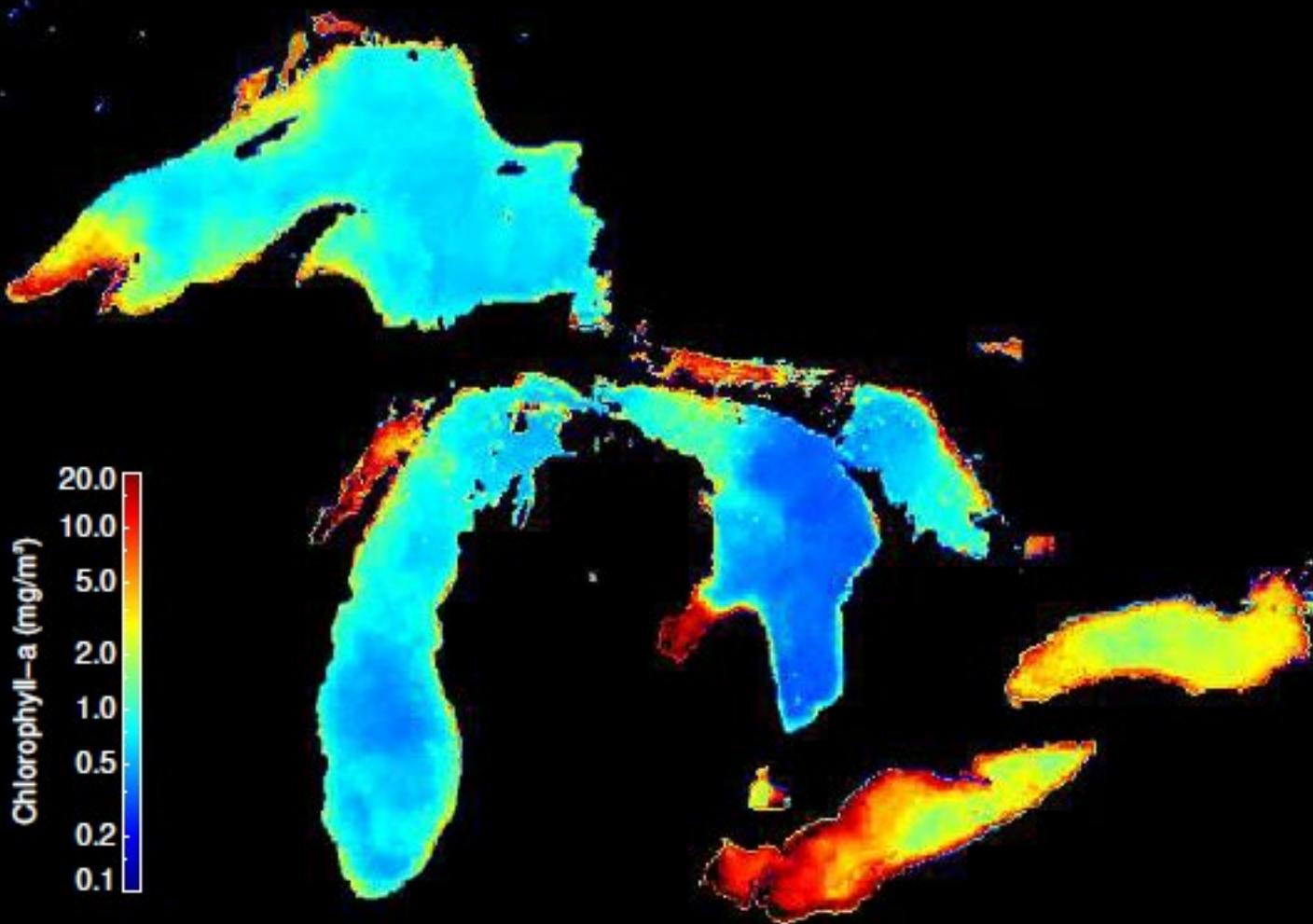


# STATUS OF THE LOWER FOOD WEB IN THE OFFSHORE WATERS OF THE LAURENTIAN GREAT LAKES

*Trends for chemical, physical, and biological variables through 2018*



March 2021  
EPA 905-R-20-007



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## ACKNOWLEDGMENTS

This work was supported under the Great Lakes Restoration Initiative by the U.S. Environmental Protection Agency (USEPA) Great Lakes National Program Office (GLNPO) as part of EPA Contract No. EP-C-15-012, Technical, Analytical, and Regulatory Mission Support for the Water Security Division, with CSRA, LLC, a General Dynamics Information Technology (GDIT) company, under the direction of Louis Blume, Project Manager as well as by agreements with Cornell University (Department of Natural Resources) under award agreement GL-00E01184 from the USEPA “Great Lakes Long Term Biological Monitoring of Zooplankton, Benthos, and Chlorophyll-*a*” and with Regents of the University of Minnesota from the USEPA under award agreements GL-00E23101-2 and GL-00E01980 “Great Lakes Biological Monitoring: Phytoplankton.” GLNPO gratefully acknowledges the support of the following team members in the preparation of this Technical Report:

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Cover Photo: *Satellite-estimated surface chlorophyll-*a* concentration in the Great Lakes – August 2018*

Citation: U.S. EPA 2021. Status of the Lower Food Web in the Offshore Waters of the Laurentian Great Lakes: Trends for chemical, physical, and biological variables through 2018. EPA 905-R-20-007.

## EXECUTIVE SUMMARY

This report presents data on selected chemical, physical, and biological variables that characterize the base of the Great Lakes ecosystem in offshore waters.

Lake Erie is currently the only Great Lake in which total phosphorus concentrations consistently (western and central basin) or intermittently (eastern basin) exceed interim substance objectives contained in the 2012 Great Lakes Water Quality Agreement (GLWQA). Summer cyanobacterial blooms are a consistent feature of the western basin, while summer/autumn chlorophyll-a has been notably higher in the central and eastern basins in the past 10 years. Abundant phytoplankton are likely contributing to late-summer hypoxia in the central basin. During summer, crustacean zooplankton biomass (volumetric) is also highest in Lake Erie, although there is considerable interannual variability; summer biomass is dominated by cladocerans and cyclopoid copepods. There has been no evidence of directional change in zooplankton or benthos communities in the past decade.

Recent total phosphorus concentrations, transparencies, and surface chlorophyll-a concentrations in Lake Ontario are characteristic of an oligotrophic system. Crustacean zooplankton communities have shifted away from species indicative of high planktivory (cyclopoids, bosminids, small daphnids, *Cercopagis*) and towards calanoid copepods, larger daphnids, and *Bythotrephes*. In addition, the amphipod *Diporeia*, absent from shallow Lake Ontario sites by 1997, had almost entirely disappeared from deep sites by 2011. Current benthos communities are dominated by *Dreissena*, which continues to increase in deep region of the lake, and oligochaetes.

The rapid shifts in the lower food web experienced by Lake Huron and, to a lesser extent, Lake Michigan, in the early to mid-2000s are moderating. The offshore lower food webs of both lakes are currently characterized by greatly increased transparency, low phytoplankton abundance, and lack of a pronounced spring chlorophyll-a maximum; summer crustacean zooplankton communities are dominated by calanoid copepods with relatively few cladocerans, and benthic communities are dominated by dreissenids, with residual populations of *Diporeia* found only in the deepest portions of the two lakes. Profundal populations of *Dreissena* are still increasing in Lake Huron but appear to have stabilized in Lake Michigan. In recent years, these lakes have exhibited ultra-oligotrophic conditions similar to those of Lake Superior. The loss of prey items favored by forage fish, such as *Daphnia* and *Diporeia*, is expected to affect higher trophic levels, particularly in Lake Huron where biomass of *Mysis*, another important prey item, is extremely low.

Proliferation of *Dreissena* has been coincident with major food web changes in the Great Lakes, especially lakes Ontario, Michigan, and Huron. Although there is uncertainty about the mechanisms by which *Dreissena* impact the food web, they can have significant effects on nutrient cycling; furthermore, mussel feeding activity has been associated with increased water transparency and reduced phytoplankton abundance in offshore waters. Changes to mussel populations have co-occurred with trends in other lower food web factors, including nutrients, water clarity, and both the abundances and community compositions of phytoplankton and zooplankton communities.

Lake Superior is consistently classified as ultra-oligotrophic based on phytoplankton and nutrient conditions. No systematic change has been seen in chlorophyll-a since 1998, although increasing spring phytoplankton abundance and opposing trends in total phosphorus and soluble silica concentrations suggest a slight long-term increase in springtime productivity. However, little evidence of directional change has been seen in crustacean zooplankton or benthos communities.

