Seasonal patterns for Secchi depth, chlorophyll *a*, total phosphorus, and nutrient limitation differ between nearshore and offshore in Lake Michigan

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ABSTRACT Data on Secchi depth, chlorophyll *a*, total phosphorus (TP), and nutrient status of phytoplankton were collected at five nearshore sites (11-17 m deep) and two offshore sites (>100 m) between the Grand River and Muskegon River outflows during March-December 2014-2018 to describe seasonal patterns and to compare the two depth regions in southeastern Lake Michigan. In contrast to the offshore, where spring chlorophyll *a* and TP concentrations declined dramatically following the dreissenid mussel expansion, the nearshore region of southeastern Lake Michigan was still characterized by low Secchi depth and elevated chlorophyll *a* and TP in the spring. During May, median Secchi depth was 5 times higher in the offshore than the nearshore, whereas chlorophyll *a* and TP were over 9 and 3 times higher in the nearshore, respectively. Even though spring chlorophyll *a* and TP have declined substantially at some of the nearshore sites compared to 1996, particularly the sites closest to tributary outflows, the overall yield of chlorophyll *a* per unit TP did not change over time in the nearshore. There were indications of P-deficiency in the nearshore in 2014-2018, but P-deficiency was even more severe in the offshore during the spring where yield of chlorophyll *a* per unit TP was also lower than in the nearshore. Although dreissenid mussels can be abundant in the nearshore, their populations are patchy and inputs from tributaries provide conditions that apparently dampen any potential filtering impacts of mussels in the nearshore compared to the offshore, especially during the spring.

Keywords: Great Lakes, tributary, coastal zone, dreissenids, thermal bar, nutrient loading

Introduction

In large lakes, such as the Lake Michigan, there is a nearshore region that separates the shoreline and the offshore pelagic zones of the lake. This nearshore region is not only the most visible region of the lake to humans, it is an economically and ecologically important region that provides water for drinking and industrial uses, recreational boating, fishing, swimming, and as well as habitat for wildlife, including fish spawning and nursery areas (Gregor and Rast, 1979; Kenaga et al., 1984). Despite the sensitivity and importance of this region, considerably less work has been done to describe and understand the conditions in the nearshore zone relative to the offshore pelagic regions, even though it has long been understood that hydrodynamic processes and proximity to tributary sources result in different water quality conditions in the nearshore than in the offshore (Schelske et al., 1980). In fact, a recent report indicated that information about the food web in the nearshore region is the biggest knowledge gap for understanding how changes in the lower trophic levels influence fish production in Lake Michigan (Bunnell et al., 2018).

The pelagic offshore region of Lake Michigan underwent a period of rapid change in the 2000s that included the nearly complete loss of the late winter and spring diatom blooms (Fahnenstiel et al., 2010; Kerfoot et al., 2010), declines in spring total phosphorus (Mida et al., 2010), increases in spring Secchi depths (Pothoven and Fahnenstiel, 2014a), lower chlorophyll yield per unit TP and increased P deficiency in phytoplankton (Pothoven and Fahnenstiel, 2014a). These changes were largely attributed to the invasion and rapid expansion of filter feeding quagga mussels (*Dreissena rostriformis bugensis*) that were found across a wider range of depths than the invasive zebra mussels (*Dreissena polymorpha*) which had been present in the lake since the late 1980s (Evans et al., 2011; Fahnenstiel et al., 2010; Vanderploeg et al., 2010). Quagga mussels appear to impact phytoplankton in the offshore region directly during the isothermal period as well as indirectly, with abundant mussels in the nearshore coastal and mid-depth zones disrupting the transfer of nutrients into offshore regions (Bootsma and Liao, 2014; Hecky et al., 2004; Kerfoot et al., 2010; Vanderploeg et al., 2010).

The sequestration of phosphorus by mussels in nearshore areas has been termed the "nearshore shunt" (Hecky et al., 2004) and is most prevalent in rocky and protected regions of Lake Michigan, where mussels are abundant because of stable substrate for attachment and colonization (Vanderploeg et al., 2010). This disruption of nutrient pathways by mussels favors production of nuisance and benthic algae in nearshore regions at the expense of pelagic production in both nearshore and offshore regions (Bootsma and Liao, 2014; Hecky et al., 2004). However, in coastal areas that are sandy and experience high wave-action during storms, such as southeastern Lake Michigan, direct filtration impacts by mussels are thought to be low because mussels are patchy and do not effectively colonize these nearshore areas (Vanderploeg et al. 2010; Nalepa et al., 2010). In turn, mussels are more abundant in mid-depth zones (30-70 m), where Vanderploeg et al. (2010) showed that the fraction of the water column cleared by mussels during the isothermal period was greater than in any other depth zone, and was as high as or higher than growth rate of the phytoplankton. Vanderploeg et al. (2010) further posited that in this region termed 'mid-depth sink,' particles and their associated nutrients are captured and a portion is likely sequestered thereby affecting both C and P in "downstream" deeper areas.

However, there are some indications in Lake Michigan on a lake-wide basis that suggest that the same trends in water quality parameters that have been observed in the offshore are occurring in the nearshore as well (Yurista et al., 2015). For example, lake-wide work based on remote sensing indicated that pelagic chlorophyll concentrations had become indistinguishable on an annual basis between the nearshore and offshore of Lake Michigan during 2010-2013

(Fahnenstiel et al., 2016). However, there can be uncertainties with nearshore estimates of water quality from remote sensing in shallow areas of the lake due to issues such as bottom reflectance and sediment resuspension (Yousef et al., 2017). Yurista et al. (2015) also found that pelagic chlorophyll concentrations on a lake-wide basis did not differ significantly between the nearshore and offshore during late summer in 2010 although total phosphorus concentrations remained higher in the nearshore region.

Although there is excellent information for the offshore of Lake Michigan that documents the dramatic seasonal changes in the lower food web since the arrival of dreissenid mussels, similar information is sparse for the nearshore areas. Modelling results indicate that mussels will not have as strong an impact in the nearshore where tributary nutrient loads help maintain higher productivity even in the presence of mussels (Rowe et al., 2017), so we expected that the nearshore would remain an important source of productivity, i.e., higher TP and chlorophyll *a* concentrations, particularly during the spring. Therefore, the goals of this study were to: 1) compare Secchi depth, chlorophyll *a*, total phosphorus, and nutrient status of phytoplankton between the nearshore and offshore during 2014-2018, 2) describe the seasonal patterns of these variables in the nearshore of southeastern Lake Michigan during 2014-2018, and 3) evaluate long term trends in Secchi depth, chlorophyll *a* and total phosphorus in the nearshore region. Southeastern Lake Michigan is of particular interest because of its high nutrient loading (Mida et al., 2010) and observations made during earlier times allow us to examine some temporal patterns.

Methods

Sampling took place in southeastern Lake Michigan between Grand Haven and Muskegon, Michigan at five nearshore stations (11 to 17 m deep) (Fig. 1). Station E (13-m deep) was located near the mouth of the Grand River which terminates directly into Lake Michigan, and Station C (16-m deep) was located off the mouth of the navigation channel connecting Lake Michigan to the drowned river mouth, Muskegon Lake. Stations GH15 (15-m deep), D (11-m deep), and M15 (17-m deep) were located between the other two nearshore sites, with Station D located near the mouth of the minor tributary Little Black Creek and the small drowned river mouth, Mona Lake (Fig. 1).

The sampling region had two major tributaries, the Grand River and Muskegon River. The Grand River has a drainage area of about 14,395 km^2 and contributes on average 518 metric tonnes of phosphorus to Lake Michigan annually, whereas the Muskegon River has a drainage area of 7,092 km^2 and contributes 72 metric tonnes of phosphorus to the lake each year (Dolan and Chapra, 2012). The watersheds of both rivers are primarily agricultural and forested, with more agriculture on the Grand River. In Lake Michigan, currents in the nearshore of this region generally flow alongshore in a counterclockwise direction (Beletsky and Schwab, 2008), i.e. northward, but current directions (and upwelling and downwelling) can be influenced by episodic wind events (Nekouee, 2010). Upwelling events bring in subsurface water from offshore into the nearshore zone and downwelling events bring surface waters from offshore into the nearshore zone. The substrate in the region is predominantly fine to medium sized sand (Chambers and Eadie, 1980; Marko et al., 2013).

