Maumee River compared to the less enriched Saginaw River (Figs. 2B, 4; 5B, 6; Stumpf et al. 2016).

The higher nutrient load in the Maumee River is due to approximately 78% of the land use being devoted to agriculture compared to 45% in the Saginaw Bay watershed (Ohio EPA, 2008). Most of the agriculture in both watersheds is devoted to cultivation of row crops (corn and soybeans). The soil types in both basins require drainage to make them agriculturally productive. As fertilizers became commonly utilized, excess P was released into streams and rivers connected to these drainage systems. Historically, efforts were undertaken in the 1970s and 1980s to reduce the total load of TP into Great Lakes watersheds as a means of reducing the intensity of cyanobacterial blooms. Significant progress was made toward meeting this goal during this period (Baker et al., 2014). Then, in the 1990s a major shift in agricultural practices occurred in the Maumee and Saginaw River watersheds with the widespread adoption of no-till farming with fertilizer being directly applied to the soil surface (Smith et al., 2015a; Jarvie et al., 2017). A major goal achieved using this approach was to stabilize or reduce export of particulate P to streams and lakes (Jarvie et al. 2017). Adoption of the no-till farming practices required large-scale installation of tile drainage systems in the Saginaw and Maumee watersheds as a way to maintain more optimal soil moisture levels. A major unintended consequence documented the

Maumee River was a doubling in dissolved reactive phosphorus (DRP) load from the mid-1990s to early 2000s while particulate phosphorus (PP) remained relatively constant (Baker et al., 2014; King et al., 2015a; Smith et al., 2015a; Stow et al., 2015; Williams et al., 2016; Baker et al. 2017; Jarvie et al. 2017). The DRP export from tile drainage systems accounted for >90% of all measured concentrations exceeding recommended levels for minimizing cyanobacterial blooms (King et al., 2015b). This increased DRP input, which is immediately utilizable by phytoplankton for growth, more than any other factor resulted in a re-eutrophication of the WLEB and contributed greatly to increased cyanobacterial biomass in the WLEB (Young et al., 1985; Kane et al., 2014; Smith et al., 2015b; Verhamme et al., 2016). It should be noted that not all nutrient loading is from row crop agriculture, and that Concentrated Animal Feeding Operations (CAFOs) are on the rise. We chose to focus on the larger and better documented source of nutrients into the system, which is row crop agriculture.

In contrast, measured TP levels in the Saginaw River Basin where forests and wetlands account for 22% and 16% of land cover, respectively, remain relatively low (Fig. 5B). Maintenance of relatively low P concentrations over time in the Saginaw River is further supported by the 37% drop in TP observed from the 1974-1991 period versus the 2001-2005 period (MDEQWB, 2010; Supplementary Fig. 2). While DRP was not measured directly in the Saginaw River, the modeling work done in this study indicates DRP concentrations for the Saginaw River are low in comparison to those in the Maumee River, consistent with the lower TP levels (Figs. 5B, 6). The higher proportion of wetlands and forest also help buffer the flow from the Saginaw River. The combination of lower FWMC of P and less variable flow caused cyanobacterial blooms in Saginaw Bay to be more consistent from year to year. Though reduced, there is still sufficient P input to cause Saginaw Bay to be classified as eutrophic with blooms comparable to years with low loading in the WLEB (Fig. 2B).

Another difference between the two systems is the extent of remaining wetland along their shorelines. Saginaw Bay is bordered by 18,000 acres of wetlands (~73 km^2), the largest coastal freshwater wetlands system in the USA (USFWS, 2019). An important component of this wetlands network is the wide swath of the three-square bulrush, *Schoenoplectus pungens*. This species is known to act as a nutrient sink preventing large pulses of phosphorus from reaching the open waters of the bay (Kohler et al., 2004). A review of 203 North American and European wetlands reported median removal rates of 93 g m^{-2} $year^{-1}$ for total nitrogen and 1.2 g m^{-2} $year^{-1}$ of total phosphorus (Land et al., 2016). Assuming the median total phosphorus removal rates reported by Land et al. (2016), Saginaw Bay's surrounding wetlands should remove 88 metric tons (29%) of total phosphorus per year, compared to the average spring input of 300 metric tons (IJC, 2019). This is sufficiently high to have a further ameliorating impact on reducing the severity of cyanobacterial blooms in Saginaw Bay. Approximately 5,100 acres (20.6 km^2) of Lake Erie's original wetlands remain in the WLEB. Using the same uptake assumptions, these marshes could remove 25 metric tons P which is a small amount (~2%) compared to the average 1,126 metric tons discharged between March and June into the WLEB (Stumpf et al., 2016).

4.2 *Nonlinear response to phosphorus loading in western Lake Erie*

A critical feature of the response of TP loading in the WLEB that warrants consideration from a management perspective is the non-linear response of cyanobacterial bloom intensity versus TP input over 500 metric tons (Stumpf et al., 2012; Obenour et al. 2014; Bertani et al. 2016; Stumpf et al., 2016; Verhamme et al., 2016; Ho et al. 2017). At TP loads less than 500 metric tons, Saginaw Bay and the WLEB experience similar sized blooms (Fig. 2B, 5B, 6). In addition at these lower TP loading levels there is a linear response of bloom size to the amount of TP input (Fig. 5B). This raises the question of why TP loading exceeding 500 metric tons causes maximal summertime cyanobacterial biomass to rise in a steep non-linear fashion (Fig. 5B). The mechanism accounting for the non-linear response, however, has not been identified. A logical hypothesis is that there is an internal cycling mechanism that causes the recent P inputs to be utilized more effectively as loading increases (Gächter and Mares, 1985). A likely possibility is that blooms of diatoms and other phytoplankton occurring in early summer are capable of effectively sequestering incoming nutrients even in high flow years (Stoermer and Theriot, 1985; Butts and Carrick, 2017; Reavie et al. 2018; O'Donnell et al., 2019). As water temperatures increase in these shallow systems, the water column stabilizes, nutrients taken up by the initial blooms can be remineralized directly via grazing or bacterial degradation as blooms senesce later in the season (Kreusad et al., 2015; Bartoli et al. 2018; Depew et al. 2018; Null et al., 2020). In essence, early blooms may provide a time release mechanism for initially capturing, then supplying, highly utilizable DRP to support more intense cyanobacterial blooms later in the season. This hypothesis is consistent with the cyanobacterial biomass pattern observed in WLEB for the wetter years in 2011, 2013, 2015, 2017, and 2019 (Fig. 2B).

4.3 *Management implications for controlling cyanobacterial blooms in the WLEB*

From a management perspective, the Saginaw Bay watershed provides a realistic model for further cyanobacterial abatement efforts in the WLEB. The results show that TP inputs into the WLEB would have to drop below 500 metric tons to regularly produce cyanobacterial blooms with comparable intensity to those observed in Saginaw Bay. This 500-metric ton threshold is less than the current loading target of 860 metric tons for the WLEB (GLWQANAS, 2019). Particular attention should be paid to reducing TP and DRP inputs as reflected in the Great Lakes Water Quality Agreement Nutrients Annex (GLWQANAS, 2019). These reductions are particularly important given the trend in increasing annual precipitation in the region over the past several decades, which has the potential to escalate nutrient loading and bloom size (Stow et al., 2015; Fig. 2). Consequently, target TP and DRP reductions may have to be even more drastic than the 40% recommended in the GLWQANAS to achieve the desired reduction in bloom intensity (Scavia et al. 2014; 2016; 2017; Iho et al., 2017; Smith et al. 2018; Wilson et al., 2018; Baker et al., 2019). Numerous approaches for reducing P inputs have been proposed, but are beyond the scope of this manuscript (e.g. Baker et al., 2017; King et al., 2018; Xia et al., 2020). The non-linear response observed with loading in the WLEB means that initial reductions in the highest P-loading rates will have the greatest benefit in terms of reducing bloom biomass (Fig. 5B). The largest loading observed in Saginaw Bay is just below the threshold where nonlinear intensification of blooms would be expected to begin (Fig. 5B). Accordingly, increases in agricultural land use or continued loss of wetlands in the Saginaw Bay watershed or surrounding the Bay will significantly increase potential for severe cyanobacterial blooms (Mitsch and Wang, 2000; USFWS, 2019).

4.4. *Secondary influences on bloom intensity, retention time and water temperature*

Cyanobacteria blooms are caused by a combination of factors. The best documented of these are temperature (Paerl and Huisman, 2009), residence (retention) times (Romo et al., 2013) and eutrophication (Paerl, 1998). Michalak et al. (2013) showed that the large bloom present in the WLEB in the summer of 2011 was partially a result of longer than usual residence times. Summer mean residence time in the WLEB is reported to be 51 days (Millie et al., 2009). This is a little less than half of the average summer residence time in Saginaw Bay, which is estimated to be about 115 days for the entire bay and 62 days for the inner bay (Nguyen et al., 2014). Therefore, residence times would indicate that Saginaw Bay should have larger blooms relative to WLEB if all other factors were equal. This reinforces the importance of the relatively low TP and estimated DRP concentrations in producing consistently moderate annual blooms in Saginaw Bay where advective losses are lower. It also argues that any future increases in nutrient loading will cause a more rapid and intense eutrophication of Saginaw Bay than occurs in the WLEB.

Temperatures in the two systems are similar to one another throughout the year and show little interannual variability (Sayers et al., 2016; Supplementary Fig. 4). While there may be small scale regional variability in the temperature data there was not sufficient temperature data to work out differences from the time period encompassed in this study. Regression analysis failed to show a correlation between temperature and maximum CI concentrations. Similarly, other climatic drivers such as wind stress and light availability were not correlated with maximum CI values. Temperature may, however, have affected the timing of the bloom which peaks 20 days earlier in Saginaw Bay (Aug 11 - Aug 20) compared to the WLEB (Sep 1 - Sep 10) (Table 2). Temperatures of 21.7 °C to 24 °C produce maximal potential *Microcystis* growth rates of 0.6 d^{-1} to 0.69 d^{-1}. The average July temperatures for the WLEB and Saginaw Bay are 24.0 °C and 21.7 °C, respectively. In August the temperatures are 24.2 °C in the WLEB and 22.0 °C in Saginaw Bay, and in September they decrease to 21.7 °C in the WLEB and 19.4 °C in Saginaw Bay. Maximal *Microcystis* growth would correspondingly decrease to ~0.62 d^{-1} in WLEB and ~0.5 d^{-1} in Saginaw Bay. The continued warm temperatures in the WLEB support stronger growth into September, which may explain why blooms peak later in WLEB compared to Saginaw Bay. However, we cannot discount the possibility that another factor, such as nitrogen limitation could be a factor in duration. Blooms in the WLEB generally switch from P-limitation to N-limitation in August and September, possibly Saginaw Bay may experience nitrogen limitation earlier than WLEB, which could promote bloom decline. However, this result could not be tested due to lack of N data.

4.5. Temporal and geographic variation in bloom intensity in Saginaw Bay

On average the cyanobacterial bloom initiates during June and begins intensifying along the southern and eastern shore in early July (Figs. 7, 8). The bloom fully develops mid-July though the end of August, begins to dissipate in early September, and is gone by mid to late October. The prevailing currents cause the bloom to be most intense along the shoreline with the middle of the Bay relatively free of cyanobacteria. During the blooms, cyanobacterial concentrations are highest along the southern shore adjacent to where the Saginaw River enters the bay (Fig. 9). Concentrations along the eastern shore are also higher than those along the western shore, consistent with the prevailing currents.