## 1 INTRODUCTION

The Great Lakes National Program Office (GLNPO) of the United States Environmental Protection Agency (USEPA) has been conducting regular surveillance monitoring of the lower trophic levels of the Great Lakes since 1983 ([Barbiero et al., 2018a](#)). This monitoring effort is focused on the relatively homogeneous offshore waters of the lakes and is currently limited to two well-defined periods during the year: the spring isothermal period and the stratified summer period. Monitoring was initially limited to Lakes Michigan, Huron, and Erie; in 1986 sampling was extended to include Lake Ontario, and in 1992 sampling of Lake Superior was added. The base monitoring program included collection of water quality data (e.g., nutrients, water clarity), along with phytoplankton samples and zooplankton samples to depths of 20 m. Zooplankton sampling to depths of up to 100 m and collection of benthos were added to the program in 1997, and mysid sampling began in 2006. Although monitoring of phytoplankton communities has always been part of the program, we only report data from 2001 to present (with greater spatial representation after 2006) due to data consistency concerns for earlier years ([Reavie et al., 2014](#)). The program has also been extended to include a remote sensing component, providing estimates of chlorophyll-a (hereafter referred to as chlorophyll) concentrations spanning from 1998 to present using an algorithm specifically tuned to the waters of the Great Lakes ([Lesht et al., 2013](#)).

This report presents data on a selection of chemical, physical, and biological variables that characterize the base of the Great Lakes open water ecosystem. A detailed report presenting the full results of the annual Great Lakes Biology Monitoring Program (GLBMP) is available elsewhere ([U.S. EPA, 2020](#)); in addition, detailed analyses of GLBMP data have recently been published for phytoplankton ([Reavie et al., 2014](#)), zooplankton ([Barbiero et al., 2019](#)), mysids ([Jude et al., 2018](#)), and benthos ([Burlakova et al., 2018](#)). The goal of this report is to integrate information from the different components of GLNPO's Water Quality Survey (WQS) to provide a general description of the status of the lower food web of all five Great Lakes. We assess the lower food web using measurements of satellite-derived chlorophyll (1998–2018), phytoplankton (2001–2018), summer crustacean zooplankton (1997–2018), the semi-benthic crustacean *Mysis diluviana* (2006–2018, also referred to as mysids), and benthic invertebrates (1997–2018).

These biological variables are supplemented by representative spring nutrient concentrations (total phosphorus and soluble silica) and transparency, as measured by spring and summer Secchi depth. Spring total phosphorus concentration has been shown to be a good indicator of average summer production, while silica is a nutrient taken up by diatoms, one of the main primary producers in the lakes. Secchi depth is correlated to algal biomass and phosphorus concentration, and it has served as the basis for the most widely used lake trophic state index ([Carlson, 1977](#)). In addition, water clarity as measured by Secchi depth is an important factor modifying interactions among visually feeding predators, such as planktivorous fish and predatory zooplankton.

## 2 METHODS

Spring surveys are conducted as early as possible after ice out conditions in the Straits of Mackinac, typically in April, and summer surveys are conducted during the period of stable thermal stratification, typically in August. Samples for nutrients, phytoplankton, and zooplankton are currently collected from 72 regular open water stations; mysid samples are taken at all regular stations visited at night. Benthos samples are collected from 33 of these open water stations, as well as from an additional 25 exclusively benthos stations ([Figure 1](#)). Historically, a greater number of WQS stations have been sampled; only

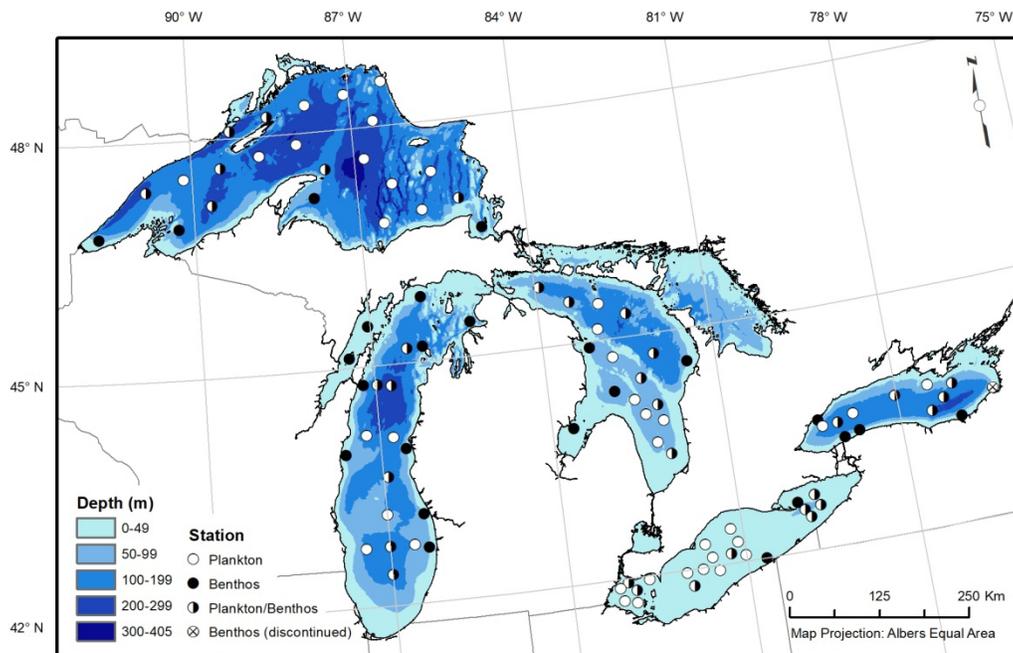
those located in lake regions that are currently sampled are included in this report. Further details on locations and characteristics of stations are available in [Barbiero et al. \(2018a\)](#) and [Lesht et al. \(2018\)](#).

Samples for nutrients (spring) are taken at discrete depths throughout the entire water column; data reported herein were averaged from discrete samples taken from depths > 10 m from the bottom (or > 2 m from the bottom in western and central Lake Erie). References to analytical methods for soluble silica (Si) and total phosphorus (TP) are provided in [Appendix A](#). Phytoplankton samples are composites of water sampled at discrete depths from the euphotic zone. Isothermal spring samples integrate water from 1, 5, 10, and 20 m. In shallower locations (Lake Erie), the 20-m sample is replaced by a collection just above the lake bottom. For summer, equal volumes are integrated from 1 m, 5 m, 10 m, and the lower epilimnion. Phytoplankton biomass is estimated using cell dimension measurements, applying historical dimension averages when required dimensions are not able to be measured.

Zooplankton samples are collected by vertical tow from the lesser of 2 meters above the bottom or 100 m using a 0.5-m diameter 153- $\mu$ m mesh net. Mysids are collected using a 1-m diameter 500- $\mu$ m mesh net (250- $\mu$ m cod end jar) towed vertically from near the bottom (3 m or 5 m off the bottom in water shallower than or deeper than 100 m, respectively). Both zooplankton and mysids are narcotized with soda water, preserved in buffered formalin, and later enumerated and measured in the lab. Biomass of zooplankton and mysids is estimated using length measurements and length-weight relationships from the literature. Samples for benthic invertebrate analysis are collected in triplicate using a Ponar grab sampler, sieved through a 500- $\mu$ m mesh net and preserved in buffered formalin with Rose Bengal. Oligochaetes and chironomids are mounted on slides and identified under a compound microscope at 63x; other organisms are identified under a dissecting microscope. *Dreissena* spp. (the zebra mussel *D. polymorpha*, and the quagga mussel *D. rostriformis bugensis*) were first enumerated in 2003. Biomass of benthos (total wet weight; with shell for molluscs) has been recorded since 2012. Further details on biological sampling and analysis methods are available from the references in [Appendix A](#).

Estimates of chlorophyll concentration in the surface waters of the offshore are estimated with data from the Sea-viewing Wide Field-of-view (SeaWiFS, 1998–2007) and Moderate resolution imaging spectroradiometer (MODIS, 2002–present) ocean color sensors using a band-ratio retrieval algorithm developed with GLNPO monitoring data ([Lesht et al., 2013; 2016](#)). To maintain consistency with other datasets presented here, satellite chlorophyll estimates from the pixels nearest to the WQS open-water sampling stations were extracted and averaged.