Stations C, D, and E were sampled during May, June, July, August, September, and November 1996. All five nearshore stations were sampled once/month in March/April through November/December during 2014-2018. M15 is part of a NOAA long term research project in the area, and was sampled more frequently than other nearshore stations, with sampling taking place 1-2 times each month in March/April through November/December in 1999-2003 (excluding 2001) and 2007-2018.

Samples were also collected at two offshore sites (Fig. 1), M110 (113-m deep) and GH100 (100-m deep). M110 is also part of a NOAA long term research project in the area, and was sampled 1-2 times each month in March/April through November/December during 2014-2018, whereas sampling took place infrequently at GH100 during 1-2 months in 2014-2016. Data from 2014-2018 for the offshore sites were compared to data collected at the same sites in 1983-1999.

During each sampling event, discrete samples of water were taken from one depth in the water column (generally 5-m deep) with a modified Niskin bottle (Fahnenstiel et al., 2002) and poured into an acid-cleaned polycarbonate carboy, which was held in a cooler in the dark until returning to the laboratory and from which all water samples were taken. Although the water column was generally mixed at the sampling depth, it is possible that sampling only in the upper part of the water column missed some vertical dynamics, including mussel depletion of near bottom seston or impacts of resuspension events. Secchi depth transparency was measured with a black/white or white 25-cm diameter disk. Water temperature and specific conductance were recorded using a Seabird SBE19 or SBE19plus CTD (Conductivity-Temperature-Depth) profiler.

For all years and stations, chlorophyll *a* and total phosphorus concentrations were determined. Water for chlorophyll *a* analysis was filtered under low vacuum onto Whatman GF/F filters (0.7 μm), extracted with N, N-dimethylformamide under low light (Speziale et al., 1984) and analyzed fluorometrically. Chlorophyll *a* data was not available for 2003 from M15. Total phosphorus (TP) samples were digested in an autoclave with 5% potassium persulfate solution and measured using standard automatic colorimetric procedures on an auto-analyzer (Laird et al., 1987).

For 2007-2018 at M15 and 2014-2018 at all stations, particulate phosphorus (PP), particulate carbon (C) and particulate nitrogen (N) were also determined. Particulate phosphorus samples were filtered onto 0.4 µm Nucleopore filters, and these filters were digested and analyzed with the same procedures used for TP. Particulate carbon (C) and nitrogen (N) samples (not screened) were filtered onto pre-combusted Whatman GF/F filters (0.7 µm) and these filters were analyzed on a Model 1110 CHN analyzer (Millie et al., 2003). For all analyses, standard protocols were followed and appropriate blanks and standards were analyzed to ensure accurate results.

To provide information on nutrient deficiency, the C:N, N:P, and C:P ratios (µmol: µmol) as well as the C:Chl *a* ratio (µmol: µg) were determined (Hecky et al., 1993). Although nutrient ratios can be influenced by various factors, including physiological status, phytoplankton composition, nutrient status, contributions of non-algal material, and photo-acclimation (Healey and Hendzel, 1979; North et al., 2012), ratios of particulate nutrients are considered the simplest way to determine nutrient status of phytoplankton (Hecky et al., 1993) and have been used previously in the Great Lakes (Guildford et al., 2005; North et al., 2012). Values for each ratio were compared to thresholds for no, moderate, and severe nutrient deficiency (see Hecky et al., 1993) defined by growing various algal species under differing nutrient conditions (Healey and Hendzel, 1979).

To evaluate seasonal patterns for the nearshore sites, data from each site during 2014-2018 were combined across years. A Kruskal-Wallis test (KW) was used to test for overall differences among months for each variable, using each observation from each month/site for the parameter of interest as the response variable. When multiple values were available for a month for a given site, the values were averaged to provide a single value for that month.

To evaluate trends over time in the nearshore, two different data sets were used. First, temporal trends in Secchi depth, chlorophyll *a*, and TP were examined over the 1999-2018 period using the data collected at M-15. To examine trends over time, the Seasonal Kendall (SK) test (Helsel et al., 2006) was used. The Seasonal Kendall test (SK) is a modification of the Mann-Kendall (MK) test where MK statistics are estimated for individual seasons (12 periods/year in this study) over the sampling record, and these are summed to give statistics for the overall trend. The SK test and a modification to correct for autocorrelation were specifically developed to determine trends in surface water quality data (see Helsel et al., 2006). For the SK test, year was input as decimal year and divided into 12 equally spaced seasons (i.e., itype =1, see Helsel et al., 2006). The tests were performed using Kendall.exe, which is available at *http://pubs.usgs.gov/sir/2005/5275/downloads/.* A *P*-value <0.05 was considered significant for all tests.

Second, data collected at Stations C, D, and E during 1996 and 2014-2018 were used to examine temporal trends in the region for Secchi depth, chlorophyll *a*, and TP. For this analysis, 95% confidence intervals for monthly values from 2014-2018 were examined relative to values in 1996 for each specific site. The data from 2014-2018 was considered different from 1996 if confidence intervals did not overlap the 1996 values. Schelske et al. (1980) sampled at sites located 0.8 km from shore at Muskegon and Grand Haven in 1972. These sites were very near our Stations C and E, so data from these 1972 sites were also included in the long term analysis. ANCOVA was used to evaluate the relationship between log chlorophyll *a* and log TP (based on all data from Stations C, D, E combined) between 1996 and 2014-2018.

To compare nearshore conditions to the offshore, all data from the nearshore and offshore were used to determine monthly mean values for each parameter for each respective depth zone for each year (2014-2018). Paired t-test were used to compare conditions for each month between the nearshore and offshore. ANCOVA was used to evaluate the relationship between log chlorophyll *a* and log TP between the nearshore and offshore during 2014-2018 after restricting data to a similar range of TP values.

Results

Nearshore – offshore comparison

During 2014-2018, Secchi depth, chlorophyll *a*, and TP differed between the nearshore and offshore during some months (paired t-tests, $P< 0.05$), with the most consistent differences found in April-June and October (Fig. 2). In all cases, Secchi depth was higher and chlorophyll *a* and TP concentrations lower in the offshore than in the nearshore. Water temperature (at 5-m depth) was higher during April-May in the nearshore, and specific conductance was higher in the nearshore during April-June (Fig. 2).

The indicators for P-deficiency, C:P and N:P, differed between the nearshore and offshore, with the most consistent differences found in April-May, when P limitations appeared more severe in the offshore than in the nearshore (Fig. 3). The C:Chl *a* ratio, which can be an indicator of general nutrient deficiency, also suggested more severe nutrient limitations in the offshore in the late spring/early summer (Fig. 3). There was little indication of nitrogen deficiency (C:N ratio) in either region (Fig. 3).

Nearshore seasonal patterns

Across all sites during 2014-2018, Secchi depth varied across months (KW test=53.1, df=9, $P<0.001$), with the lowest median value occurring in May (3.5 m) and higher values occurring in the fall, especially September (8.8 m; see Fig. 2). Chlorophyll *a* concentrations differed among months (KW test = 56.4, df=9, P<0.001), with the highest overall median concentration found during May (6.3 µg/L) and values ≤ 4.3 µg/L for all other months. Similarly, TP concentrations also differed among months (KW=48.7, df=9, P<0.001), with the highest median concentration again occurring in May (10 µg/L), compared to ≤ 7.2 µg/L for all other months.

All nutrient ratios indicated monthly differences (KW >23, df=9, P<0.006). Both indicators for phosphorus deficiency had levels that indicated moderate to severe deficiency, i.e., C:P ratios were generally indicative of moderate phosphorus deficiency for all months, whereas N:P ratios were generally indicative of severe phosphorus deficiency for most months (see Fig. 3). The C:N ratios for all months did not indicate nitrogen deficiency during any month. The C:Chl *a* ratio was consistently in the range of moderate to severe deficiency, with the highest values found in late summer months and the lowest values in May and November.