5. Conclusions

Saginaw Bay has less variable, lower biomass cyanobacterial blooms than the WLEB. This difference is driven by lower and less variable P-inputs from the Saginaw River compared to the Maumee River. Equivalent P-loading in both systems produced similar intensity blooms. A key difference between the two systems is that the WLEB has TP loads exceeding 500 metric tons. TP inputs into Saginaw Bay ranged from ~120-450 metric tons and overlapped levels observed in the WLEB in lower input years. In this range, equivalent phosphorus loads produce equivalent biomass blooms. Above 500 metric tons, cyanobacterial bloom biomass in the WLEB increases rapidly in a non-linear fashion (Fig. 5B).

From a management perspective, these results indicate that reductions in TP loading, particularly the DRP component, below the current maximal loading values in the WLEB will disproportionately reduce boom intensity (Fig. 5B). If loading into the WLEB were reduced to approximately 500 metric tons, blooms would be expected to be equivalent to those observed in Saginaw Bay. Conversely, if P-inputs in Saginaw Bay are increased because of some factor, such as a shift toward more intense agricultural land use, or additional destruction of wetlands, the blooms are likely to intensify significantly. The highest P-inputs into Saginaw Bay are already near the 500 metric tons P threshold and it is reasonable to predict loads above this threshold will begin to produce non-linear intensification of cyanobacterial blooms.

Acknowledgements

This work was partially supported by the U.S. EPA Great Lakes Research Initiative. Andrew Meredith maintains the image processing system. The authors would like to thank Bryan Eder for assistance in making the map in Figure 1.

References:

Baker, D.B., Confesor, R., Ewing, D.E., Johnson, L.T., Kramer, J.W., Merryfield, N.J., 2014. Phosphorus loading to Lake Erie from the Maumee, Sandusky, and Cuyahoga rivers: The importance of bioavailability. J. Great Lakes Res. 40, 5502-517.

Baker, D.B., Johnson, L.T., Confessor, R.B., Crumrine, J.P., 2017. Vertical stratification of soil phosphorus as a concern for dissolved phosphorus runoff in the Lake Erie Basin. J. Environ. Qual. 46, 1287–1295.

Baker, D.B., Johnson, L.T., Confesor, Jr., R.B., Crumrine, J.P., Guo, T., Manning, N.F., 2019. Early-term adjustments for Lake Erie phosphorus target loads to address western basin cyanobacterial blooms. J. Great Lakes Res. 45, 203-211.

Bartoli, M., Zilius, M., Bresciani, M., Vaiciute, D., Vybernaite-Lubiene, I., Petkuviene, J., Giordani, G., Daunys, D., Ruginis, T., Benelli, S., Giardino, C., Bukaveckas, P.A., Zemlys, P., Griniene, E., Gasiunaite, Z.R., Lesutiene, J., Pilkaitytė, R. Baziukas-Razinkovas, A., 2018. Drivers of cyanobacterial blooms in a hypertrophic lagoon. Front. Mar. Sci. https://doi.org/10.3389/fmars.2018.00434

Bierman, V.J., Dolan, D.M., Kasprzyk, R., Clark, J.L., 1984. Retrospective analysis of the response of Saginaw Bay, Lake Huron to reductions in phosphorus loadings. Environ. Sci. Technol. 18, 23-31.

Bertani, I., Obenour, D.R., Stegar, C.E., Stow, C.A., Gronewold, A.D., Scavia, D., 2016. Probabilistically assessing the role of nutrient loading in harmful algal bloom formation in western Lake Erie. J. Great Lakes Res. 42, 1184-1192.

Boedecker, A.R., Niewinski, D.N., Newell, S.E., Chaffin, J.D., McCarthy, M.J., 2020. Evaluating sediments as an ecosystem service in western Lake Erie via quantification of nutrient cycling pathways and selected gene abundances. J. Great Lakes Res. 46(4), 920-932.

Bosse, K.R., Sayers, M.J., Shuchman, R.A., Fahnenstiel, G.A., Ruberg, S.A., Fanslow, D.L., Stuart, D.G., Johengen, T.H., Burtner, A.M. 2019. Spatio-temporal variability of in situ cyanobacteria vertical structure in western Lake Erie: Implications for remote sensing observations. J. Great Lakes Res. 45, 480-489.

Brooks, B.W., Lazorchak, J.M., Howard, M.D.A., Johnson, M.V., Morton, S.L., Perkins, D.A.K., Reavie, E.D., Scott, G.I., Smith, S.A., Steevens, J.A., 2016. Are harmful algal blooms becoming the greatest inland water quality threat to public health and aquatic ecosystems? Environ. Toxicol. Chem. 35, 6-13.

Budd, J.W., Drummer, T.D., Nalepa, T.F., Fahnenstiel, G.L., 2001. Remote Sensing of biotic effects: Zebra mussels (*Dreissena polymorpha*) influence on water clarity in Saginaw Bay, Lake Huron. Limnol. Oceanogr. 46, 213-223.

Butts, E., Carrick, H.J., 2017. Phytoplankton Seasonality along a Trophic Gradient of Temperate Lakes: Convergence in Taxonomic Composition during Winter Ice-Cover. Northeastern Naturalist, 24(sp7):B167-B187. Eagle Hill Institute. https://doi.org/10.1656/045.024.s719

Cha, Y., Stow, C.A., Reckhow, K.H., DeMarchi, C., Johnengen, T.H., 2010. Phosphorus load estimation in the Saginaw River, MI using a Bayesian hierarchical/multilevel model. Water Res. 44, 3270-3282.

Chaffin, J.D., Bridgeman, T.B., Bade, D.L., 2013. Nitrogen constrains the growth of late summer cyanobacterial blooms in Lake Erie. Adv. Microbiol. 3, 16–26.

Chaffin, J.D., Davis, T.W., Smith, D.J., Baer, M.M., Dick, G.J., 2018. Interactions between nitrogen form, loading rate, and light intensity on Microcystis and Planktothrix growth and microcystin production. Harmful Algae 73, 84–97.

Chorus, I., Bartram, J., 1999. Toxic Cyanobacteria in Water: A Guide to Their Public Health Consequences, Monitoring and Management. World Health Organization, London, UK.

Clark, J.M., Schaeffer, B.A., Darling, J.A., Urquhart, E.A., Johnson, J.M., Ignatius, A.R., Myer, M.H., Loftin, K.A., Werdell, J., Stumpf, R.P., 2017. Satellite monitoring of cyanobacterial harmful algal bloom frequency in recreational waters and drinking water sources. Ecol. Indic. 80, 84-95.

Conley, D.J., Paerl, H.W., Howarth, R.W., Boesch, D.F., Seitzinger, S.B., Havens, K.E., Lancelot, C., Likens, G.E., 2009. Controlling eutrophication: nitrogen and phosphorus. Science 323, 1014-1015.

Davis T. W., Stumpf R., Bullerjahn G. S., McKay R. M. L., Chaffin J. D., Bridgeman T. B., Winslow, C., 2019. Science meets policy: a framework for determining impairment designation criteria for large waterbodies affected by cyanobacterial harmful algal blooms. Harmful Algae 81, 59–64. 10.1016/j.hal.2018.11.016

Davis, T.W., Watson, S.B., Rozmarynowycz, M.J., Ciborowski, J.J.H., McKay, R.M., Bullerjahn, G.S. 2014. Phylogenies of microcystin-producing cyanobacteria in the lower Laurentian Great Lakes suggest extensive genetic connectivity. PLOS ONE. https://doi.org/10.1371/journal.pone.0106093

Depew, D.C., Koehler, G., Hiriart-Baer, V., 2018. Phosphorus dynamics and availability in the nearshore of eastern Lake Erie: Insights from oxygen isotope ratios of phosphate. Front. Mar. Sci. https://doi.org/10.3389/fmars.2018.00215

Fishman, D.B., Adlerstein, S.A., Vanderploeg, H.A., Fahnenstiel, G.L., Scavia, D., 2010. Phytoplankton community composition of Saginaw Bay, Lake Huron, during the zebra mussel (*Dreissena polymorpha*) invasion: A multivariate analysis. J. Great Lakes Res. 36, 9-19.

Gächter, R., Mares, A., 1985. Does settling seston release-soluble reactive phosphorus in the hypolimnion of lakes? Limnol. Oceanogr. 30, 364-371.

Gardner, W.S., Yang, L., Cotner, J.B., Johengen, T.H., Lavrentyev, P.J., 2001. Nitrogen dynamics in sandy freshwater sediments (Saginaw Bay, Lake Huron). J. Great Lakes Res. 27, 84-97.

GES-DISC Interactive online visualization and analysis infrastructure (Giovanni), 2020. Giovanni.gsfc.nasa.gov. Last accessed online 5/20/2020.

Gobbler, C.J., Burkholder, J.M., Davis, T.W., Harke, M.J., Johengen, T., Stow, C.A., Van de Waal, D.B., 2016. The dual role of nitrogen supply in controlling the growth and toxicity of cyanobacterial blooms. Harmful Algae 54, 87-97.

Gorham, T., Jia, Y., Shum, C.K., Lee, J. 2017. Ten-year survey of cyanobacterial blooms in Ohio’s waterbodies using satellite remote sensing. Harmful Algae. 66:13-19.

Gower, J., King, S., 2007. Validation of chlorophyll fluorescence derived from MERIS on the west coast of Canada. Int. J. Remote Sens. 28(3), 625-635.

Great Lakes Water Quality Agreement Nutrients Annex Subcommittee (GLWQANAS), 2019. Lake Erie Binational Phosphorus Reduction Strategy. https://binational.net/wp-content/uploads/2019/06/19-148_Lake_Erie_Strategy_E_accessible.pdf. Last accessed 4/25/2020.

Hallegraeff, G.M., 1993. A review of harmful algal blooms and their apparent global increase. Phycologia 32, 79-99.

Hampel, J.J., McCarthy, M.J., Neudeck, M., Bullerjahn, G.S., McKay, R.M.L., Newell, S.E., 2019. Ammonium recycling supports toxic *Planktothrix* blooms in Sandusky Bay, Lake Erie: Evidence from stable isotope and metatranscriptome data. Harmful Algae 81, 42–52.

Hawley, N. Redder, T., Beletsky, R., Verhamme, E., Beletsky, D., DePinto, J., 2014. Sediment resuspension in Saginaw Bay. J. Great Lakes Res. 40, 18-27.

Heath, R.T., Fahnenstiel, G.L., Gardner, W.S., Cavaletto, J.F., Hwang, S., 1995. Ecosystem-level effects of zebra mussels (*Dreissena polymorpha*) and enclosure experiment in Saginaw Bay, Lake Huron. J. Great Lakes Res. 21, 501-516.

Heidelberg University National Center for Water Quality Research, 2019. https://ncwqr.org/monitoring/data/. Last accessed 5/26/2020.

Hilborn, E.D., Beasley, V.R., 2015. One health and cyanobacteria in freshwater systems: Animal illnesses and deaths are sentinel events for human health risks. Toxins. 7, 1374-1395.

Ho, J.C., Stumpf, R.P., Bridgeman, T.B., Michalak, A.M., 2017b. Using Landsat to extend the historical record of lacustrine phytoplankton blooms: a Lake Erie case study. Remote Sens. Environ. 191, 273–285.