Monotonic trends in water quality variables were assessed with Spearman rank correlations with year. Being a rank-based test, it assesses trends by testing for successive increases/decreases in a variable over time, without regard to the magnitude of change. Similarly, phytoplankton trends were assessed with Kendall's rank correlation test. Significance for all tests was assessed at  $\alpha = 0.05$ .



**Figure 1.** Map of GLNPO long-term monitoring stations for annual spring and summer nutrient and plankton sampling (includes phytoplankton, zooplankton, *Mysis*) and summer benthos sampling.

## 3 RESULTS

### 3.1 WATER QUALITY VARIABLES

#### 3.1.1 Spring Total Phosphorus

Spring TP has increased significantly since 1983 in the western basin of Lake Erie, although inter-annual variability has been high (Figure 2). Years with elevated TP levels have been particularly apparent since the early 2000s. No trends in TP were observed in the central or eastern basins of Lake Erie. All three basins have exceeded Great Lakes Water Quality Agreement (GLWQA) interim substance objectives for TP concentrations in open waters in some years, the western and central basins most consistently.

Spring TP concentrations have declined in lakes Ontario, Huron, and Michigan since the mid-1980s (Figure 2; Table 1). The most notable declines in Lake Ontario were between the mid-1980s and the late 1990s, with some evidence of further, more moderate decreases during the last decade. Recent TP concentrations in Lake Ontario are less than half those seen at the beginning of our surveys in 1986. The longer time series collected by Environment and Climate Change Canada shows that the decline in spring TP was even larger in the late 1970s and early 1980s, prior to the initiation of the GLNPO WQS (Dove and Chapra, 2015). TP concentrations in Lake Michigan have declined by nearly 50% since the start of our monitoring in 1983. Declines in Lake Huron first became apparent in the mid-1990s; recent (2014–2018) concentrations are approximately 35% lower than those seen at the beginning (1983–1987) of our program. Since approximately 2005–2010, declines in both lakes have abated, with concentrations in Lake Huron increasing slightly. Concentrations in lakes Ontario, Huron, and

Michigan are currently substantially below GLWQA interim substance objectives for TP concentrations in open waters.

Spring TP has increased in Lake Superior ([Table 1](#)), though the absolute increase has been slight. Currently, spring concentrations in lakes Superior and Huron are virtually identical (2018: 2.5 and 2.6  $\mu\text{g P/L}$ , respectively) while concentrations in Lake Michigan are slightly higher (2018: 3.2  $\mu\text{g P/L}$ ). Based on TP concentrations, the upper lakes (Michigan, Huron, and Superior) are considered ultraoligotrophic ([Ryding and Rast, 1994](#)). Spring TP in Lake Ontario is only slightly higher than that in the three upper lakes (2018: 3.8  $\mu\text{g P/L}$ ).

### 3.1.2 Spring Soluble Silica

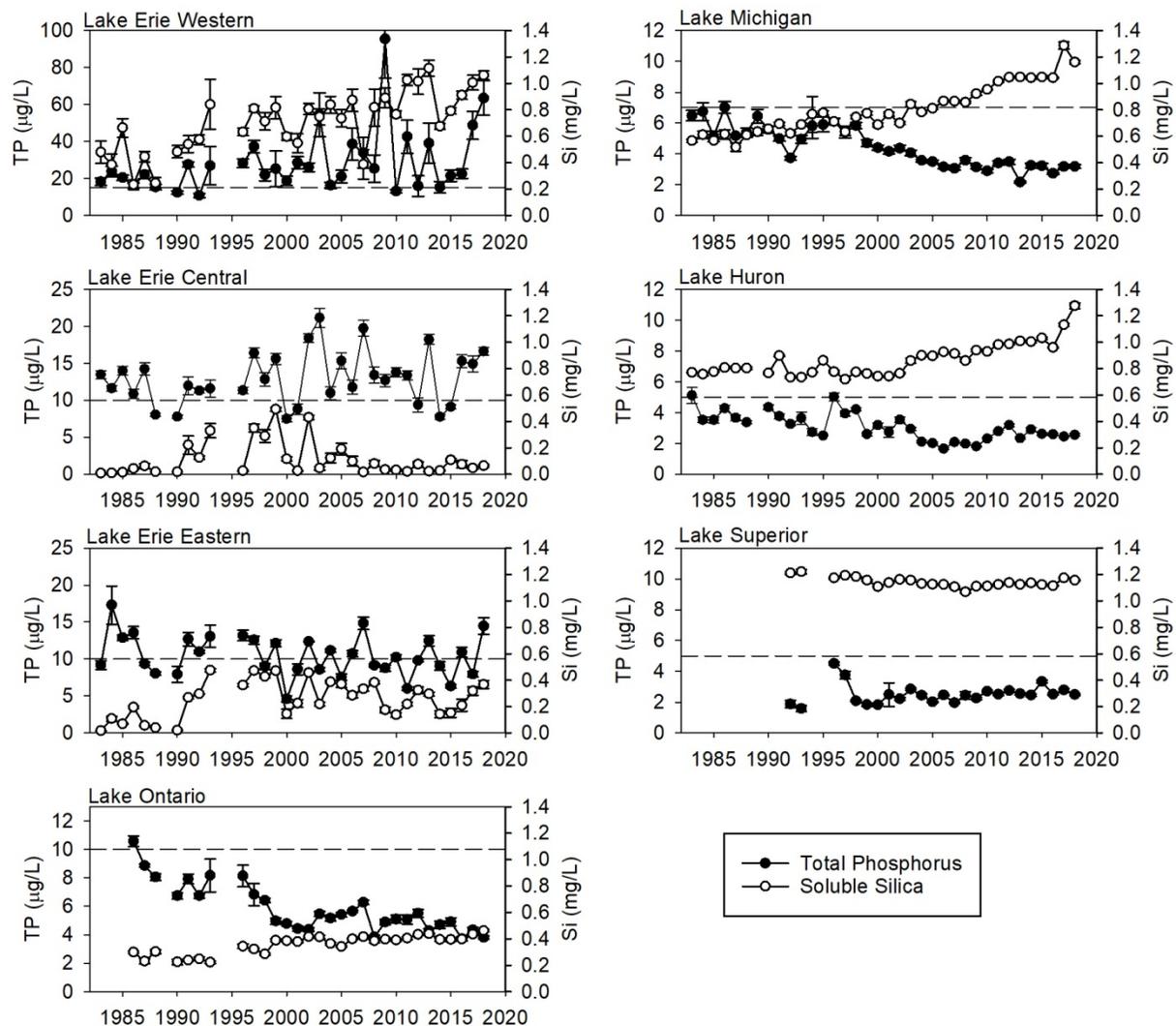
The western basin of Lake Erie has shown a significant increasing trend in soluble silica ([Figure 2](#); [Table 1](#)), perhaps influenced by increased concentrations in Lake Huron, which provides the majority of water input to Lake Erie. In the central basin, elevated silica concentrations were seen in the 1990s–early 2000s, a period corresponding to peak dreissenid abundance in that basin ([Karatayev et al., 2018](#)). Although there are no significant long-term trends for the period presented, silica concentrations have been lower in the central basin since 2003, likely due to growth of large centric diatoms during the winter-spring bloom ([Reavie et al., 2016](#)). In the eastern basin, spring silica concentrations increased notably during the mid-1990s and have remained elevated since. This was accompanied by a reduction in the size of the spring phytoplankton community and a shift towards centric diatom species with high silica requirements, changes that were likely due to dreissenid grazing ([Barbiero et al., 2006](#)).

As might be expected given the decreases in TP, silica has increased in lakes Ontario, Huron, and Michigan ([Figure 2](#)). These increases in silica are consistent with limitation of diatom growth through reduced availability of phosphorus, leading to lower diatom production and/or increased grazing, e.g., by dreissenid mussels ([Mida et al., 2010](#)), perhaps in combination with decreased long-term burial rates of silica ([Barbiero et al., 2002](#)). It is worth noting that Lake Huron experienced a marked increase in silica concentrations in 2003, a year associated with a notable decline in spring phytoplankton ([Barbiero et al., 2011a](#)), owing mainly to a loss in pelagic diatoms ([Reavie et al., 2014](#)); this change was accompanied by drastic changes to the zooplankton community as well ([Kovalenko et al., 2018](#)). Both lakes Michigan and Huron experienced further increases in soluble silica in 2017 and 2018, although these were not accompanied by notable changes in transparency or chlorophyll (see below).