Long-term trends

At the M15 site during the 1999-2018 period, there was a significant decrease in TP concentrations (SK test; S= -205, P=0.04), an increase in Secchi depth (SK test; S= 132, P=0.04), and no change in chlorophyll *a* concentrations (SK test; S= 57, P=0.34; Fig. 4).

Overall, trends in nearshore Secchi depth, chlorophyll *a*, and TP between 1996 and 2014-2018 depended on site, with the strongest changes noted at Station E, especially in spring and summer, a few changes noted at Station C, and almost no changes noted at Station D. Secchi depths were generally higher in 2014-2018 than in 1996 at Station E during spring and summer, but at Stations C and D, there were few differences between time periods (Fig. 5). Chlorophyll *a* concentrations did not differ much between 1996 and 2014-2018 at Station D or at Station C. By contrast, chlorophyll *a* concentrations at Station E were much lower in 2014-2018 compared to 1996 for May, June and August, but were similar between periods for September and November (Fig. 5). TP differed little between time periods at Station D, but for both Station C and E, TP concentrations were higher during 1996 than 2014-2018 in May-August, but were similar between time periods in September and November (Fig. 5). At the offshore site, Secchi depth was higher and chlorophyll *a* and TP were lower in 2014-2018 compared to the 1980s and 1990s, especially during the spring, i.e., April-June (Fig. 5).

Chlorophyll a *: TP ratios*

Across nearshore sites (i.e., Stations C, D, and E), the chlorophyll *a* : TP ratio did not differ between 1996 and 2014-2018 (ANCOVA, $F_{1,147} = 0.73$, P=0.40; Fig. 6A). However, the chlorophyll *a* : TP ratio differed significantly between the nearshore and offshore in 2014-2018 (ANCOVA, $F_{1,172} = 0.20.8$, P<0.001), with a higher yield of chlorophyll *a*/unit TP in the nearshore (Fig. 6B). Mean log chlorophyll *a* (adjusted for log TP) was 0.31 and 0.11 µg/L in the nearshore and offshore, respectively (from ANCOVA).

Discussion

During the early 2000s, the offshore of Lake Michigan underwent dramatic changes in water quality, with declines in TP and chlorophyll *a* most evident during the spring (Fahnenstiel et al., 2010). In 2014-2018, in our study, although there were substantial declines in chlorophyll *a* and TP over time at some sites in the nearshore region of southeastern Lake Michigan, these changes were not consistent across sites. In turn, water quality variables in the nearshore of southeast Lake Michigan were still overall characterized by consistent seasonal patterns, most notably, Secchi depths were lowest and chlorophyll *a* and TP concentrations were highest in the spring, especially during May.

A number of factors likely contributed to chlorophyll *a* and TP remaining elevated in the spring in the nearshore region of the study area. Seasonal tributary inputs and to a lesser degree, resuspension events increase TP concentration and stimulate primary productivity in nearshore regions (Johengen et al., 2008; Rowe et al. 2017; Vanderploeg et al., 2007). Resuspension has a smaller impact compared to tributary loading because soluble P is a smaller fraction of TP in resuspension events and because of the negative impacts of resuspension on water clarity (Vanderploeg et al., 2007). Spring is the period of high tributary flow (see Fig. 7) which can lead to elevated nutrient levels (Chambers and Eadie, 1980; Schelske et al., 1980). The higher specific conductivity in the nearshore than the offshore in the spring reflects the relatively higher tributary influence on the nearshore at this time of year in our study region. Furthermore, during the spring, the nearshore warms faster than the offshore (see Fig. 2) and the thermal bar traps nutrients in the region leading to heightened productivity, including the development of the spring diatom bloom (Moll and Brahce, 1986). In the summer, TP and chlorophyll *a* concentrations in the nearshore decline as tributary flow is reduced, photosynthetic rates increase, and nutrients from tributaries are dispersed as the thermal bar moves offshore (Moll and Brahce, 1986).

High spring phytoplankton biomass, as inferred from chlorophyll *a* concentrations, could be important for fish production in the nearshore region. High food availability in the spring can allow zooplankton abundance to increase rapidly (Luecke et al., 1990), which in turn, provides a critical food source for fish. For example, abundance and survival of age-0 yellow perch (*Perca flavescens*) in Lake Michigan has been linked to June zooplankton density (Dettmers et al., 2003; Redman et al., 2011). Increased zooplankton prey availability in the spring has also been linked to lower overwinter energy losses for juvenile alewife in Lake Michigan (Pothoven and Fahnenstiel, 2014b).

Although there were long-term declines in spring chlorophyll *a* concentrations at some sites, the spring remained the season with the highest chlorophyll *a* concentrations in the nearshore. Elevated chlorophyll *a* concentrations in the spring in the nearshore contrast with conditions at deeper offshore sites in the same region. Overall, median chlorophyll *a* and TP concentrations were over 9 and 3 times higher respectively, in the nearshore than in the offshore in May, whereas Secchi depth was 5 times higher in the offshore (see Fig. 2). During the 1980s and 1990s, chlorophyll *a* concentrations in the offshore also peaked during May (approximately 2.5-3 µg/L) during the spring bloom period, but following the expansion of dreissenid mussels, the spring bloom was largely eliminated in the offshore of Lake Michigan (see Fig. 5; Fahnenstiel et al., 2010; Pothoven and Fahnenstiel, 2014a), consistent with high mussel filtering impacts in mid-depth zones of southeastern Lake Michigan (Rowe et al. 2015; Vanderploeg et al., 2010). In turn, seasonal patterns shifted so that peak chlorophyll *a* concentrations in the surface mixed layer in the offshore occurred in the fall, when chlorophyll *a* concentrations changed little over time (see Figs. 2 and 5; Fahnenstiel et al., 2010). During the late summer however, TP and chlorophyll *a* concentrations were similar between the nearshore and offshore. This is consistent with lake-wide late summer data that found that chlorophyll *a* concentrations were more similar between the nearshore (< 30 m) and offshore regions in 2010 than they had been in the late 1970s, although TP concentrations remained higher in the nearshore (Yurista et al., 2015). Fahnenstiel et al. (2016) found no difference in nearshore (< 30 m) mean annual chlorophyll *a* concentrations between the nearshore and offshore based on lake-wide remote sensing data. Similarly, in Lake Ontario, TP concentrations were more similar between the nearshore and offshore after the dreissenid mussel invasion than in prior decades (Hall et al., 2003).

Indicators of P deficiency did not demonstrate a strong seasonal pattern in the nearshore, where P-deficiency was generally moderate (C:P) or severe (N:P). However, during the spring, P-deficiency was consistently more severe in the offshore than in the nearshore. These indicators could have been biased low, because filter size for C and N was 0.7 µm, compared to filter size for PP, which was 0.4 µm, although limited comparisons suggest that this was not an issue. The C: Chl ratio, which can indicate either P or N deficiency, also indicated more severe nutrient deficiency in the offshore than the nearshore in the spring. The C: Chl ratio can also reflect changes in phytoplankton light acclimation (North et al., 2012; Guildford et al., 2013), so it is not necessarily as useful an indicator as other indicators (Healey and Hendzel, 1979). Secchi depths were highest in the spring in the offshore and lowest in the spring in the nearshore, so it seems reasonable that photo-acclimation of chlorophyll affected C: Chl ratios in each area differently. Higher water clarity in the offshore does not necessarily mean that phytoplankton in the offshore experienced higher light exposure because the photic depth to mixing depth ratio under isothermal conditions could be lower offshore simply because of greater water depth (e.g., Vanderploeg et al., 2007). However, considering that trends in nutrient status based on C: Chl ratios were consistent with the C:P and N:P ratios at least during the spring, high C: Chl ratios also support the idea of higher P-deficiency in the offshore than the nearshore during that period.