Ho, J.C., Michalak, A.M., Pahlevan, N., 2019. Widespread global increase in intense lake phytoplankton blooms since the 1980s. Nature 574, 667–670.

Horst, G.P., Sarnelle, O., White, J.D., Hamilton, S.K., Kaul, R.B. and Bressie, J.D., 2014. Nitrogen availability increases the toxin quota of a harmful cyanobacterium, *Microcystis aeruginosa*. Water Research, 54, pp.188-198.

Iho, A., Ahlvik, L., Ekhyolm, P., Lehtoranta, J., Kortelainen, P., 2017. Optimal phosphorus abatement redefined: insights from coupled element cycles. Ecol. Econ. 137, 13–19.

International Joint Commission (IJC), 2019. The coastal wetlands of Lake Erie: Have we lost our Swiss Army knife? Water Matters Newsletter. https://www.ijc.org/en/coastal-wetlands-western-lake-erie-have-we-lost-our-swiss-army-knife. Last accessed 5/20/2020.

Jarvie, H.P., Johnson, L.T., Sharpley, A.N., Smith, D.R., Baker, D.B., Bruulsema, T.W., Confesor, R., 2017. Increased soluble phosphorus loads to Lake Erie: Unintended consequences of conservation practices? J. Environ. Qual. 46, 123–132.

Kane, D.D., Conroy, J.D., Richards, R.P., Baker, D.B., Culver, D.A., 2014. Re-eutrophication of Lake Erie: correlations between tributary nutrient loads and phytoplankton biomass. J. Great Lakes Res. 40, 496–501.

King, K.W., Williams, M.R., Macrae, M.L., Fausey, N.R., Frankenberger, J., Smith, D.R., Kleinman, P.J., Brown, L.C., 2015a. Phosphorus transport in agricultural subsurface drainage: a review. J. Environ. Qual. 44, 467–485.

King, K.W., Williams, M.R., Fausey, N.R., 2015b. Contributions of systematic tile drainage to watershed scale phosphorus transport. J. Environ. Qual. 44, 486–494.

King, K.W., Williams, M.R., LaBarge, G.A., Smith, D.R., Reutter, J.M., Duncan, E.W., Pease, L.A., 2018. Addressing agricultural phosphorus loss in artificially drained landscapes with 4R nutrient management practices. J. Soil Water Conserv. 73, 35–47.

Kohler, E.A., Poole, V.L., Reicher, Z.J., Turco, R.F., 2004. Nutrient, metal, and pesticide removal during storm and nonstorm events by a constructed wetland on an urban golf course. Ecol. Eng. 23, 285-298.

Kreusad, M., Scharta, M., Enge, A., Nausc, M., Vos, M., 2015. Variations in the elemental ratio of organic matter in the central Baltic Sea: Part I—Linking primary production to remineralization. Cont. Shelf Res. 100, 25-45.

Land, M., Graneli, W., Grimvall, A., Hoffman, C.C., Mitsch,W.J., Tonderski, K.S., Verhoeven, J.T.A., 2016. How effective are created or restored freshwater wetlands for nitrogen and phosphorus removal? A systematic review. Environ. Evid. 5:9. https://doi.org/10.1186/2047-2382-2-16

Lunetta, R.S., Schaeffer, B.A., Stumpf, R.P., Jacobs, S.A., Murphy, M.S., 2015. Evaluation of cyanobacteria cell count detection derived from MERIS imagery across the eastern USA. Remote Sens. Environ. 157, 24-34.

Manning, N. F., Wang, Y., Long, C. M., Bertani, I., Sayers, M., Bosse, K., Shuchman, R., and Scavia, D. 2019. Extending the forecast model: Predicting Western Lake Erie harmful algal blooms at multiple spatial scales. Journal of Great Lakes Research, 45(3), 587-595.

Michalak, A.M., Anderson, E.J., Beletsky, D., Boland, S., Bosch, N.S., Bridgeman, T.B., Chaffin, J.D., Cho, K., Confesor, R., Daloglu, I., DePinto, J.V., Evans, M.A., Fahnenstiel, G.L., He, L., Ho, J.C., Jenkins, L., Johnengenjep, T.H., Kuo, K.C., LaPorte, E., Liu, X., McWilliams, M.R., Moore, M.R., Posselt, D.J., Richards, R.P., Scavia, D., Steiner, A.L., Verhamme, E., Wright, D.M., Zagorski, M.A., 2012. Record-setting algal bloom in Lake Erie caused by agricultural meteorological trends consistent with expected future conditions. Proc. Natl. Acad. Sci. USA 110, 6448-6452.

Michigan Department of Environmental Quality Water Bureau (MDEQWB), 2010. Update of phosphorus load data for Saginaw Bay. MI/DEQ/WB-10/006. https://www.baycounty-mi.gov/Docs/DrainComm/Approved%20WMP/Appendix_L.pdf. Last accessed 5/27/2020.

Millie, D.F., Fahnenstiel, G.L., Dyble Bressie, J., Pigg, R.J., Rediske, R.R., Klarer, D.M., Tester, P.A., Litaker, R.W., 2009. Late-summer phytoplankton in wester Lake Erie (Laurentian Great Lakes): bloom distributions, toxicity, and environmental influences. Aquat. Ecol. 43, 915-934.

Mishra, S., Stumpf, R.P., Schaeffer, B.A., Werdell, P.J., Loftin, K.A., and Meredith, A., 2019. Measurement of cyanobacterial bloom magnitude using satellite remote sensing. Sci Rep. 9(1), 18310. doi:10.1038/s41598-019-54453-y

Mitsch, W.J., Wang, N., 2000. Large-scale coastal wetland restoration on the Laurentian Great Lakes: Determining the potential for water quality improvement. Ecol. Eng. 15, 267-282.

Mitsch, W.J., 2017. Solving Lake Erie's harmful algal blooms by restoring the Great Black Swamp in Ohio. Ecological Engineering. 108, 406-413.

National Aeronautics and Space Administration (NASA) SeaDAS Software Package, 2019. https://seadas.gsfc.nasa.gov/. Last accessed 5/26/2020.

Newell, S.E., Davis, T.W., Johengen, T.H., Gossiaux, Burtner, A., Palladino, D., McCarthy, M.J., 2019. Harmful Algae. 81, 86-93.

Nguyen, T.D., Thupaki, P., Anderson, E.J., Phanikumar, M.S., 2014. Summer circulation in the Saginaw Bay –Lake Huron system. J. Geophys. Res. Oceans. 119, 2713-2734.

Null, G., Errera, R., Fanslow, D.L., 2020. OB14F-0426 - Identifying seasonal shifts in freshwater phytoplankton assemblages through optimizing a flow imaging microscopy technology for the Great Lakes. Ocean Sciences Meeting, 16-21 February, San Diego, CA USA.

Obenour, D.R., Gronewold, A.D., Stow, C.A., Scavia, D., 2014. Using a Bayesian hierarchical model to improve Lake Erie cyanobacteria bloom forecasts. Water Resour. Res. 50, 7847-7860.

O'Donnell, D.R., Conine, A., Hood, J.M., 2019. Time Series Analysis of Lake Erie Phytoplankton dynamics final report for the Ohio Lake Erie Commission, grant number SG-531-2018. https://lakeerie.ohio.gov/Portals/0/LEPF/LEPF%20Final%20Report%20531-18%20sm.pdf?ver=2020-02-10-151947-517. Last accessed 5/26/2020.

Ohio Environmental Protection Agency (Ohio EPA), 2008. Evaluation of land use/land Cover characteristics in Ohio drainages to Lake Erie. Ohio Phosphorus Task Force. https://www.epa.ohio.gov/portals/35/lakeerie/ptaskforce/OPTF_Landuse_20081001_hres.pdf. Last accessed 5/26/2020.

Paerl, H.W., 1988. Nuisance phytoplankton blooms in coastal, estuarine, and inland waters. Limnol. Oceanogr. 33, 823-847.

Paerl, H.W., Huisman, J., 2008. Blooms like it hot. Science 320, 57-58.

Paerl, H.W., Huisman, J., 2009. Climate change: A catalyst for global expansion of harmful cyanobacterial blooms. Environ. Microbiol. Rep. 1, 27-37.

Paerl, H.W., Paul, V.J., 2012. Climate change: Links to global expansion of harmful cyanobacteria. Water Res. 46, 1349-1363.

Paerl, H.W., Otten, T.G., 2013. Harmful cyanobacterial blooms: causes, consequences, and controls. Microb. Ecol. 65, 995-1010.

Paerl, H.W., Scott J.T., McCarthy M.J., Newell S.E., Gardner W.S., Havens K.E., Hoffman D.K., Wilhelm S.W., Wurtsbaugh W.A. 2016. It takes two to tango: when and where dual nutrient (N & P) reductions are needed to protect lakes and downstream ecosystems. Environ. Sci. Technol. 50, 10805–10813.

Pillsbury, R.W., Lowe, R.L., Pan, Y.D., Greenwood, J.L., 2002. Changes in the benthic algal community and nutrient limitation in Saginaw Bay, Lake Huron, during the invasion of the zebra mussel (*Dreissena polymorpha*). J. N. Am. Benthol. Soc. 21, 238-252.

Pope, R.M., Fry, E.S., 1997. Absorption spectrum (380-700 nm) of pure water. II. Integrating cavity measurements. Appl. Opt. 33, 8710-8723.

Reavie, E.D., Cai, M., Twiss, M.R., Carrick, H.J., Davis, T.W., Johengen, T.H., Gossiaux, D., Smith, D.E., Palladino, D., Burtner, A., Sgro, G.V., 2016. Winter-spring diatom production in Lake Erie is an important driver of summer hypoxia. J. Great Lakes Res. 42, 608–618.

Reynolds, C.S., Oliver, R.L., Walsby, A.E., 1987. Cyanobacterial dominance: the role of buoyancy regulation in dynamic lake environments. New Zeal. J. Mar. Fresh. Res. 21, 379-390.

Rockwell, D.C., G.J. Warren, P.E. Bertram, D.K. Salisbury, and N.M. Burns. 2005. The US EPA indicators monitoring program 1983-2002: Trends in phosphorus, silica, and chlorophyll a in the central basin. J. Great Lakes Res. 31, 23-34.

Romo, S., Soria, J., Fernandez, F., Ouahid, Y., Baron-Sola, A., 2013. Water residence time and the dynamics of toxic cyanobacteria. Freshw. Biol. 58, 513-522.

Saginaw 2020; Source of Your Drinking Water https://www.saginaw-mi.com/departments/wastewaterandwatertreatmentservices/watertreatment/sourceofyourdrinkingwater.php. Last accessed September 20, 2020.

Sayers, M., Fahnenstiel, G.L., Shuchman, R.A., Whitley, M., 2016. Cyanobacteria blooms in three eutrophic basins of the Great Lakes: a comparative analysis using remote sensing. Int. J. Remote Sens. 37, 4148-4171.

Scavia, D., Allan, J.D., Arend, K.K., Bartell, S., Beletsky, D., Bosch, N.S., Brandt, S.B., Briland,R.D., Daloglu, I., DePinto, J.V., Dolan, D.M., Evans, M.A., Farmer, T.M., Goto, D., Han,H., Hook, T.O., Knight, R., Ludsin, S.A., Mason, D., Michalak, A.M., Richards, R.P.,Roberts, J.J., Rucinski, D.K., Rutherford, E., Schwab, D.J., Sesterhenn, T.M., Zhang, H., Zhou, Y., 2014. Assessing and addressing the re-eutrophication of Lake Erie: central basin hypoxia. J. Great Lakes Res. 40, 226–246.