In contrast to the other lakes, the Lake Superior silica concentration has decreased significantly, although the absolute change is modest. This might indicate an increase in productivity ([Schelske et al., 1983](#)), which is supported by the observed increasing trends in both TP and spring phytoplankton (see below).

### 3.1.3 Secchi Depth

The western basin of Lake Erie experienced a significant reduction in spring transparency during the mid-1990s ([Figure 3](#)), despite high abundances of dreissenid mussels during those years ([Karatayev et al., 2014](#)). The lack of a dreissenid impact on transparency in the western basin has been ascribed to high sediment inputs and resuspension of unassimilated non-algal particulates ([Barbiero and Tuchman, 2004](#)). No changes were seen in the central basin of Lake Erie. In contrast, transparency has increased in the eastern basin of Lake Erie, with most of this change taking place in the mid-1990s, a likely consequence of dreissenid activity ([Karatayev et al., 2018](#)). Despite these long-term changes in spring Secchi depth (western and eastern basins), there were no statistically significant trends in summer Secchi depth for any basin of Lake Erie ([Table 1](#)).



**Figure 2.** Spring total phosphorus (TP) and soluble silica (Si) from 1983 to 2018 in the Great Lakes. Bars indicate one standard error. The horizontal dashed line within each plot indicates the 2012 interim substance objectives for TP concentrations in open waters. Note different Y-axis scales in TP plots.

As might be expected from other indicators of oligotrophication, spring and summer Secchi depths showed marked increases in lakes Ontario, Michigan, and Huron over the time series. However, the trajectories of increase were different in the three lakes. Spring transparency in Lake Ontario has been notably higher, albeit quite variable, since the early 2000s (Figure 3). Although our data lack information from 1992 to 1995, other sampling programs show that summer Secchi disk depth increased continuously from the 1980s to 2000, and then stabilized around 7 m (Rudstam et al., 2017). The continued increase in water clarity from 1990s to 2018 mirrors an increased lake-wide biomass of dreissenid mussel in the lake (Birkett et al., 2015), suggesting an effect of filtering by dreissenid mussels (see also Barbiero et al., 2006).

Trends in lakes Michigan and Huron Secchi depth have been remarkably similar ([Barbiero et al., 2018b](#)), with steady increases in spring and summer transparency throughout most of the last 20 years and some evidence of a recent stabilization. After a short period of relatively high values at the beginning of our data series, which has been attributed to high zooplankton herbivory ([Scavia et al., 1986](#)), Secchi depth in Lake Michigan decreased and remained low (<10 m) through the 1990s. Secchi depth then increased dramatically (to ~15 m in spring) from approximately 2000 to 2005 and has remained elevated since. The increase in transparency in Lake Huron began somewhat earlier (late 1990s) than in Lake Michigan and has also remained relatively stable since then.

In Lake Superior, there has been no change in spring or summer Secchi depths, which have averaged approximately 15 m and 12 m, respectively, over the time series ([Figure 3](#)).

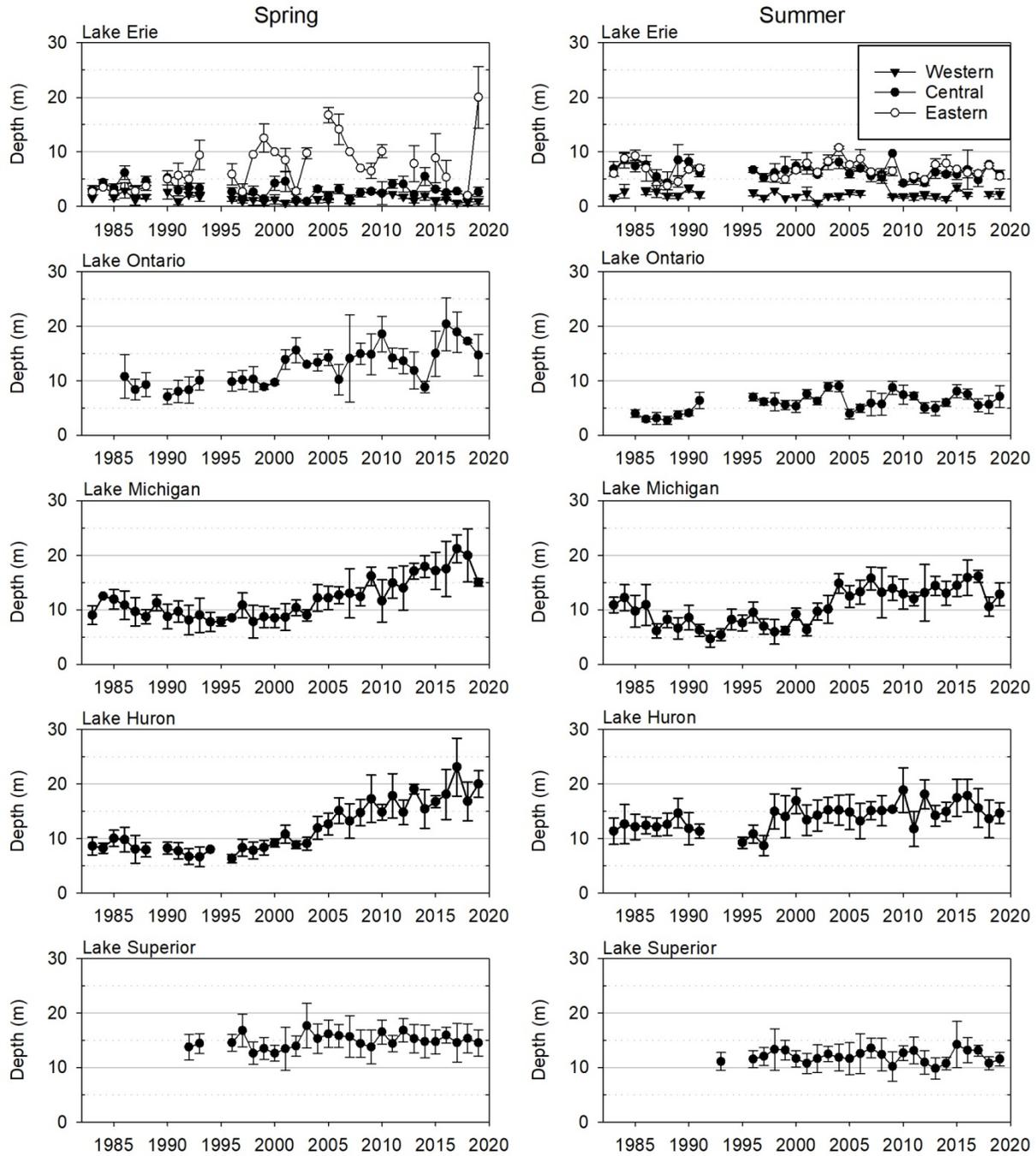
### 3.1.4 Chlorophyll-a

Lake Erie was the only lake in which surface chlorophyll concentration increased over time ([Figure 4](#)). Both the eastern and the central basins showed increases in late summer/early autumn chlorophyll beginning in 2006. Both early summer (June–July) and late summer/early autumn (August–October) showed statistically significant positive trends in both basins. The western basin has shown consistently high chlorophyll concentrations in late summer; while some years have been notable for the duration of high chlorophyll concentrations (e.g., 2011), there has been no indication of trends since 1998. Lake Ontario chlorophyll concentrations were considerably lower, consistent with its oligotrophic status, and there were no significant long-term trends. However, Lake Ontario has exhibited considerable inter-annual variability in chlorophyll, particularly regarding the timing of seasonal peaks.