The long term trends in chlorophyll *a* and TP in the nearshore depended on site as well as season. Although chlorophyll *a* and TP in the nearshore of our study region have not decreased to the same low levels found in the offshore, there have been changes in water quality, including during the spring, at some sites. Both chlorophyll *a* and TP declined dramatically between 1996 and 2014-2018 during May-August at the site located off the Grand River (Station E), whereas only TP consistently declined over the same period at the site located off the Muskegon channel outflow (Station C), and no changes were noted at a site located in between the other two (Station D). Furthermore, little change in either chlorophyll *a* or TP was noted between time periods during late summer or fall at any of these sites. Similarly, Yurista et al. (2015) found that on a lake-wide basis, chlorophyll *a* and TP concentrations during late summer had remained relatively stable between 1994/95 and 2010 following declines between the 1970s and 1994/95.

Tributary loading has a significant influence on nearshore nutrient and phytoplankton conditions (Johengen et al., 2008; Moll and Brahce, 1986; Rowe et al., 2017; Schelske et al., 1980). Because the changes in TP and chlorophyll *a* concentrations between 1996 and 2014-2018 were most evident at the two sites near tributary outflows, especially the site off the Grand River, it seems reasonable that a change in tributary loading could have led to these declines. However, based on the most recent available data from Dolan et al. (2012), despite high year to year variability, P loading estimates for both the Grand River (Mann-Kendall test, S=-9, P=0.69) and Muskegon River (Mann-Kendall test, S=13, P=0.55) did not trend either positively or negatively between 1994 and 2008. Also, there was no evidence that river flow was any higher in 1996 than in 2014-2018 for either the Grand or Muskegon rivers (see Fig. 7). So, decreases in loading or discharge do not appear to explain the decline in TP and/or chlorophyll *a* concentrations at Stations C and E between 1996 and 2014-2018.

At nearshore sites, the water column is generally well mixed and benthic dreissenid mussels have nearly year round access to phytoplankton (Rowe et al., 2015; Vanderploeg et al. 2010), so their impact is expected to be even more pronounced than in the offshore, where the direct impact of mussel filtering is limited to the isothermal period. On the other hand, even though quagga mussels don't need hard substrate to colonize a region, mussel populations in sandy nearshore regions are thought to be limited by unstable substrate, wave resuspension, thermal instability, and fish predation (Glyshaw et al., 2015; Nalepa et al. 2010; Vanderploeg et al., 2010). Although there is limited information on dreissenids in nearshore regions, especially from areas < 16 m deep, we do know that zebra mussels were present in our sampling region (16-30 m depth zone) by 1992, but densities remained low (<1000/m^2) through 2000 (Nalepa et al., 1998, 2006), and soon thereafter quagga mussels replaced zebra mussels. At a 25-m site located about 3 km from the M15 site, quagga mussel densities rose quickly between 2004-2008 and 2010, when average annual density was around 25,000/m^2, although mussels at this site were extremely patchy (Glyshaw et al., 2015). By 2013 mussel densities had declined at the 25-m site to around 8811/m^2 (SE=3589), similar to average densities at a 45-m site located between M15 and M110 (Glyshaw et al., 2015). During 2014-2018, mussel densities based on 2-3 collections annually at the 25-m site averaged 7664/m^2 (SD=3637), ranging from 1883/m^2 (SD=1891) in 2016 to 11,300/m^2 (SD=9595) in 2014 (S. Pothoven, unpublished data). Therefore, it appears that mussels are potentially an important factor in nearshore water quality dynamics, although it is unclear if a highly patchy population of mussels could have as strong effect on local water quality conditions as the populations that are found further offshore. Clearly, a better understanding of mussel population abundance, biomass and filtering capacity in shallow waters of Lake Michigan is needed, especially in areas near major tributaries.

Despite rising mussel densities in the nearshore during the late 2000s, there was evidence that direct impacts by mussels alone do not fully explain the declines in chlorophyll *a* and TP that were observed between 1996 and 2014-2018 at some of our sites. First, the relationship between chlorophyll *a* and TP did not change between 1996 and 2014-2018, whereas studies in nearshore regions of lakes Erie and Ontario demonstrated that there is a lower yield of chlorophyll *a* per unit TP following dreissenid invasions, because of mussel filtering that led to larger contributions of non-algal P to the TP pool (Hall et al., 2003; Nicholls et al., 2001; North et al., 2012). The chlorophyll *a* yield per unit TP also declined in the offshore of Lake Michigan following mussel expansion (Pothoven and Fahnenstiel, 2014a), and was much lower than in the nearshore in this study. Secondly, there was little change in TP or chlorophyll *a* at Station D between 1996 and 2014-2018, and at M15, where extensive sampling took place, TP concentrations only declined slightly and chlorophyll *a* concentrations did not change between 1999 and 2018. Our finding that direct impacts of dreissenid mussels do not fully explain the long-term changes noted for TP and chlorophyll *a* is consistent with modeling results from Rowe et al. (2017), which found that tributary loads could support higher chlorophyll *a* concentrations in the nearshore even in the presence of mussels. However, it is somewhat paradoxical and not clear why long term declines in TP and chlorophyll *a* were most notable at the sites that were closest to tributaries outflows.

Dreissenid mussels in the Great Lakes have been shown to have indirect impacts on offshore regions, whereby mussels in nearshore and mid-depth regions intercept nutrients before they reach the offshore regions (Hecky et al., 2004; Vanderploeg et al., 2010). It is possible that there are also indirect impacts of mussels in the nearshore region as a whole or in localized areas, such as tributary outflows, but these mechanisms have not been well studied. Some possibilities for future studies that could provide better insight into mussel dynamics and impacts in nearshore regions include: 1) an accurate assessment of mussel dynamics in nearshore regions, especially areas <16 m deep, 2) the impact of mussel filtering in nearshore areas and on alongshore nutrient transport within the nearshore, 3) the impact of mussel facilitation of benthic algae such as

Cladophora, which shunts nutrients into benthic algal pathways (Hecky et al., 2004), 4) the impact of mussel filtering along tributary outflows that are hardened with piers and breakwaters and provide substrate for dreissenid mussels that filter water immediately before discharge into the lake, 5) the impact of mussels in drowned river mouth lakes such as Muskegon Lake, which is considered a substantial sink for nutrients (Marko et al., 2013).

Although the reason that TP and chlorophyll *a* concentrations changed at sites near tributaries but not at other sites is somewhat unclear, the end result is that the range of these measures across the nearshore sites within any given month has decreased in our sampling region (see Fig. 5). For example, in May, the range of chlorophyll *a* concentrations among Stations C, D, and E was 5.2 to 21.6 µg/L in 1996 compared to 7.4 to 9.0 µg/L in 2014-2018. Similarly, the range of TP concentrations in May among these stations was 10 to 85 µg /L in 1996 compared to 9.7 to 12.7 µg/L in 2014-2018. Similarly, Yurista et al. (2015) reported that although the nearshore region was quite variable on a lake-wide basis, regional landscape processes result in much lower variability in water quality measures within more localized areas.

By contrast to the offshore, the nearshore region of southeastern Lake Michigan still has low Secchi depths and elevated chlorophyll *a* and TP in the spring, especially May, compared to other months. Although chlorophyll *a* and TP have declined substantially at some nearshore sites since the mid 1990s, it appears that high spring inputs from nearby tributaries combined with earlier warming than in the offshore that creates a thermal bar still provide for conditions that help mitigate any potential dreissenid impacts in the nearshore. However, even though yield of chlorophyll *a* per unit TP has not changed in the nearshore, there are indications of P-deficiency in the region, although P-deficiency is not as high as in the offshore during the spring. Furthermore, even though tributaries appear critical to maintaining the primary productivity of the nearshore in southeastern Lake Michigan, somewhat paradoxically, the sites located nearest to these tributaries experienced the largest changes in chlorophyll *a* and TP over time.

Although the nearshore region is a critical link between tributaries and the offshore, much less work has been done to understand the dynamics and ongoing changes that may be occurring in this area of Lake Michigan compared to the offshore. Therefore, it seems reasonable that greater attention be given to more fully understanding the dichotomy between tributary loading and mussel filtering on productivity dynamics in the nearshore region, including in areas without strong tributary influences or in rocky, sheltered areas where mussel impacts could be expected to be higher than in our study area.