Scavia, D., DePinto, J.V., Bertani, I., 2016, A multi-model approach to evaluating target phosphorus loads for Lake Erie. J. Great Lakes Res. 42, 1130–1150.

Scavia, D., Kalcic, M., Muenich, R.L., Read, J., Aloysius, N., Bertani, I., Boles, C., Confessor, R., DePinto, J., Gildow, M., Martin, J., Reddar, T., Robertson, D., Sowa, S., Wang, Y., Yen, H., 2017. Multiple models guide strategies for agricultural nutrient reductions. Front. Ecol. Environ. 15, 126–132.

Schaeffer, B.A., Bailey, S.W., Comney, R.N., Galvin, M., Ignatius, A.R., Johnston, J.M., Keith, D.J., Lunetta, R.S., Parmar, R., Stumpf, R.P., Urquhart, E.A., Werdell, P.J., Wolfe, K., 2018. Mobile device application for monitoring cyanobacteria harmful algal blooms using Sentinel-3 satellite Ocean and Land Colour Instruments. Environ. Modell. Softw. 109, 93-103.

Schaeffer, B. A., Loftin, K., Stumpf, R.P., Werdell, P. J., 2015. Agencies collaborate, develop a cyanobacteria assessment network, EOS 96, doi:10.1029/2015EO038809.

Sigleo, A., Frick, W., 2003. Seasonal Variations in River Flow and Nutrient Concentrations in a Northwestern USA Watershed. pp. 370-376. In: K.G. Renard, S.A. McElroy, W.J. Gburek, H.E. Canfield, and R.L. Scott [eds.], First interagency conference on research in the watersheds. U.S. Department of Agriculture.

Smayda, T.J. 1990. Novel and nuisance phytoplankton blooms in the sea: Evidence for a global epidemic. pp 29-40. In: Graneli E. [ed.] Toxic marine phytoplankton, Elsevier, New York, NY, USA.

Smith, D.R., King, K.W., Johnson, L., Francesconi, W., Richards, P., Baker, D., Sharpley, A.N., 2015a. Surface Runoff and Tile Drainage Transport of Phosphorus in the Midwestern United States. Journal of Environmental Quality 44(2), 495.

Smith, D.R., King, K.W., Williams, M.R., 2015b. What is causing harmful algal blooms in Lake Erie? J. Soil Water Conserv. 70, 27A–29A.

Smith, D.R., Wilson, R.S., King, K.W., Zwonitzer, M., McGrath, J.M., Harmel, R.D., Haney, R.L., Johnson, L.T., 2018. Lake Erie, phosphorus, and microcystin: is it really the farmer's fault? J. Soil Water Conserv. 73, 48–57.

Smith, V.H., 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science 221(4611), 669–671.

Steffen, M.M., Belisle, B.S., Watson, S.B., Boyer, G.L., Wilhelm, S.W. 2014. Status, causes and controls of cyanobacterial blooms in Lake Erie. J. Great Lakes Res. 40, 215-225.

Steffen, M.M., Davis, T.W., McKay, R.M., Bullerjahn, G.S., Krausfeldt, L.E., Stough, J.M.A., Neitzey, M.L., Gilbert, N.E., Boyer, G.L., Johengen, T.H., Gossiaux, D.C., Burtner, A.M., Palladino, D., Rowe, M., Dick, G.J. Meyer, K., Levy, S., Boone, B., Stumpf, R., Wynne, T.T., Zimba, P.V., Gutierrez, D.B., Wilhelm, S.W., 2017. Ecophysiological examination of the Lake Erie *Microcystis* bloom in 2014: linkages between biology and the water supply shutdown of Toledo, Ohio. Environ. Sci. Technol. 51, 6745-6755.

Stoermer, E.F., Theriot, E., 1985. Phytoplankton Distribution in Saginaw Bay. J. Great Lakes Res. 11(2), 132-142.

Stow, C.A., Dyble, J., Kashian, D.R., Johengen, T.H., Peters Winslow, K., Peacor, S.D., Francour, S.N., Burtner, A.M., Palladino, D., Morehead, N., Gossiaux, D., Cha, Y.K., Qian, S.S., Miller, D., 2014. Phosphorus targets and eutrophication objectives in Saginaw Bay: A 35 year assessment. J. Great Lakes Res. 40, 4-10.

Stow, C. A., Y. Cha, L. T. Johnson, R. Confesor, and R. P. Richards. 2015. Long-term and seasonal trend decomposition of Maumee River nutrient inputs to western Lake Erie. Environ. Sci. Technol. 49: 3392–3400. doi:10.1021/es5062648

Stumpf, R.P., Werdell, P.J., 2010. Adjustment of ocean color sensor calibration through multi-band statistics. Opt. Express 18, 401-412.

Stumpf, R.P., Wynne, T.T., Baker, D.B., Fahnenstiel, G.L., 2012. Interannual variability of cyanobacterial blooms in Lake Erie. PLOS ONE. 7 e42444.

Stumpf, R.P., Johnson, L.T., Wynne, T.T., Baker, D.B., 2016. Forecasting annual cyanobacterial bloom biomass to inform management decisions in Lake Erie. J. Great Lakes Res. 42, 1174-1183.

U.S. Fish and Wildlife Service (USFWS), 2019. Michigan Wetland Resources. https://www.fws.gov/wetlands/data/Water-Summary-Reports/National-Water-Summary-Wetland-Resources-Michigan.pdf. Last accessed 5/26/2020.

Urquhart, E.A., Schaeffer, B.A., Stumpf, R.P., Loftin, K.A., Werdell, P.J., 2017. A method for examining temporal changes in cyanobacteria harmful algal bloom spatial extent using satellite remote sensing. Harmful Algae. 67, 144-152.

Vanderploeg, H.A., Jiebig, J.R., Carmichael, W. W., Agy, M.A., Johengen, T.H., Fahnenstiel, G.L., Nalepa, T.F., 2001. Zebra Mussel (*Dreissena polymorpha*) selective filtration promoted toxic *Microcystis* blooms in Saginaw Bay (Lake Huron) and Lake Erie. Can. J. Fish. Aquat. Sci. 58, 1208-1221.

Verhamme, E.M., Redder, T.M., Schlea, D.A., Grush, J., Bretton, J.F., DePinto, J.V., 2016. Development of the Western Lake Erie Ecosystem Model (WLEEM): application to connect phosphorus loads to cyanobacteria biomass. J. Great Lakes Res. 42, 1193–1205.

Wang, G., Lee, Z., and Mouw, C. 2018. Multi-spectral remote sensing of phytoplankton pigment absorption properties in cyanobacteria bloom waters: a regional example in the western basin of Lake Erie. Remote Sensing. 10(2), 302.

Watson, S.B., Ridal, J., Boyer, G.L., 2008. Taste and odor can cyanobacterial toxins: Impairment, prediction, and management in the Great Lakes. Can. J. Fish. Aquat. Sci. 65, 1779-1796.

Williams, M.R. King, K.W., Ford, W., Buda, A.R., Kennedy, C.D. 2016. Effect of tillage on macropore flow and phosphorus transport to tile drains. J. Environ. Qual. 46, 1306–1313.

Wilson, A.E., Wilson, W.A., Hay, M.E., 2006. Intraspecific variation in growth and morphology on the bloom-forming cyanobacterium *Microcystis aeruginosa*. Appl. Environ. Microbiol. 72, 7386-7389.

Wilson, R.S., Beetstra, M.A., Reutter, J.M., Hesse, G., DeVanna-Fussell, K.M., Johnson, L.T., King, K.W., LaBarge, G.A., Martin, J.F., Winslow, C., 2018. Commentary: achieving phosphorus reduction targets for Lake Erie. J. Great Lakes Res. 45(1):4-11.

Withers, P.J.A., Jarvie, H.P., 2008. Delivery and cycling of phosphorus in rivers: A review. Sci. Total Environ. 400, 379-395.

Wynne, T.T., Stumpf, R.P. 2015. Spatial and temporal patterns in the seasonal distribution of toxic cyanobacteria in western Lake Erie from 2002-2014. Toxins 7, 1649-1663.

Wynne, T.T., Stumpf, R.P., Tomlinson, M.C., Warner, R.A., Tester, P.A., Dyble, J., Fahnenstiel, G.L. 2008. Relating spectral shape to cyanobacterial blooms in the Laurentian Great Lakes. Int. J. Remote Sens. 29, 3665–3672.

Wynne, T.T., Stumpf, R.P., Tomlinson, M.C., Dyble, J., 2010. Characterizing a cyanobacterial bloom in western Lake Erie using satellite imagery and metrological data. Limnol. Oceanogr. 55, 2025–2036.

Wynne, T.T., Stumpf, R.P., Tomlinson, M.C., Fahnenstiel, G.L., Schwab, D.J., Dyble, J., Joshi, S., 2013a. Evolution of a cyanobacterial bloom forecast system in western Lake Erie: Development and initial evaluation. J. Great Lakes Res. 39, 90–99.

Wynne, T.T., Stumpf, R.P. Briggs, T.O., 2013b. Comparing MODIS and MERIS spectral shapes for cyanobacterial bloom detection. Int. J. Remote Sens. 34, 6668–6678.

Wynne, T.T., Meredith, A., Stumpf, R.P., Briggs, T.O., Litaker, R.W., 2018. Harmful algal bloom forecasting branch ocean color satellite imagery processing guidelines. NOAA Technical Memorandum NOS NCCOS 252. https://repository.library.noaa.gov/view/noaa/20270. Last accessed 5/20/2020.

Xu, H., Paerl, H.W., Qin, B., Zhu, G., Gaia, G., 2009. Nitrogen and phosphorus inputs control phytoplankton growth in eutrophic Lake Taihu, China. Limnol. Oceanogr. 55, 420-432.

You, J., Mallery, K., Hong, J., Hondzo, M. 2018, Temperature effects on growth and buoyancy of *Microcystis aeruginosa*. J. Plank. Res. 40(1), 16–28.

Young, T.C., DePinto, J.V., Martin, S.C., Bonner, J.S., 1985. Algal-available particulate phosphorus in the Great Lakes Basin. J. Great Lakes Res. 11, 434–446.

Zhang, F., Hu, C., Shum, C.K., Liang, S. and Lee, J. 2017. Satellite remote sensing of drinking water intakes in Lake Erie for cyanobacteria population using two MODIS-based indicators as a potential tool for toxin tracking. Front. Mar. Sci. https://doi.org/10.3389/fmars.2017.00124

Figure Legends

Figure 1. Maps of the two study areas. (Top) Bathymetry and other relevant features of Saginaw Bay. (Middle) Geographic location of Saginaw Bay and the WLEB relative to one another. The Saginaw and Maumee Rivers supply a majority of the nutrients to Saginaw Bay and the WLEB respectively. (Bottom) The bathymetry and other relevant features of the WLEB.

Figure 2. Monthly variations in cyanobacterial biomass in Saginaw Bay and the WLEB. (A) The maximal cumulative cyanobacterial index (CI) values from every 10-day composite (see Table 1) available for Saginaw Bay for 2000-2019. (B) The maximal commutative CI values for the WLEB (light bars) and Saginaw Bay (dark bars) allowing comparison of relative differences in the biomass of the cyanobacterial blooms in the two systems. The vertical black lines delimit the bloom season for each year, which starts on June 1 – June 10 and ends October 20-October 31 (See Table 1). Each bloom year was divided into the same 15, 10-day composite periods.