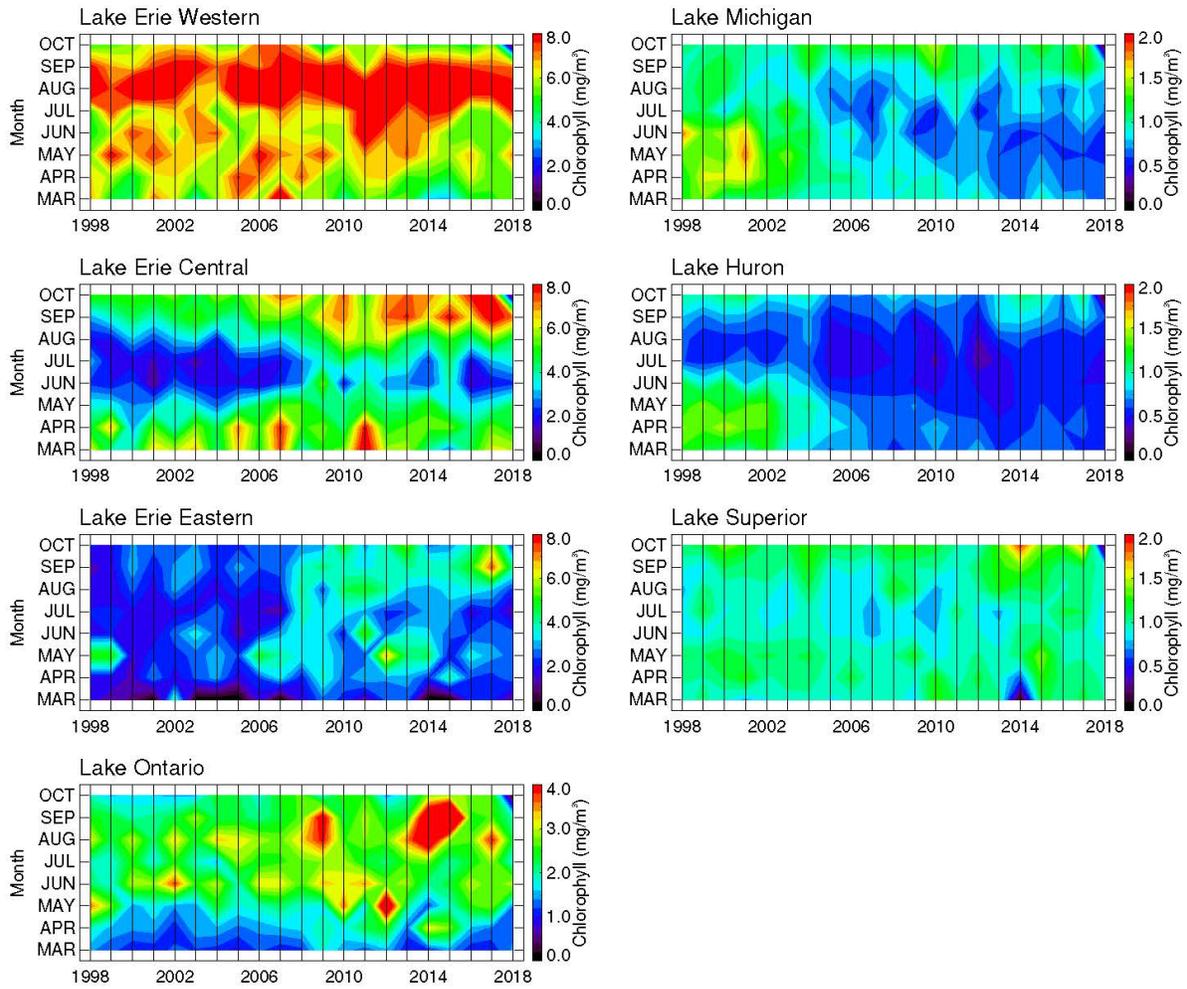
Lakes Huron and Michigan have experienced similar trends in spring chlorophyll, with highly significant reductions in both lakes ([Table 1](#)) beginning in the early 2000s and continuing through the mid-2010s. These spring reductions have been associated with declines in large diatoms, which historically had been spring dominants (see below; [Barbiero et al., 2018b](#)). Summer concentrations also decreased significantly in Lake Michigan, but not in Lake Huron. With the reduction in spring chlorophyll and the continuation of the summer minimum, particularly in Lake Michigan, seasonal peaks in surface chlorophyll in both lakes now occur in late summer/early autumn. It is notable that the reductions in chlorophyll in these two lakes continued after the apparent stabilization in TP, which occurred around 2006.

By multiple accounts (e.g., [Barbiero et al., 2018b](#), [Kovalenko et al., 2018](#), [Dove and Chapra 2015](#)), lakes Huron and Michigan have transitioned to more oligotrophic water quality conditions as a result of food web modification over the past two decades. The recent shift to high transparency, low spring chlorophyll, and low phytoplankton abundance (see below; [Reavie et al., 2014](#)) is associated with the direct and indirect effects of the dreissenid expansion. Mechanistically, the loss of phytoplankton biomass could be associated with direct filter-feeding of sinking microorganisms (such as heavy diatoms) by dreissenids. This impact is likely exacerbated by the sequestration of nutrients by dreissenids in the nearshore ([Hecky et al., 2004](#)) and nutrient retention by deeper living dreissenids ([Vanderploeg et al., 2010](#)).

In contrast, Lake Superior has shown no evidence of trends in chlorophyll concentrations over the course of our time series. In general, water quality variables in Lake Superior have been relatively stable over the time series and exhibited no definitive long-term changes.



**Figure 3.** Spring (left panels) and summer (right panels) Secchi depth from 1983 to 2019 in the Great Lakes. Bars indicate one standard error.



**Figure 4.** Monthly averaged (March–October) surface chlorophyll concentrations at GLNPO WQS station locations in the Great Lakes, 1998–2018. Note different color scales in Erie and Ontario compared to the other three lakes.

## 3.2 BIOLOGY VARIABLES

### 3.2.1 Phytoplankton

The Great Lakes phytoplankton community includes hundreds of unique taxa including diatoms, chrysophytes, green algae, cryptomonads, cyanophytes, euglenoids and dinoflagellates ([Figure 5](#)). Temporal changes in phytoplankton abundance over 18 years are shown through histograms that summarize within-lake averages (within-basin averages for Erie; [Figure 5](#)). In many cases, these changes are attributed to food web shifts and changes in water quality. Likely reasons for these changes include size-specific preferences of food organisms by successful grazers ([Barbiero et al., 2018](#)), nutrient shifts (e.g., increases in soluble reactive phosphorus loads in Lake Erie; [Kane et al., 2014](#)) and climate-related changes in physical properties of the lakes ([Reavie et al., 2017](#)). These mechanisms are discussed in greater detail in respective, published manuscripts.

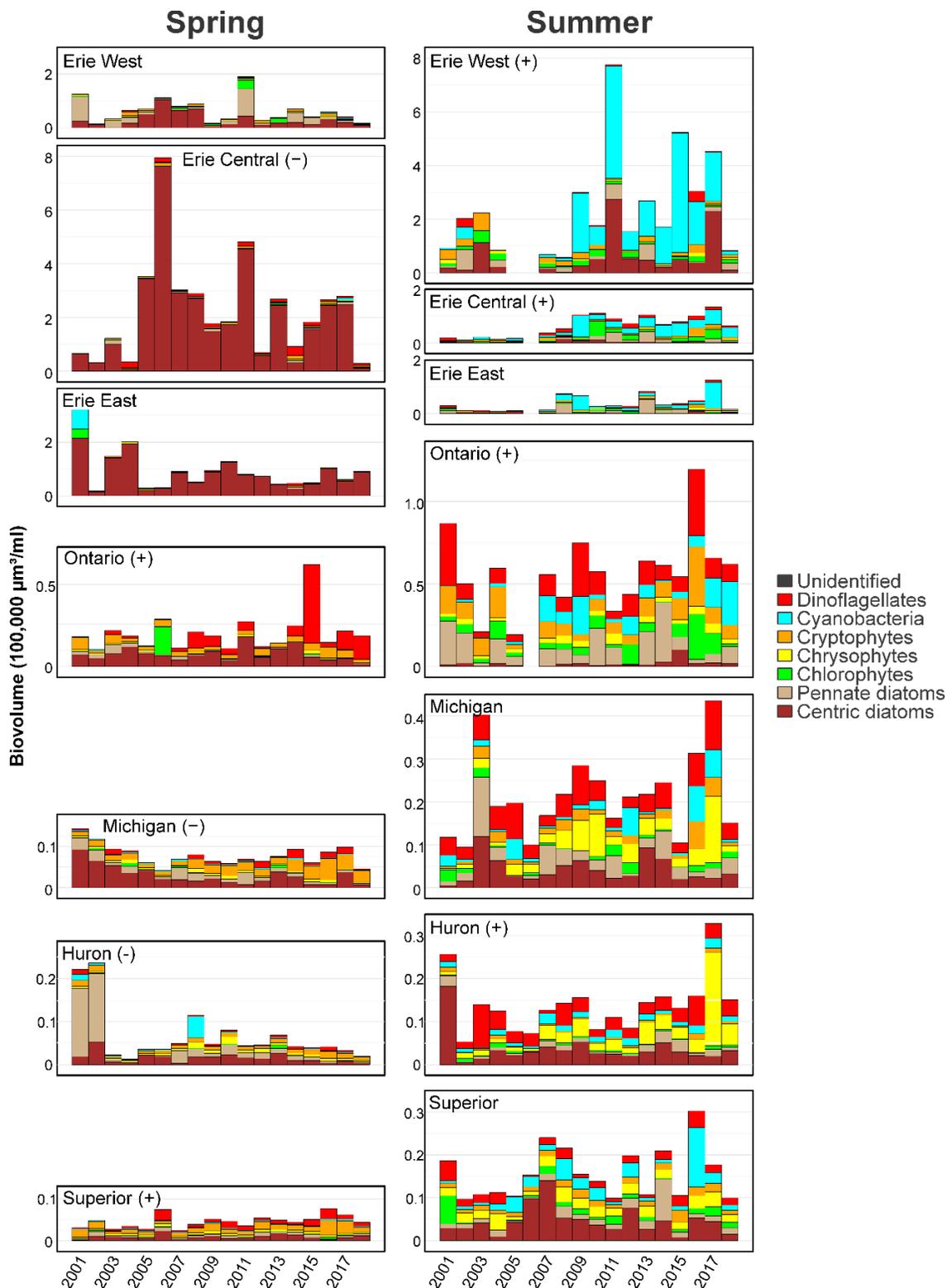
Spring phytoplankton biovolumes are highest in Lake Erie, which is overwhelmingly dominated by diatoms (especially the centric diatom *Aulacoseira islandica*), particularly in the central basin ([Reavie et al., 2014](#)). Very high spring biovolumes of diatoms, relative to that of other taxa later in the year, have been linked to late-summer hypoxia ([Reavie et al., 2016](#)). It is notable that there have been erratic fluctuations in algal abundance and composition in the spring, but summer has exhibited a persistent increase in cyanophytes (dominated by *Aphanocapsa* and *Microcystis*). During summer, phytoplankton biovolumes are typically highest in Lake Erie's western basin, where there are often especially high abundances of the nuisance cyanophyte *Microcystis aeruginosa* ([Bridgeman et al., 2013](#)), although there are also some high abundances of diatoms, chrysophytes, dinoflagellates, and cryptophytes.