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Figure Legends

Fig. 1. Map showing locations of five nearshore sampling stations and two offshore stations in southeastern Lake Michigan.

Fig. 2. Box plots of Secchi depth, chlorophyll *a* concentration, total phosphorus concentration, specific conductivity, and water temperature (at 5-m) for each month during 2014-2018 across five nearshore sites (open) and two offshore sites (shaded) in southeastern Lake Michigan. The horizontal line in the box represents the median. An asterisk above a month grouping represents a significant difference between the offshore and nearshore for that month (paired t test, $P<0.05$).

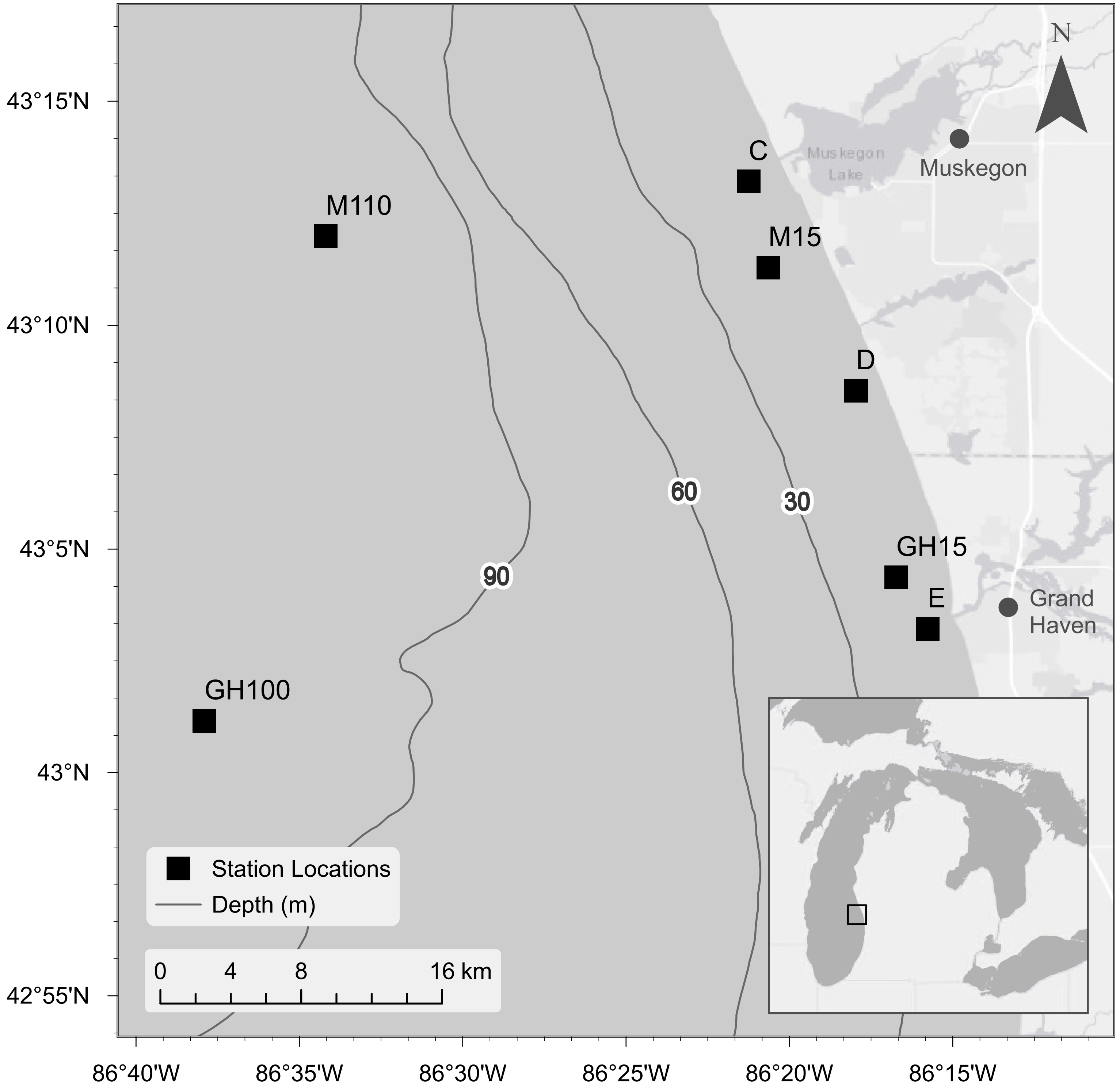
Fig. 3. Box plots of nutrient status ratios for each month during 2014-2018 across five nearshore sites (open) and two offshore sites (shaded) in southeastern Lake Michigan. The horizontal line in the box represents the median. The dashed horizontal lines denote no deficiency, moderate deficiency, and severe deficiency levels (Hecky et al., 1993). An asterisk above a month grouping represents a significant difference between the offshore and nearshore for that month (paired t test, $P<0.05$).

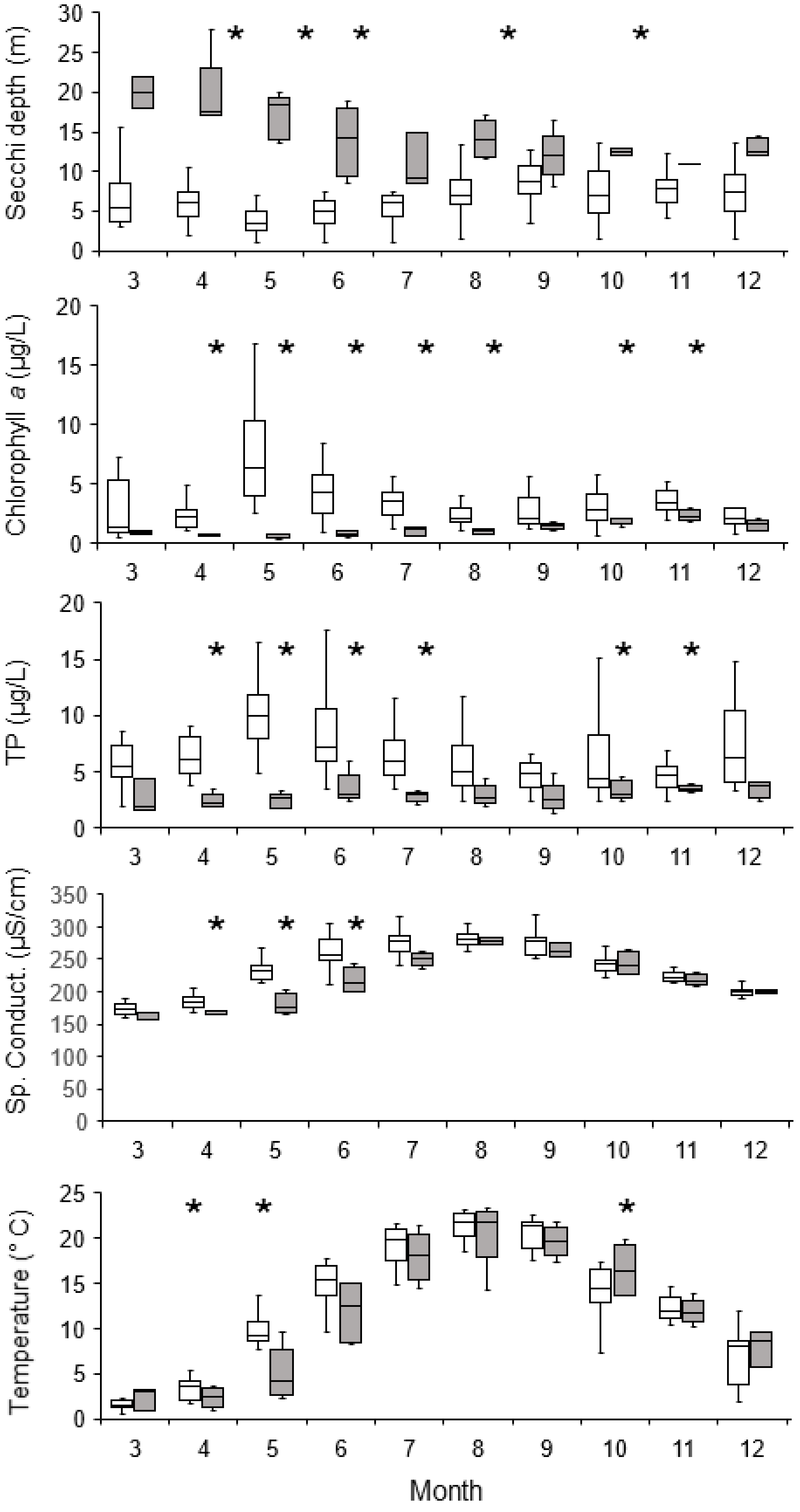
Fig. 4. Secchi depth, chlorophyll *a* concentration, and total phosphorus concentration during 1999-2018 at M15, a nearshore station located in southeastern Lake Michigan. Each point represents a sampling event. The dashed line represents the trends line from the Seasonal-Kendall test.