Figure 3. Relationship between the maximal annual CI value (*) in Saginaw Bay and cumulative volumetric output from the Saginaw River for the time periods. Circles (-o-) indicate volumetric output per water year which is October previous year to September of the current year. This encompasses the progression of annual blooms from their demise in October in one year through the summertime bloom and late summer/early fall decline the following year. Symbols (...+...) represents volumetric output of the Saginaw River from March - June and (–x–) the March - July output.

Figure 4. Monthly discharge from the Saginaw and Maumee Rivers. (A) Mean and standard deviation for monthly discharge from the Saginaw River between 2000-2019. The data are plotted from October 1 to September 30 to correspond to the end of the bloom the previous year and the decline of the bloom the following September. (B) Same data for the Maumee River processed as detailed in A.

Figure 5. Relationship between (A) March - June discharge from the Saginaw and Maumee Rivers from 2000-2008 and (B) March - June total phosphate loading (from 2000-2008) from the Saginaw and Maumee Rivers versus the corresponding maximal 10-day Cyanobacterial Index in Saginaw Bay (*) and the WLEB (o), respectively.

Figure 6. Observed annual maximum 10-day, Cyanobacterial Index (CI) values vs modeled maximal CI based on total phosphorus (TP) input from the Maumee (o) and Saginaw (*) Rivers. The models used for predicting CI from TP were originally developed using data available for the WLEB (Stumpf et al. 2016). The diagonal line indicates a 1:1 correspondence between actual and modeled maximum CI values.

Figure 7. Time series showing the average maximal Cyanobacterial Index (CI) values for every pixel in Saginaw Bay obtained for each of the 15, ten-day periods in a bloom season (Table 1). Warmer colors indicate higher levels of cyanobacteria, while cooler colors indicate lower levels. The composited images for each 10-day period were then arranged in chronological order to show development and decline of the bloom. Data for each image were determined by extracting the maximal CI values for the same pixel in every corresponding 10-day period between 2000 and 2019 and then averaging those data to provide a mean pixel value for a given 10-day period across all years. The center of the bay has lower cyanobacterial concentrations relative to the shoreward areas due to prevailing circulation within the bay. The inner bay also has higher concentration relative to the outer bay.

Figure 8. Time series showing the percent of the years in the study maximal Cyanobacterial Index (CI) values for every pixel in Saginaw Bay exceeded one of two thresholds. (A) The percent of time a pixel exceeded a (CI) of 0 in each of the 15, ten-day periods in a bloom season

over the 20 year cyanobacterial time series from Saginaw Bay. A CI=0 is estimated to be ~20,000 cells mL^{-1} (Stumpf et al., 2012). This graphic provides a probability estimate of a cyanobacterial bloom being present in a given location in each of the 15 of the 10-day periods from June 1 to October 31. (B) Same as A except it is percent of time the CI value was ≥ 0.001, which is equivalent to a concentration of 10^5 cells mL^{-1}.

Figure 9. (A) Saginaw Bay was subdivided into 5 regions to examine geographic variation in bloom intensity. The cumulative maximal CI values for each 10-day composites from each of these five regions was then plotted as time series from 2000 to 2019. (B) Map showing the different subregions of the Bay. (C) The average of the cumulative maximal CI values for each subregion over all 20 years of the study normalized to surface area. Region 1, closest to the primary nutrient source, the Saginaw River, had the highest CI value. The inner bay (R2, R3), had a higher CI value than the outer bay subregions (R4, R5). Values for the eastern shore subregions (R3, R5) were higher than the corresponding ones on the eastern shore (R2, R4).

Supplementary Fig. 1. March to July loads of total phosphorus load versus total bioavailable phosphorus for the Maumee River.

Supplementary Fig. 2. (A) Regression analysis of the relationship between annual volume of water from the Saginaw River and total annual phosphorus load from the 1974- 1991 (MDEQWB, 2010) (B) Same as for (A) except for the 2001-2005 time period (MDEQWB, 2010). The slope of the regression lines represents the flow weighted mean concentration (FWMC) of TP (mg mL^{-1}) for both time periods. The differences in the FWMC concentrations during the two periods are consistent with phosphorus abatement strategies begun in the 1970s having reduced TP loading into Saginaw Bay from the Saginaw River by 37% in the early to mid-2000s.

Supplementary Fig. 3. Regression analysis of the CI from the Stumpf et al. (2016) model on western Lake Erie against the CI from the MODIS data used in the current study. The slope (m) and the slope intercept (b) of the relationship shown here was used to adjust equation 6.

Supplementary Fig. 4. Relationship between mean monthly water temperature in the WLEB versus Saginaw Bay from 2002-2019.

Tables

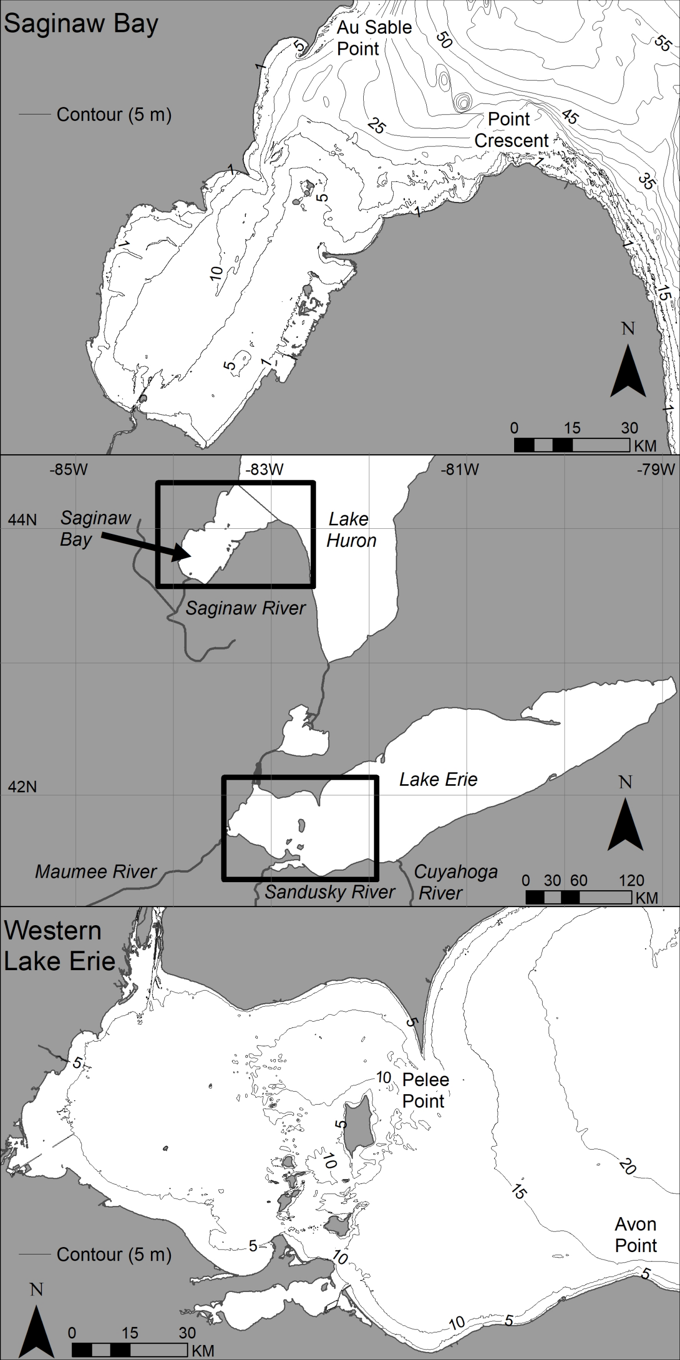
Table 1: The 10-day composite numbering system used for each year in both Saginaw Bay and western Lake Erie basin.

Composite Number	Start Date	End Date
1	June 1	June 10
2	June 11	June 20
3	June 21	June 30
4	July 1	July 10
5	July 11	July 20
6	July 21	July 31
7	August 1	August 10
8	August 11	August 20
9	August 21	August 31
10	September 1	September 10

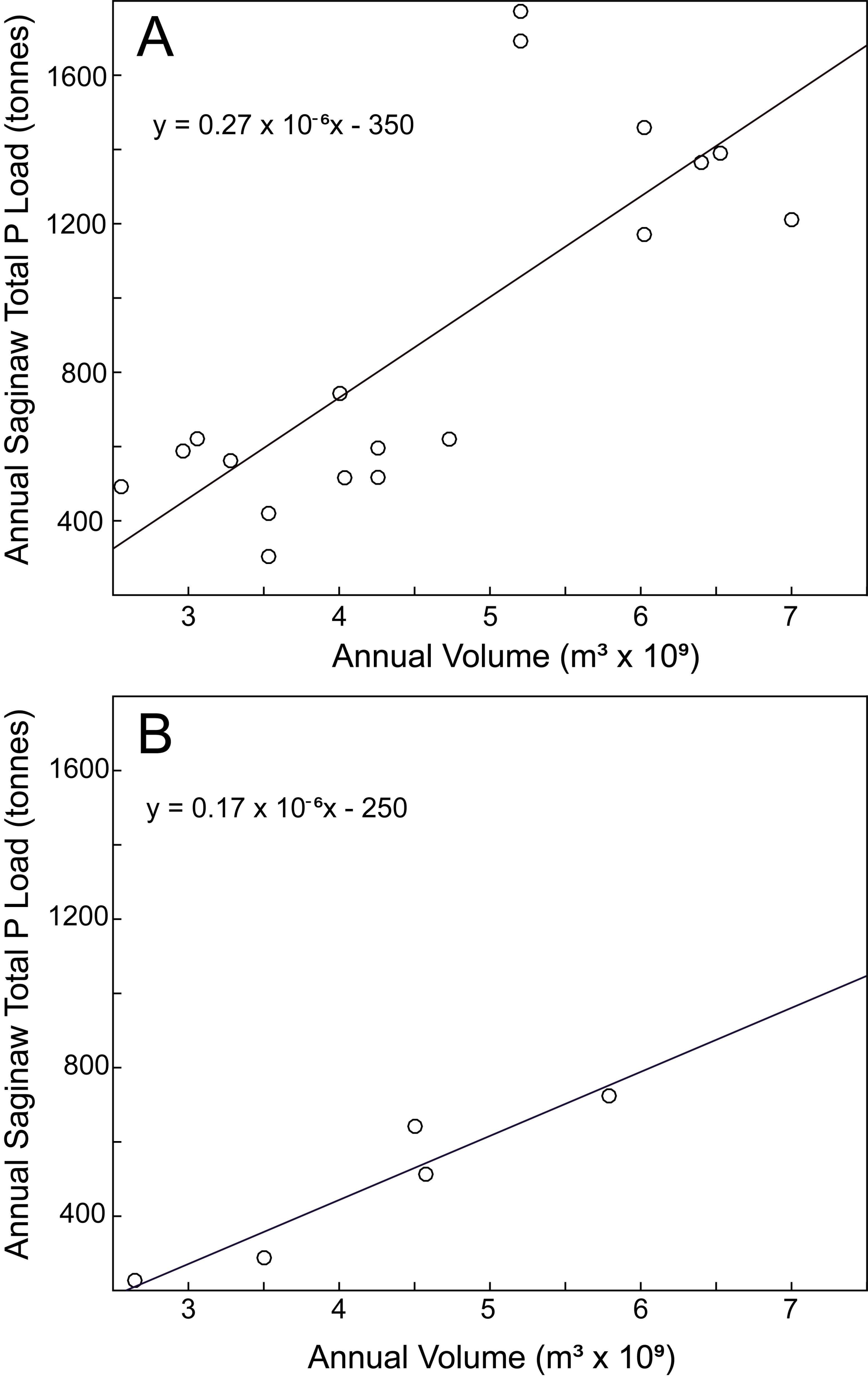
11	September 11	September 20
12	September 21	September 30
13	October 1	October 10
14	October 11	October 20
15	October 21	October 31

Table 2: The 10-day composite periods (in parentheses) exhibiting the highest mean, median, and mode integrated CI values during the 20-year MODIS time series. Details on how values were calculated are given in section 2.3.