Lake Ontario has been dominated by centric diatoms and dinoflagellates in the spring and pennate diatoms, cryptophytes, chlorophytes, and dinoflagellates in the summer. While not easily apparent in the histograms ([Figure 5](#)), total phytoplankton density and biovolume exhibited a slight increase over the last 18 years. During that time, the abundance of dinoflagellates (*Peridinium*) increased, as did that of summer cyanophytes (largely *Aphanocapsa*).

Algal abundance overall is lower in the upper lakes. Spring dominants tend to be opportunistic diatom taxa (*Aulacoseira*, *Stephanodiscus*) that make use of abundant nutrients, such as phosphorus and silica. As nutrient limitation is established later in the year, cyanophytes and dinoflagellates increase in abundance. In terms of biovolume, spring in Lake Michigan is dominated by centric diatoms with an increasing relative abundance of flagellates such as cryptophytes ([Figure 5](#)). Total spring phytoplankton biovolume has decreased in Lake Michigan, largely due to a decline in centric diatoms. Summer phytoplankton abundance has fluctuated, showing no long-term trend, although relative contributions from chrysophytes may be increasing ([Figure 5](#)).

Lake Huron is dominated by diatoms and cryptophytes in the spring, and by diatoms, chrysophytes, and dinoflagellates in the summer. Spring diatom biovolume plummeted after 2002, while summer data reveal a less dramatic decline followed by a gradual recovery in algal abundance favoring chrysophytes and dinoflagellates. This decline is associated with concurrent declines in nutrients, chlorophyll, zooplankton, and benthos ([Kovalenko et al., 2018](#)), as well as with the rapid spread of dreissenids.

Lake Superior is dominated by diatoms, chrysophytes, cryptophytes and dinoflagellates in the spring, with the addition of cyanophytes by summer. Although algal abundance has consistently represented an oligotrophic system, spring data suggest an increase in biovolume over the period presented ([Figure 5](#)), which appears to be driven by increased flagellated cryptophytes; there were no significant trends in summer algal abundance or composition.



**Figure 5.** Basin-wide averages of phytoplankton biovolume in spring (left) and summer (right) from 2001 to 2018. Spring/summer scales are aligned (except for Lake Erie) for easier comparison. A significant increasing (+) or decreasing (-) trend (Kendall's rank correlation test,  $p < 0.05$ ) for the 18-year period is indicated following each lake/basin name.

### 3.2.2 Crustacean Zooplankton

Crustacean zooplankton communities differ from lake to lake, both in abundance and composition; data from 1997 to 2016 were recently analyzed by [Barbiero et al. \(2019\)](#). Volumetric biomass is highest in the western and central basins of Lake Erie, followed by Erie's eastern basin and Lake Ontario, and similarly low biomass in lakes Michigan, Huron, and Superior ([Figure 6](#)). At the start of the time series, the crustacean zooplankton community was dominated by cladocerans and cyclopoids in lakes Erie and Ontario, by cladocerans and calanoids in lakes Michigan and Huron, and by calanoids in Lake Superior. This pattern is consistent with a greater prevalence of cladocerans and cyclopoids in more highly productive systems, although zooplankton community structure also depends on the degree of fish predation.

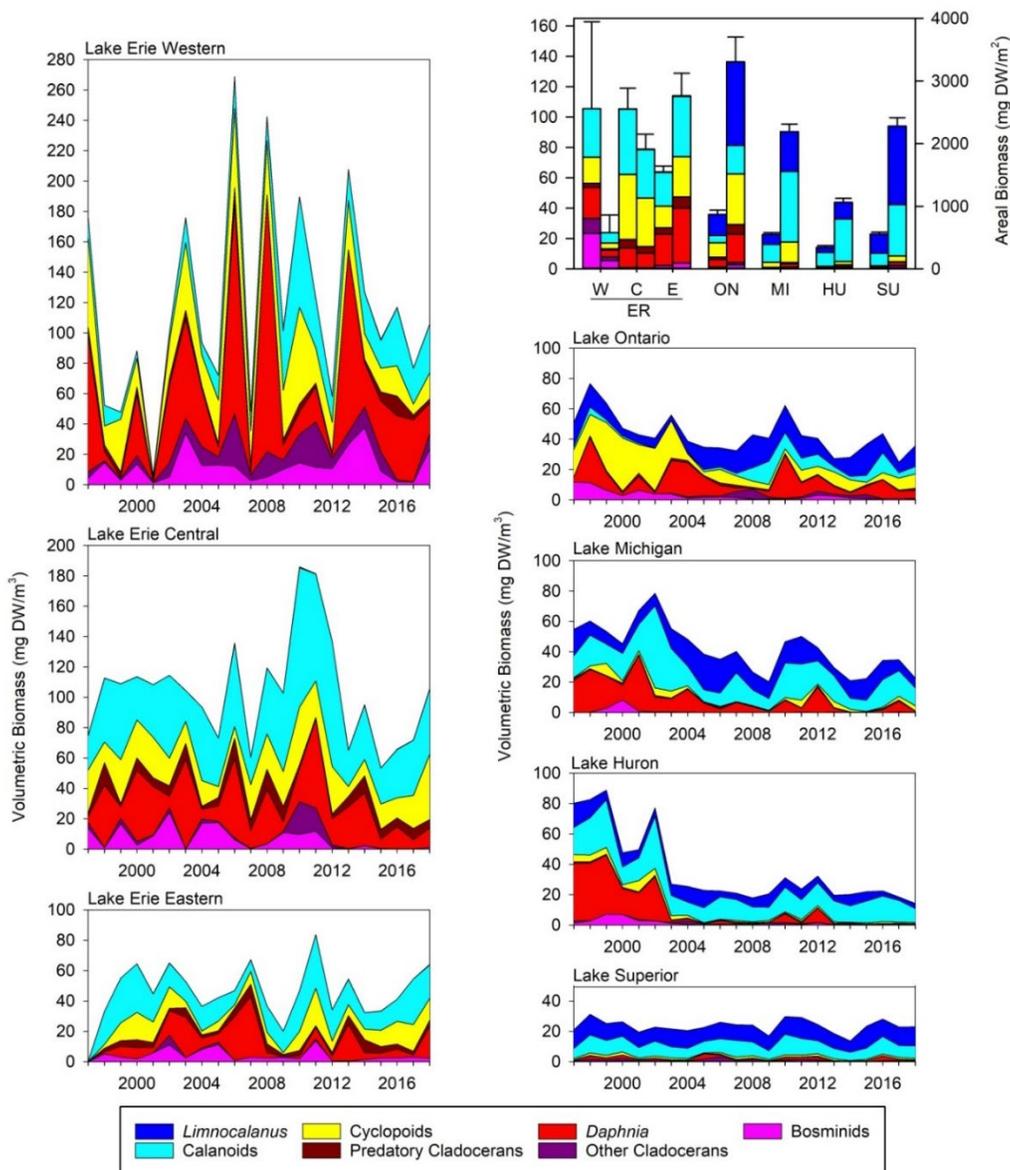
The western basin of Lake Erie shows a high degree of inter-annual variability, as would be expected in this very dynamic and relatively productive system; both the highest (2006) and the lowest (2001) volumetric biomass values in our dataset were recorded in this basin. There has been no evidence of directional change in community composition. The western basin was also unique in having the native *Leptodora kindtii* as the dominant predatory cladoceran. The central and eastern basins of Lake Erie also have shown high inter-annual variability and little evidence of directional change. Unlike the western basin, the non-native *Bythotrephes longimanus* was the dominant predatory cladoceran in the eastern and central basins, where its biomass was higher than in any other region of the Great Lakes.