Fig. 5. Secchi depth (left column), chlorophyll *a* concentration (center column), and total phosphorus concentration (right column) at three nearshore sites in southeastern Lake Michigan during 2014-2018 (mean, 95% CI), 1996, and 1972 (from Schelske et al., 1980) and from the offshore (M110, GH100 combined) during 1983-1989, 1990-1999, and 2014-2018 (mean, 95% CI). Note different scales for the y-axis across sites.

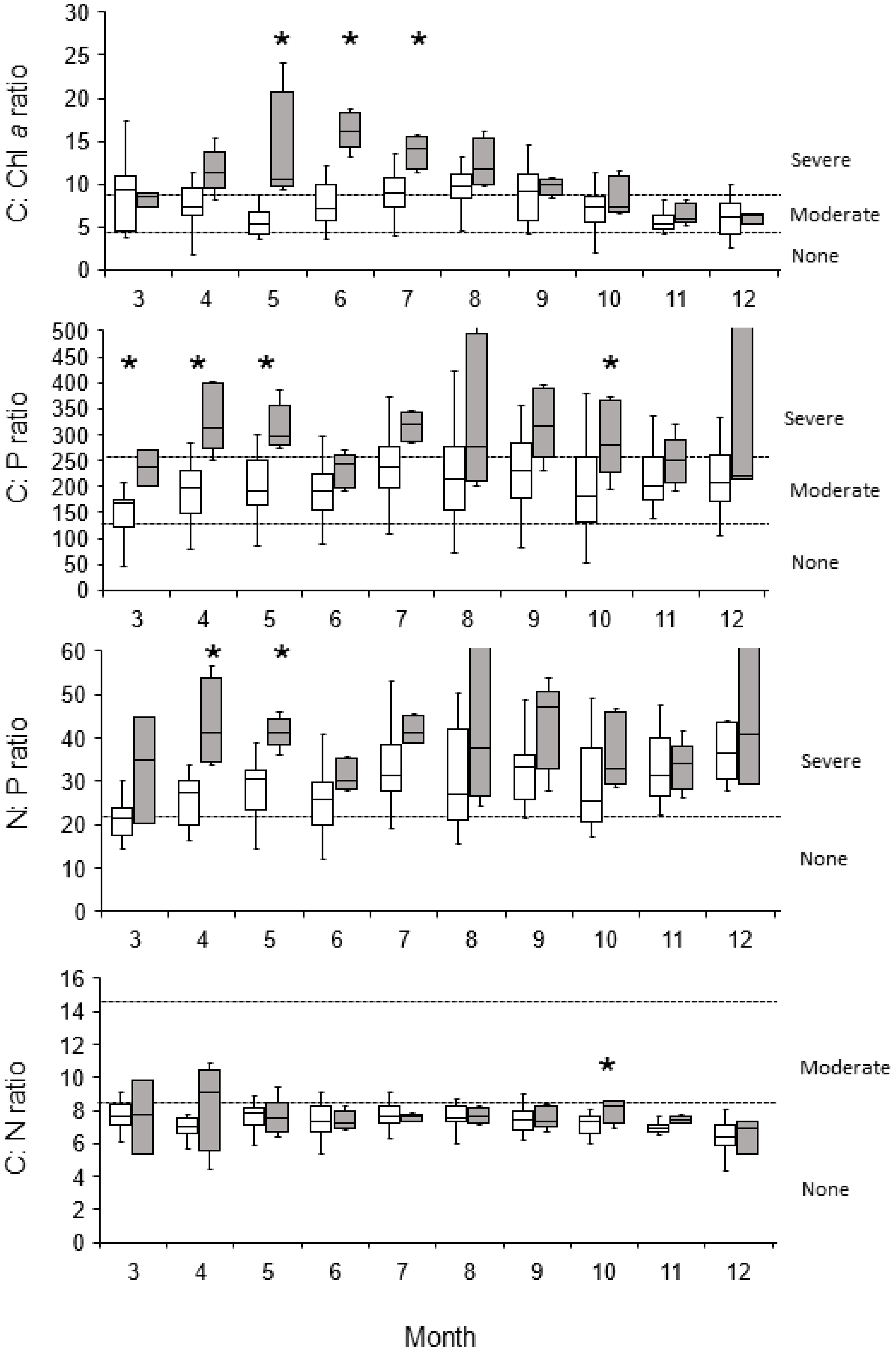
Fig. 6. Log chlorophyll *a* as a function of log TP in A) the nearshore during 1996 and 2014-2018, and B) the nearshore and offshore during 2014-2018. Data for the nearshore to offshore comparison was restricted to log TP ≤ 0.8 µg/L.

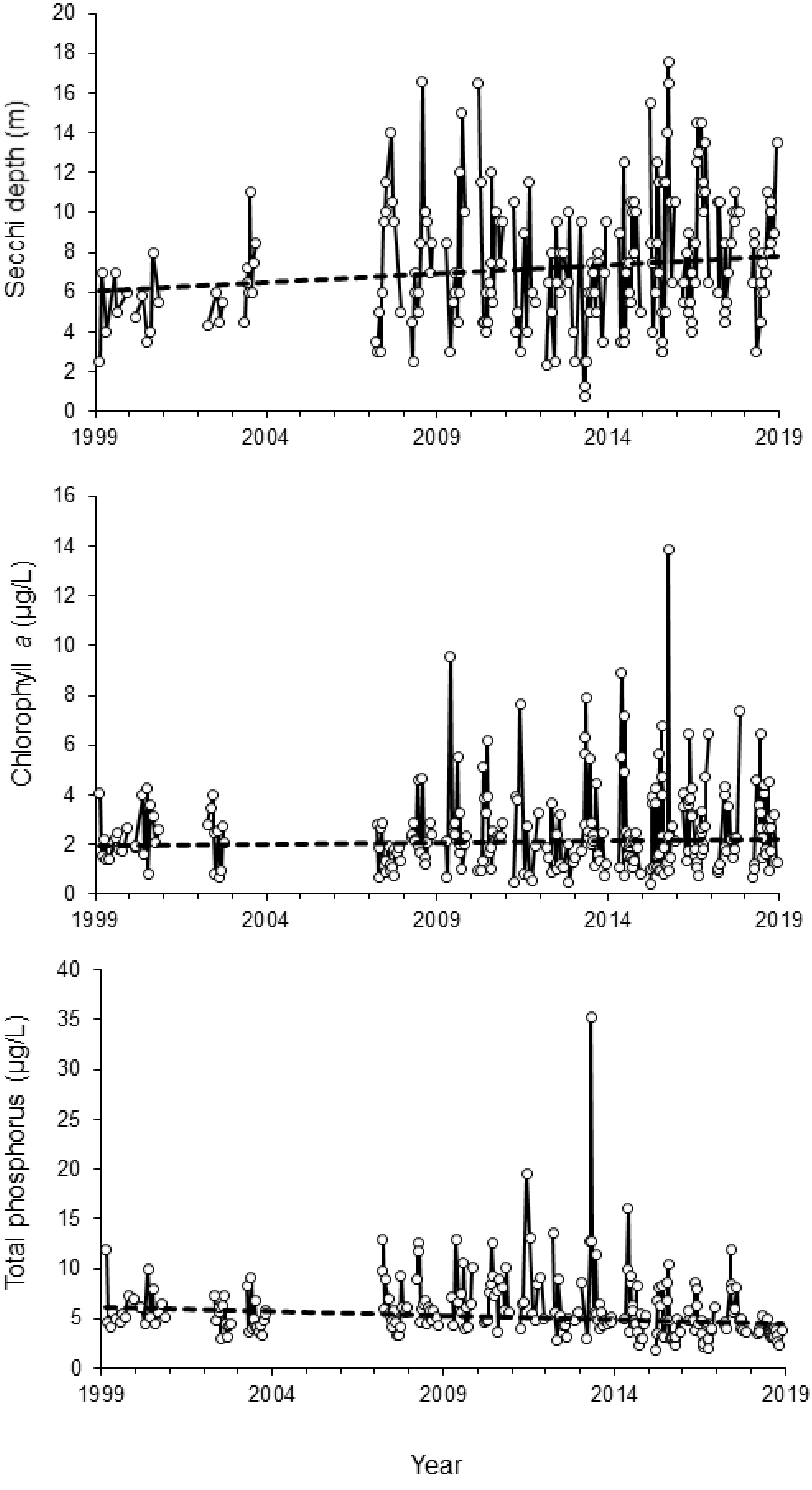
Fig. 7. Monthly river flow rate (mean, 95% CI) for the A) Grand River at Grand Rapids and B) Muskegon River at Croton Dam. Data retrieved from Grand Rapids gage USGS 04119000, data available at *https://waterdata.usgs.gov/nwis/uv?04119000*, and Croton Dam gage USGS 04121970, data available at *https://waterdata.usgs.gov/mi/nwis/uv?site_no=04121970*.