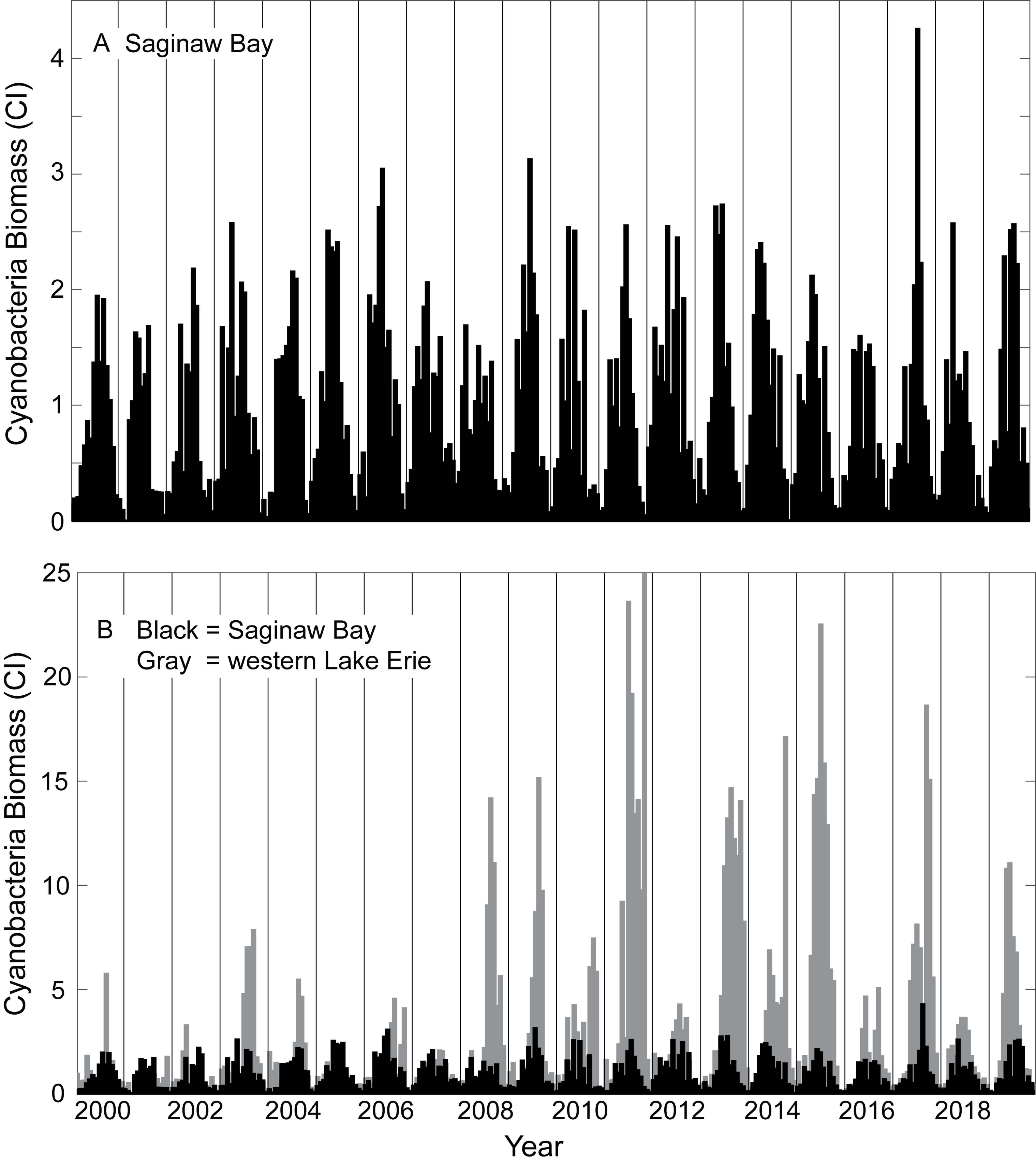
Statistic	western Lake Erie Basin	Saginaw Bay
Mean ± SD	9.7 ± 2.4 (Sep 1 - Sep 10)	7.75± 1.7 (Aug 11 - Aug 20)
Median	10.0 (Sep 1 - Sep 10)	7.5 (Aug 11 - Aug 20)
Mode	10.0 (Sep 1 - Sep 10)	9.0 (Aug 21 - Aug 31)

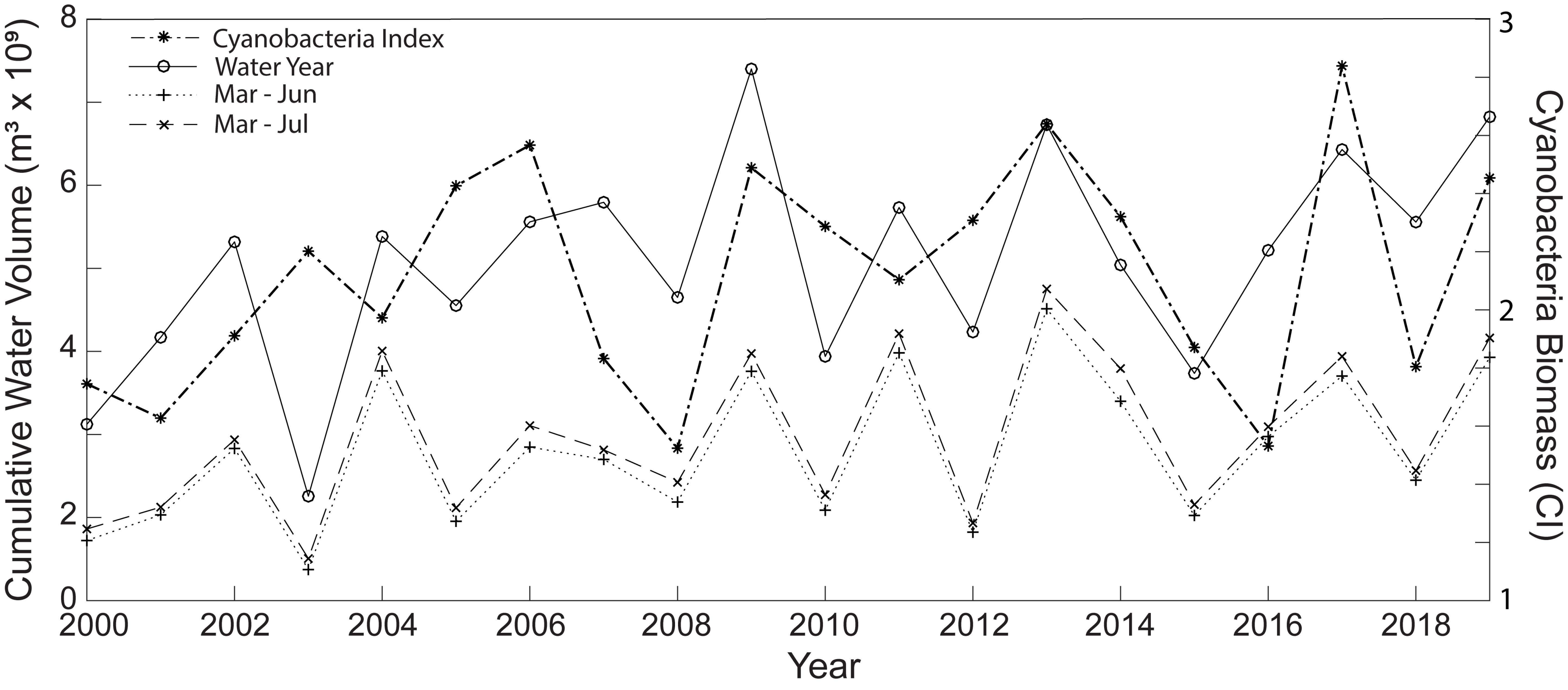


Saginaw Bay
Contour (5 m)
Au Sable Point
Point Crescent
50
55
45
35
25
15
10
5
1
N
0 15 30 KM
-85W
-83W
-81W
-79W
44N
42N
Saginaw Bay
Lake Huron
Saginaw River
Lake Erie
Maumee River
Sandusky River
Cuyahoga River
N
0 30 60 120 KM
Western Lake Erie
Contour (5 m)
Pelee Point
Avon Point
5
10
15
20
N
0 15 30 KM