The zooplankton community in Lake Ontario has undergone substantial change since 1997. An initial assemblage dominated by cyclopoid copepods (mostly *Diacyclops thomasi*), *Daphnia retrocurva*, and bosminids, and with the invasive *Cercopagis pengoi* as the dominant predatory cladoceran, shifted to one characterized by reduced numbers of cyclopoids, a more varied predatory cladoceran community, and increased biomass of calanoid copepods. A further change occurred in 2008, with increased biomass of the calanoid copepod *Leptodiaptomus sicilis*, occasional dominance by *Bythotrephes longimanus*, and the appearance in substantial numbers of *Daphnia mendotae*. Total crustacean biomass has declined since 1997 ([Table 1](#)). The shifts in Lake Ontario crustaceans have not been accompanied by notable reductions in chlorophyll; the replacement of cyclopoids and smaller cladocerans (*Daphnia retrocurva*, bosminids) with calanoids and larger cladocerans (*D. mendotae*, *B. longimanus*) instead are consistent with decreased fish predation ([Barbiero et al., 2014](#); [Rudstam et al., 2015](#)). Species composition has been variable in recent years (2014–2018); while cyclopoid biomass has remained relatively low, dominant cladoceran species and calanoids have varied from year to year, perhaps indicating variations in the intensity of planktivory by fish.

Lakes Michigan and Huron also have experienced marked shifts in summer zooplankton community size and composition since 1997; these trends have been similar between the lakes, but the change is much more pronounced in Lake Huron. In both cases, declines in cladocerans have occurred, with the resulting communities dominated by calanoid copepods (diaptomids and *Limnocalanus macrurus*). The reduction in cladocerans has not been as dramatic in Lake Michigan as in Lake Huron. Since 2003, total crustacean biomass in Lake Huron has been approximately a third of that observed between 1997 and 2002, with relatively little variation. In contrast, Lake Michigan total biomass in recent years been approximately half that of 1997–2002, with more notable inter-annual variation. In both lakes, declines have been statistically significant ([Table 1](#)) and followed declines in spring chlorophyll ([Barbiero et al., 2018b](#)), suggesting declining resources as a causal factor. The strongest evidence of bottom-up regulation of the lower food web has been seen in Lake Huron; evidence in Lake Michigan has been more ambiguous ([Barbiero et al., 2011a](#); [Bunnell et al., 2014](#)).

Lake Superior has had the lowest and most consistent zooplankton biomass over time. Calanoid copepods accounted for over 85% of total biomass, on average, over the full time series; the vast majority of this calanoid biomass was contributed by two large, deep-living species: *L. macrurus* and *Leptodiaptomus sicilis*.

The loss of cladocerans and the increased importance of calanoids in lakes Huron and Michigan have altered the size- and depth-distributions of crustacean biomass, reducing biomass in intermediate (1.5 – 2.5 mm) size categories and likely shifting biomass deeper in the water column. Crustacean community structure in these lakes is currently similar to that of Lake Superior. The increased importance of calanoids in Lake Ontario, in turn, has shifted its community structure closer to those characteristic of lakes Huron and Michigan during the late 1990s–early 2000s.



**Figure 6.** Summer crustacean volumetric biomass (mg DW/m<sup>3</sup>), by major taxonomic group, for the Great Lakes, 1997–2018. The upper right graph shows zooplankton volumetric (left axis; left bars) and areal (right axis; right bars) biomass for all five lakes in 2018.

### 3.2.3 Mysids

The opossum shrimp *Mysis diluviana* (formerly *M. relicta*) is a large omnivorous crustacean zooplankton that inhabits bottom sediments during the day and migrates into the upper hypolimnion or lower metalimnion at night. It is both an important predator on other zooplankton and an important food item for many Great Lakes fish due to its size, year-round availability, and high lipid content. A detailed analysis of the time series from 2006 to 2016 is in [Jude et al. \(2018\)](#).

*M. diluviana* occurs in all five of the Great Lakes, but it is rare in Lake Erie. Among the four deeper lakes, biomass was highest in Lake Ontario, somewhat lower in lakes Michigan and Superior, and substantially lower in Lake Huron ([Figure 7](#)). Since 2006, both lakes Michigan and Huron have exhibited statistically significant declining trends in spring mysid biomass; an increasing trend in spring biomass was seen in Lake Superior. No trends were apparent in summer.

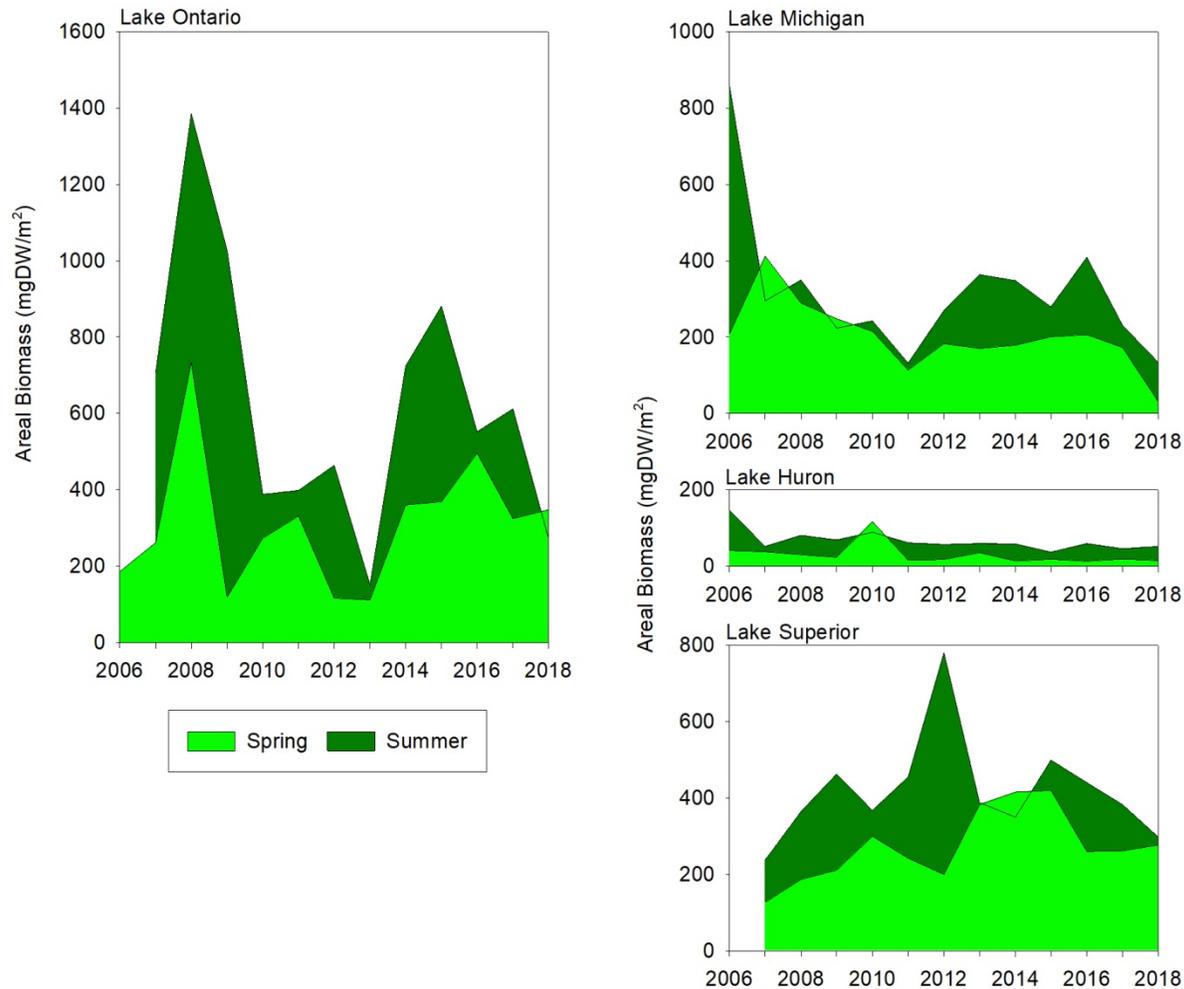
Because our data series begins in 2006, we cannot assess whether *M. diluviana* populations exhibited declines similar to those seen in other crustacean groups in the early 2000s in lakes Huron and Michigan. [Pothoven and Vanderploeg \(2017\)](#) reported 54% declines in *M. diluviana* between 1995–2002 and 2007–2015 at a 110-m site in southeastern Lake Michigan. Predictions of the effect of declines in epilimnetic production on mysid populations is complicated by the fact that mysids feed below the thermocline in the deep chlorophyll layer at night ([O'Malley et al., 2017](#)); the biomass of both algae and zooplankton in this layer varies by lake ([Scofield et al., 2020a](#); [Scofield et al., 2020b](#)). In Lake Ontario, where the major declines in production occurred earlier than in lakes Michigan and Huron, *M. diluviana* populations during the 2000s were approximately half those in the 1990s ([Johannsson et al., 2011](#)). [Holda et al., \(2019\)](#), in an analysis of spatially extensive mysid data from Lake Ontario in 2013, suggested that the decline was due to increased mortality.