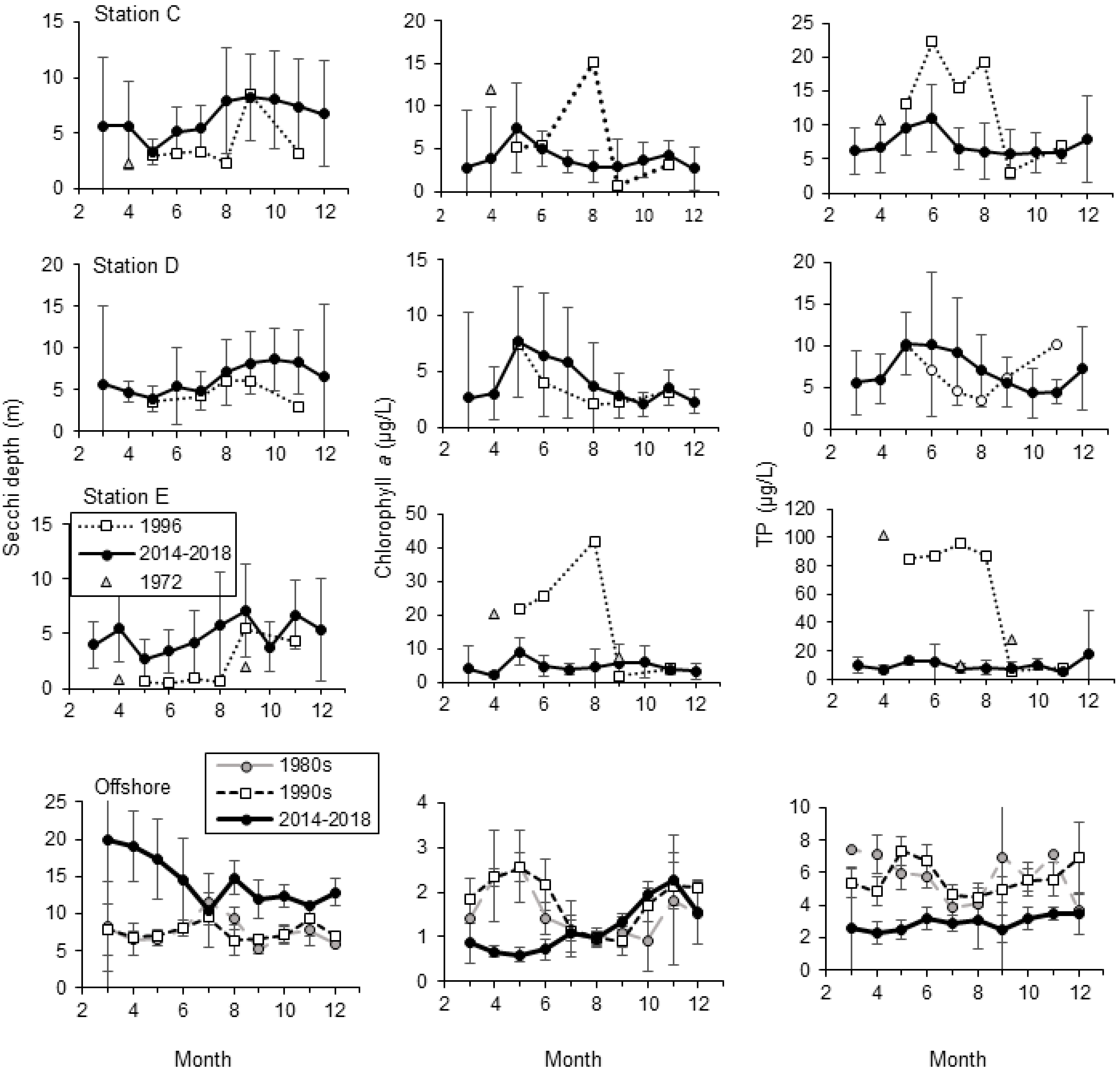

N
43°15'N
43°10'N
43°5'N
43°N
42°55'N
86°40'W
86°35'W
86°30'W
86°25'W
86°20'W
86°15'W
C
M110
M15
D
GH15
E
GH100
60
30
90
Muskegon Lake
Muskegon
Grand Haven
Station Locations
Depth (m)
0
4
8
16 km