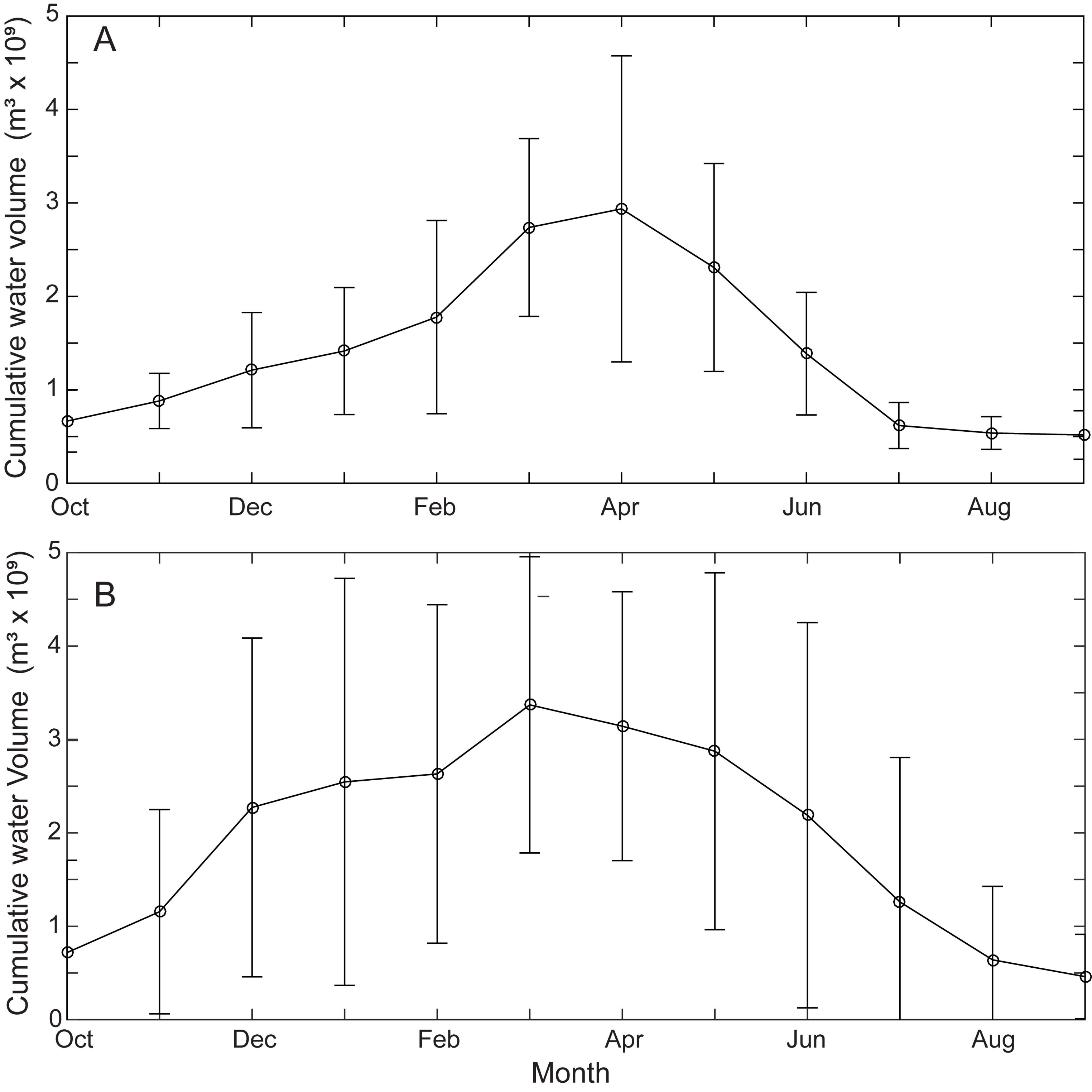


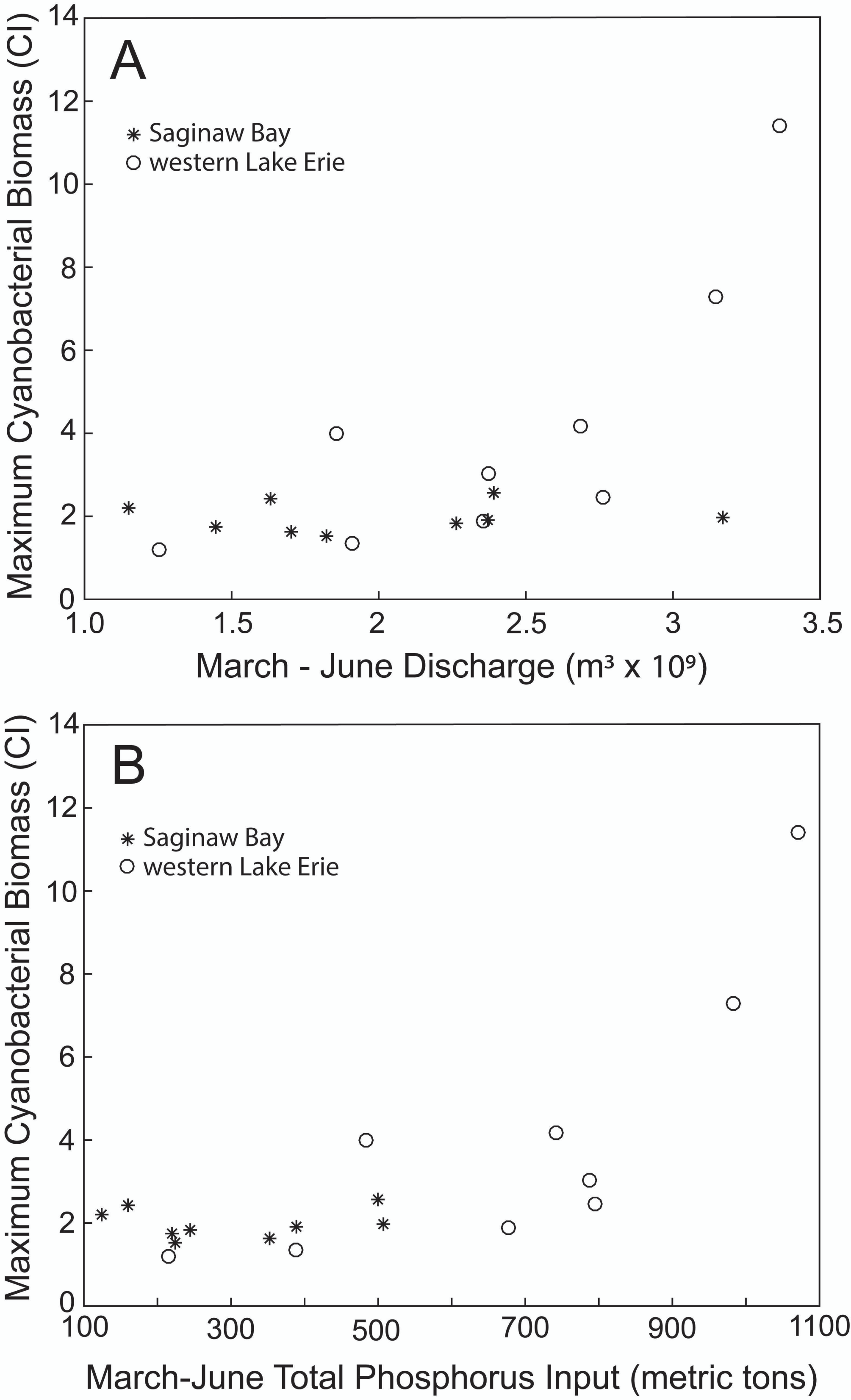
A
y = 0.27 x 10⁻⁶x - 350
Annual Saginaw Total P Load (tonnes)
400
800
1200
1600
3
4
5
6
7
Annual Volume (m³ x 10⁹)
B
y = 0.17 x 10⁻⁶x - 250
Annual Saginaw Total P Load (tonnes)
400
800
1200
1600
3
4
5
6
7
Annual Volume (m³ x 10⁹)


A Saginaw Bay
B Black = Saginaw Bay
Gray = western Lake Erie
Cyanobacteria Biomass (CI)
Year
0
1
2
3
4
5
10
15
20
25
2000
2002
2004
2006
2008
2010
2012
2014
2016
2018

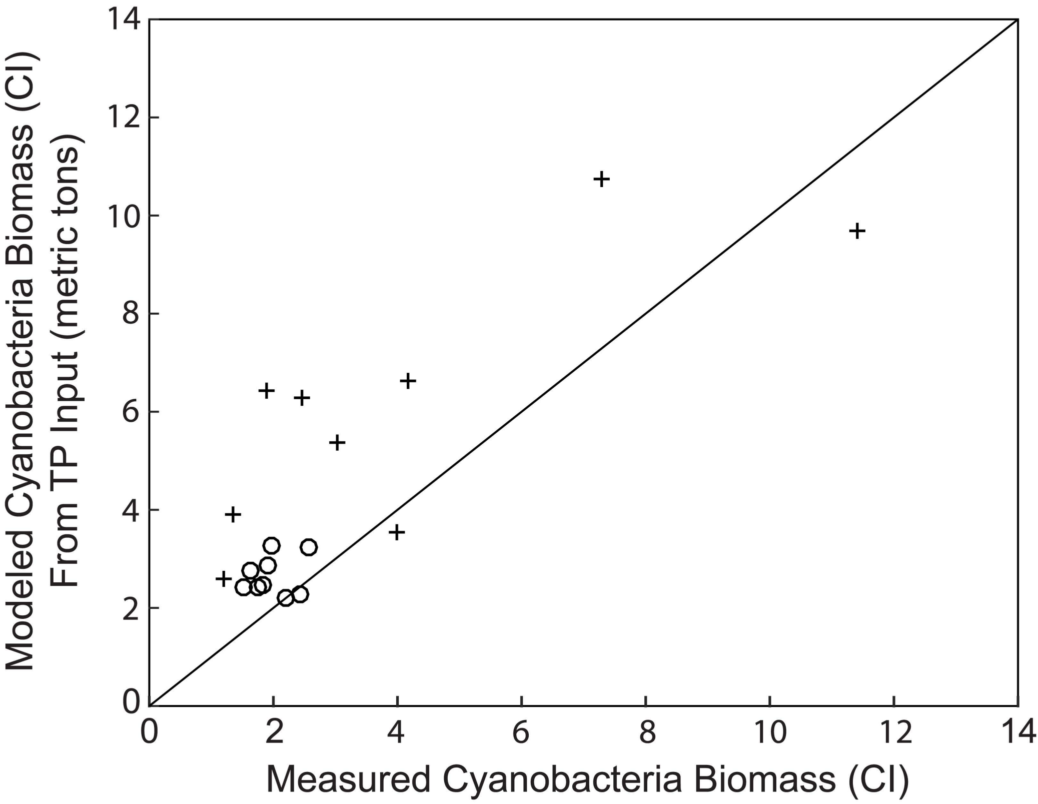


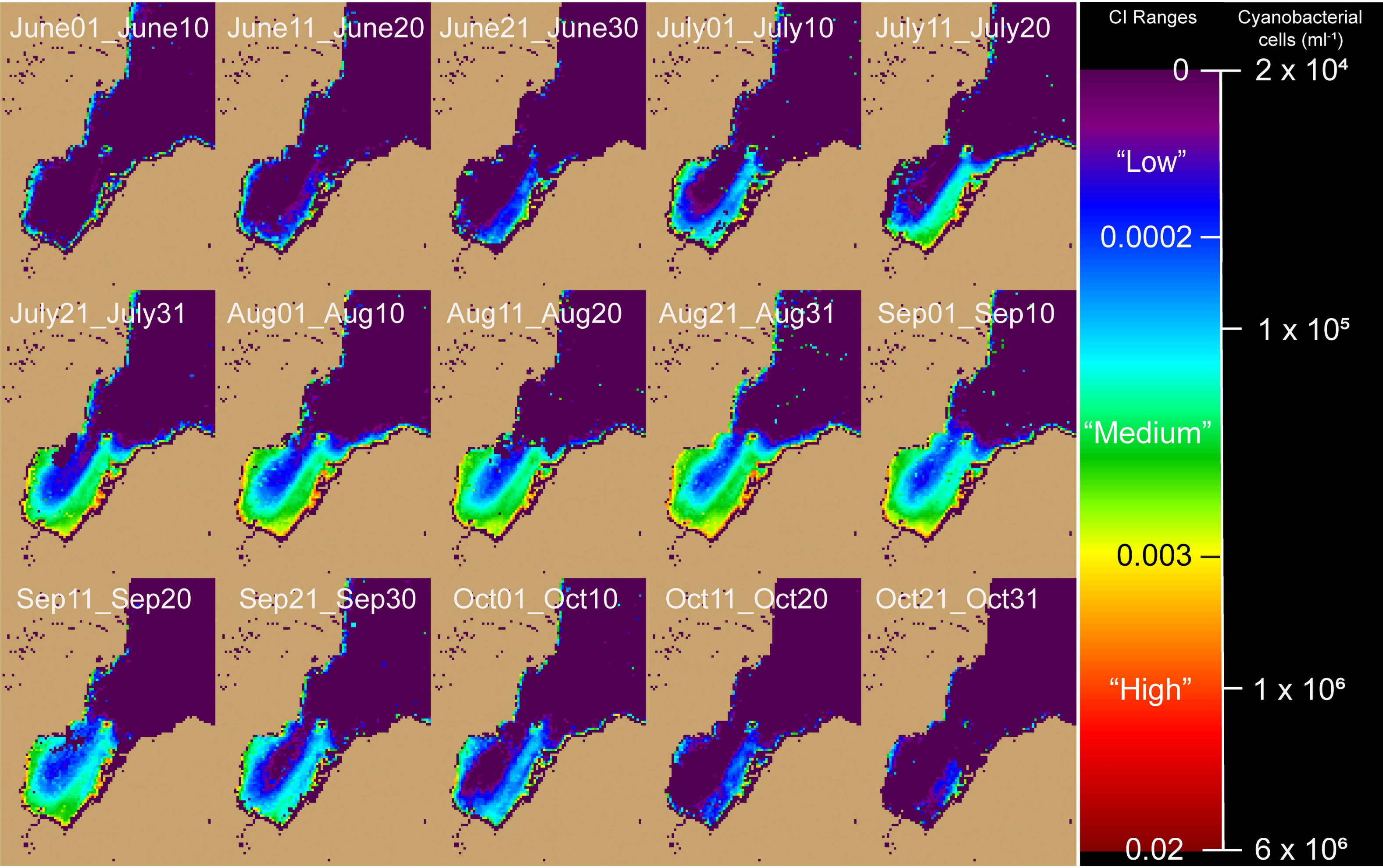
Cyanobacteria Index
Water Year
Mar - Jun
Mar - Jul
Cumulative Water Volume (m³ x 10⁹)
Cyanobacteria Biomass (CI)
Year
0
2
4
6
8
1
2
3
2000
2002
2004
2006
2008
2010
2012
2014
2016
2018