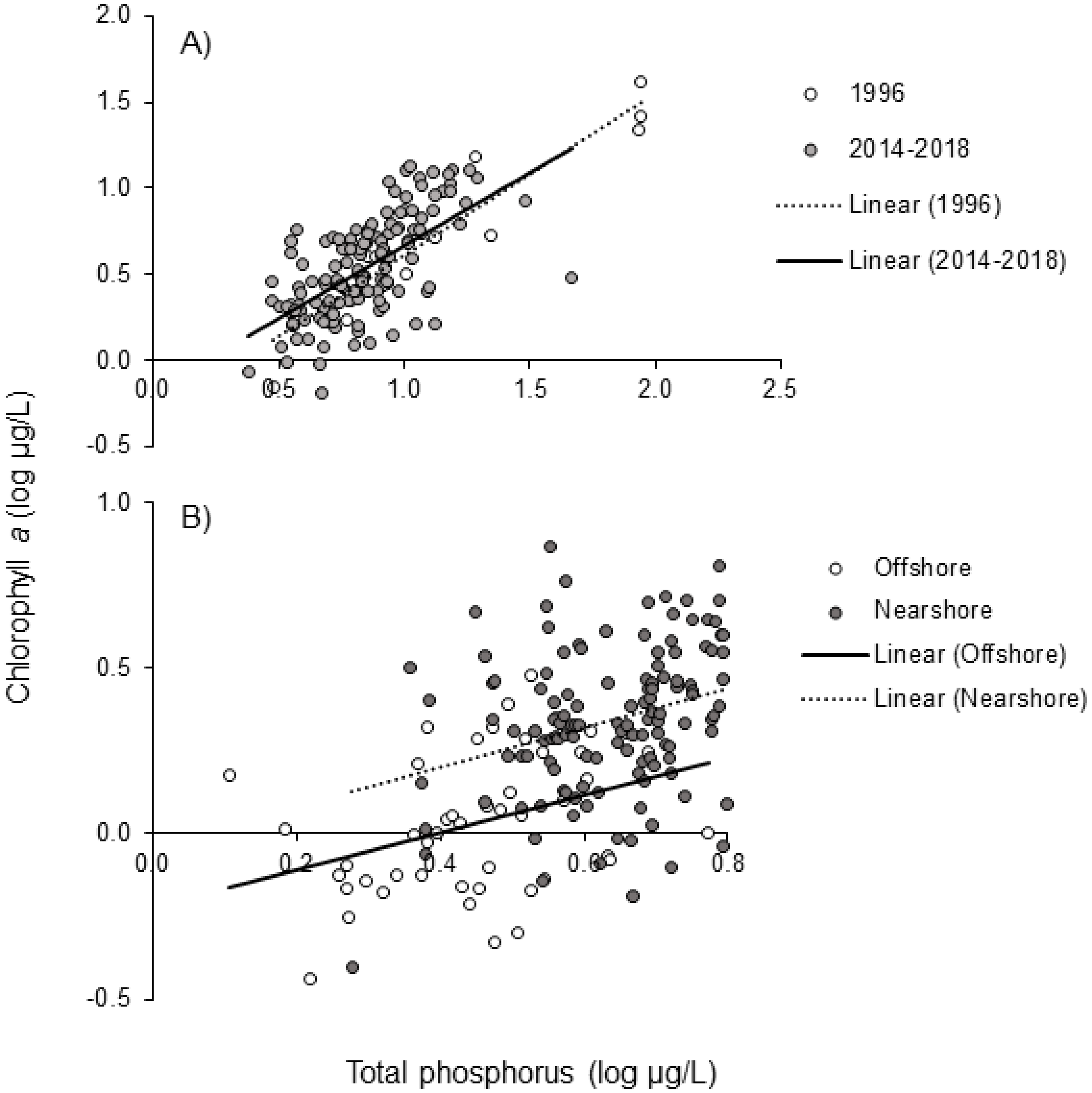


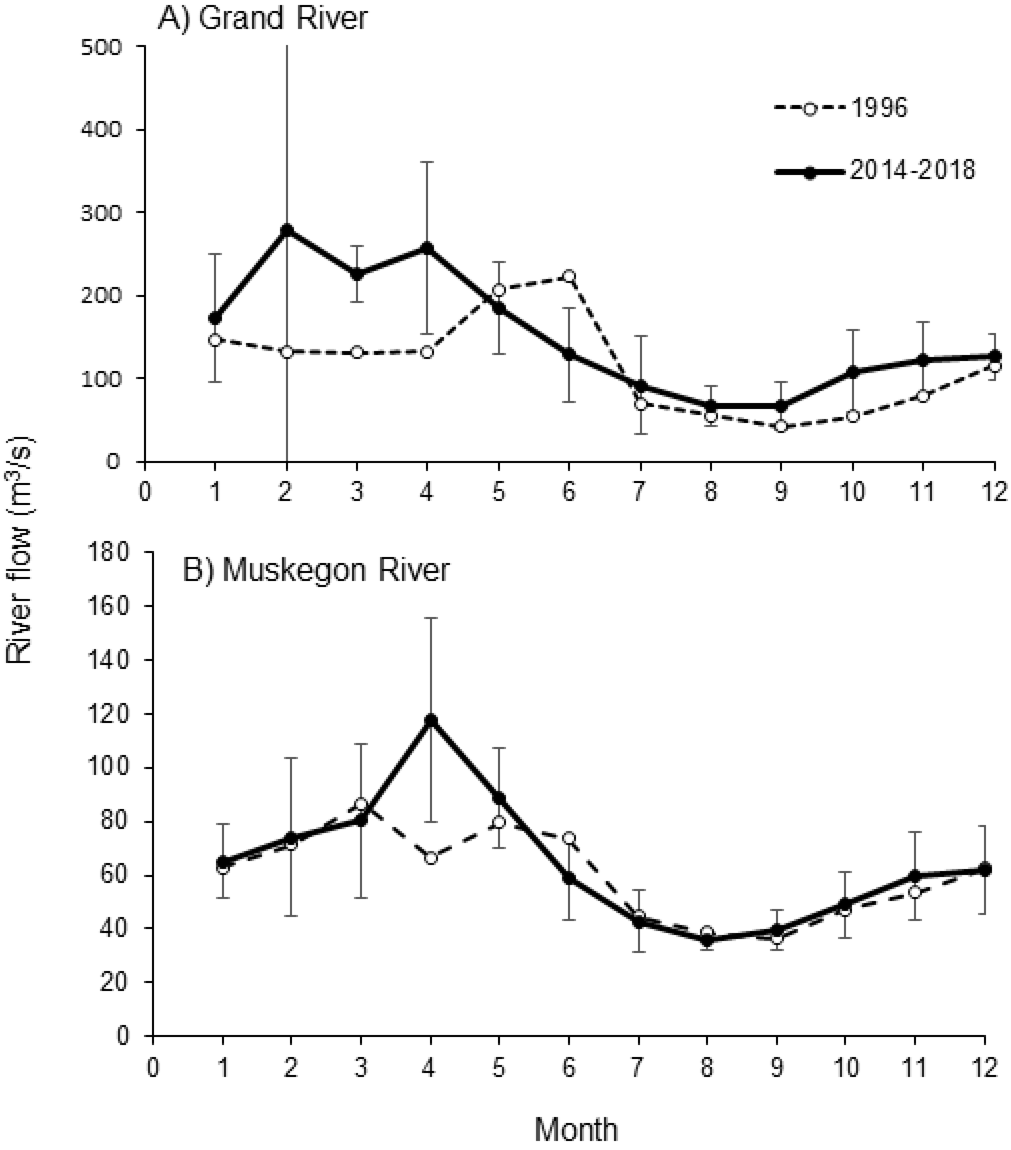
Secchi depth (m)
0
5
10
15
20
25
30
Chlorophyll *a* (µg/L)
0
5
10
15
20
TP (µg/L)
0
5
10
15
20
Sp. Conduct. (µS/cm)
0
50
100
150
200
250
300
350
Temperature (° C)
0
5
10
15
20
25
*
3
4
5
6
7
8
9
10
11
12
Month


C: Chl a ratio
30
25
20
15
10
5
0
*
*
*
Severe
Moderate
None
3
4
5
6
7
8
9
10
11
12
C: P ratio
500
450
400
350
300
250
200
150
100
50
0
*
*
*
*
Severe
Moderate
None
3
4
5
6
7
8
9
10
11
12
N: P ratio
60
50
40
30
20
10
0
*
*
Severe
None
3
4
5
6
7
8
9
10
11
12
C: N ratio
16
14
12
10
8
6
4
2
0
*
Moderate
None
3
4
5
6
7
8
9
10
11
12
Month


Secchi depth (m)
20
18
16
14
12
10
8
6
4
2
0
1999
2004
2009
2014
2019
Chlorophyll a (µg/L)
16
14
12
10
8
6
4
2
0
1999
2004
2009
2014
2019
Total phosphorus (µg/L)
40
35
30
25
20
15
10
5
0
1999
2004
2009
2014
2019
Year


Station C
Station D
Station E
Offshore
Secchi depth (m)
Chlorophyll a (µg/L)
TP (µg/L)
1996
2014-2018
1972
1980s
1990s
2014-2018
Month
Month
Month


A)
2.0
1.5
1.0
0.5
0.0
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
1996
2014-2018
Linear (1996)
Linear (2014-2018)
B)
1.0
0.5
0.0
-0.5
0.0
0.2
0.4
0.6
0.8
Offshore
Nearshore
Linear (Offshore)
Linear (Nearshore)
Chlorophyll a (log µg/L)
Total phosphorus (log µg/L)


A) Grand River
B) Muskegon River
1996
2014-2018
River flow (m3/s)
Month
500
400
300
200
100
0
180
160
140
120
100
80
60
40
20
0
0
1
2
3
4
5
6
7
8
9
10
11
12