A
B
Cumulative water volume (m³ x 10⁹)
Cumulative water Volume (m³ x 10⁹)
0
1
2
3
4
5
Oct
Dec
Feb
Apr
Jun
Aug
Month

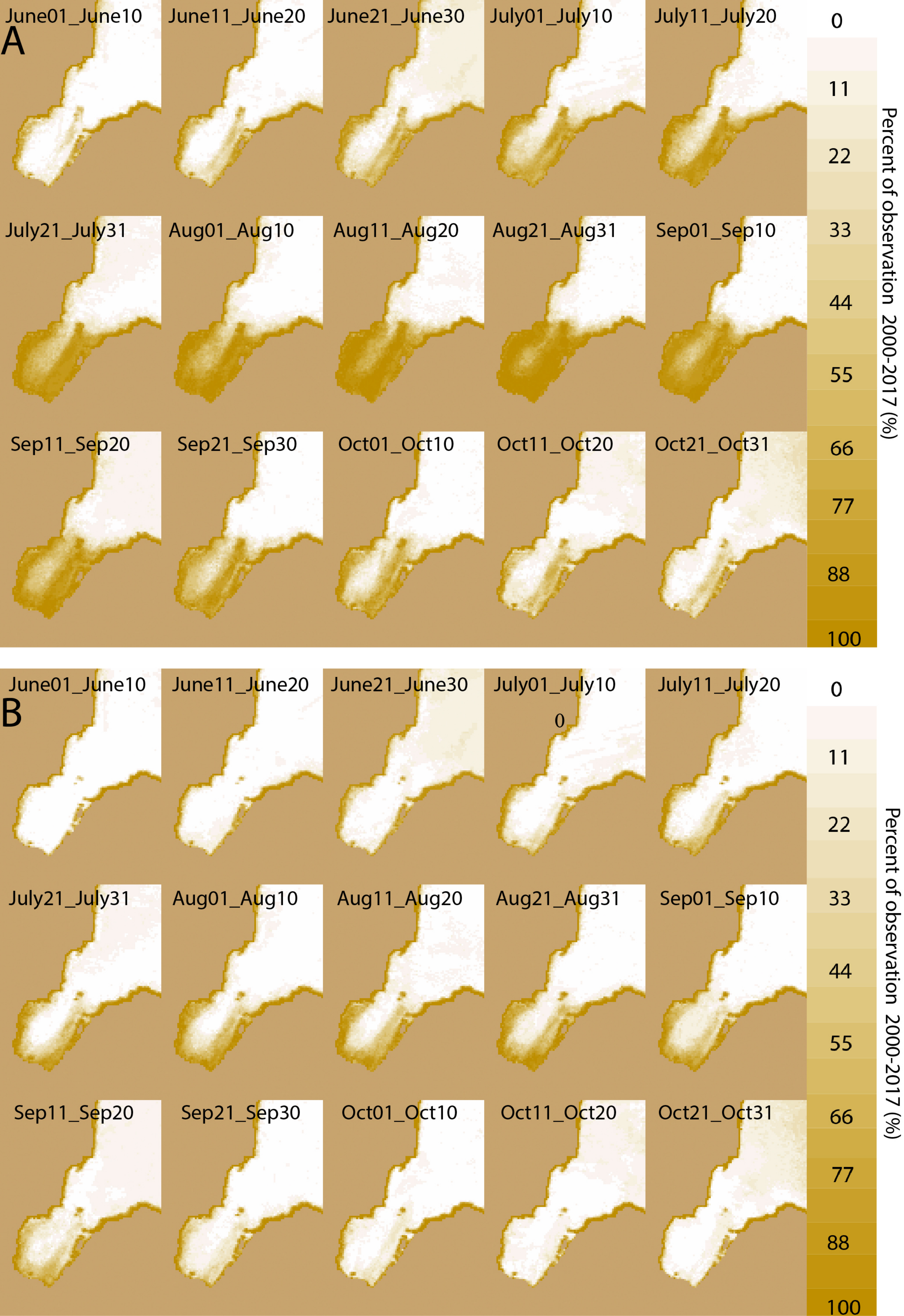


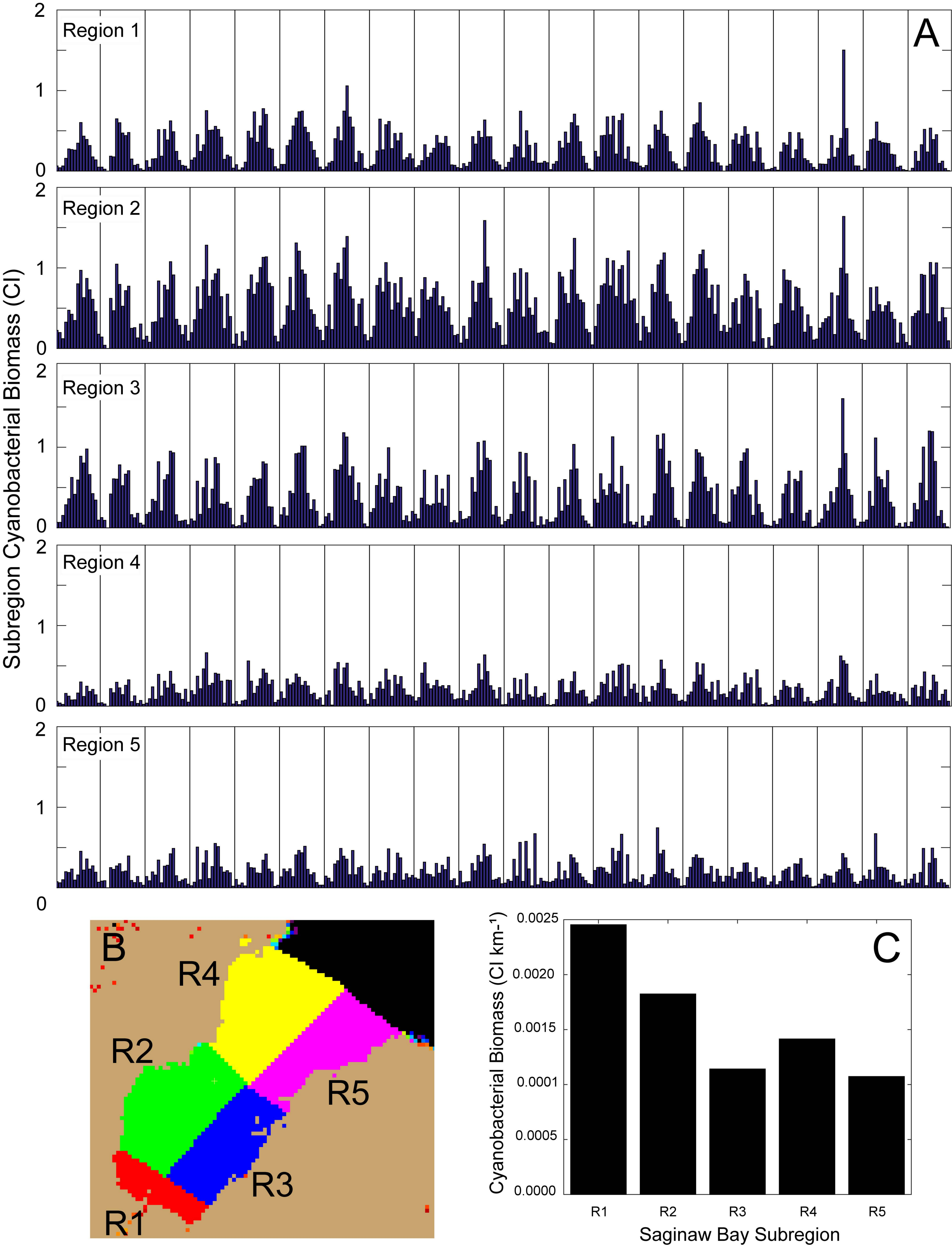
A
Saginaw Bay
western Lake Erie
Maximum Cyanobacterial Biomass (CI)
March - June Discharge (m³ x 10⁹)
0
2
4
6
8
10
12
14
1.0
1.5
2
2.5
3
3.5
B
Saginaw Bay
western Lake Erie
Maximum Cyanobacterial Biomass (CI)
March-June Total Phosphorus Input (metric tons)
100
300
500
700
900
1100


Modeled Cyanobacteria Biomass (CI)
From TP Input (metric tons)
0
2
4
6
8
10
12
14
Measured Cyanobacteria Biomass (CI)



June01_June10
June11_June20
June21_June30
July01_July10
July11_July20
July21_July31
Aug01_Aug10
Aug11_Aug20
Aug21_Aug31
Sep01_Sep10
Sep11_Sep20
Sep21_Sep30
Oct01_Oct10
Oct11_Oct20
Oct21_Oct31
CI Ranges
Cyanobacterial cells (ml⁻¹)
0
2 x 10⁴
"Low"
0.0002
1 x 10⁵
"Medium"
0.003
"High"
1 x 10⁶
0.02
6 x 10⁶


A
June01_June10
June11_June20
June21_June30
July01_July10
July11_July20
July21_July31
Aug01_Aug10
Aug11_Aug20
Aug21_Aug31
Sep01_Sep10
Sep11_Sep20
Sep21_Sep30
Oct01_Oct10
Oct11_Oct20
Oct21_Oct31
0
11
22
33
44
55
66
77
88
100
Percent of observation 2000-2017 (%)
B
June01_June10
June11_June20
June21_June30
July01_July10
0
July11_July20
July21_July31
Aug01_Aug10
Aug11_Aug20
Aug21_Aug31
Sep01_Sep10
Sep11_Sep20
Sep21_Sep30
Oct01_Oct10
Oct11_Oct20
Oct21_Oct31
0
11
22
33
44
55
66
77
88
100
Percent of observation 2000-2017 (%)



A
Region 1
Region 2
Region 3
Region 4
Region 5
Subregion Cyanobacterial Biomass (CI)
2
1
0
B
R1
R2
R3
R4
R5
C
Cyanobacterial Biomass (CI km-1)
0.0025
0.0020
0.0015
0.0001
0.0005
0.0000
R1
R2
R3
R4
R5
Saginaw Bay Subregion