### 3.2.4 Benthos

Benthos community size and structure in the Great Lakes has been shown to vary with depth, with a notable breakpoint occurring at 70 m ([Burlakova et al., 2018](#)). Therefore, data are presented separately for shallow (< 70 m) and deep (> 70 m) regions, for both dreissenids ([Figure 8](#)) and the whole benthic community ([Figure 9](#)). Abundances (excluding dreissenids) were highest in Lake Erie, where all sites were < 70 m ([Figure 9](#)). Within lakes, abundances were often higher at shallower sites, particularly in recent years. Detailed analysis of the 1998 to 2016 benthos data are in [Burlakova et al. \(2018\)](#).

The highest total wet weight biomass of benthos in our most recent year of data (2018) was found in Lake Ontario, followed by, in order of decreasing biomass, Lake Erie, Michigan, Huron, and Superior ([Figure 9](#)). The largest contributor of biomass (wet weight with shells) in all lakes except Superior was *Dreissena* (largely *D. r. bugensis*), which has increased in abundance over the time series ([Figure 8](#)) and now contributes more than 99% of total benthos biomass in the other four lakes. In 2018, the highest lake-wide average *Dreissena* biomass occurred in Lake Ontario, followed by lakes Erie and Michigan; the lowest biomass was found in Lake Huron, but it has increased five-fold since 2014. Excluding *Dreissena*, the highest areal benthos biomass was found in Lake Erie and the highest biomass in the > 70 m zone was found in Lake Huron. In all lakes, non-dreissenid communities were dominated by oligochaetes except for Lake Superior, where *Diporeia* continue to dominate benthos density and biomass. *Dreissena* populations are not established in Lake Superior.

One of the most dramatic changes over time was the loss of the amphipod *Diporeia* from Lake Ontario and from shallow regions of lakes Michigan and Huron, and its extreme declines in deeper regions of lakes Michigan and Huron. Like *M. diluviana*, *Diporeia* is a relatively large, lipid-rich prey item consumed by many fish species, and its populations have historically been reliant upon the spring diatom bloom ([Gardner et al., 1990](#)).



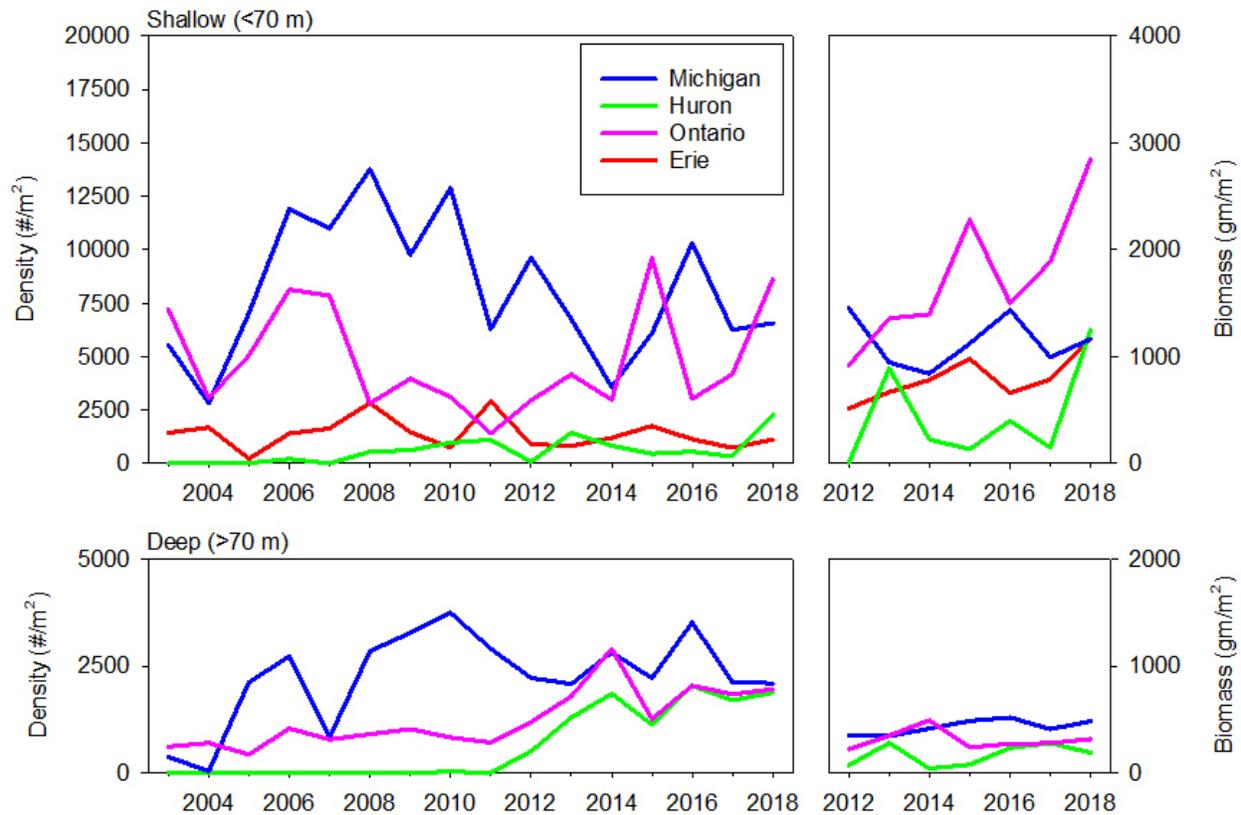
**Figure 7.** *Mysis diluviana* areal density (mg DW/m<sup>2</sup>) from 2006–2018 from stations deeper than 30 meters in Lakes Ontario, Michigan, Huron, and Superior. *Mysis* were not sampled during the following cruises: Lake Ontario (summer 2006) and Lake Superior (spring and summer 2006).

*Diporeia* was once among the dominant components of the benthic fauna in the eastern basin of Lake Erie, but has been absent from that lake since the late 1990s (Figure 9; Dermott and Dow, 2008; Barbiero et al., 2011b). In Lake Ontario, *Diporeia* was largely absent from shallow sites at the initiation of our program in 1997, and since 2011 has only been encountered sporadically at our deep stations in that lake. In lakes Michigan and Huron, *Diporeia* at shallow sites underwent marked, coincident declines between 2002 and 2005, and have only occasionally been found since 2010. Deep populations of *Diporeia* underwent marked declines at the same time but have remained relatively stable since 2005. The only Great Lake where *Diporeia* continue to dominate benthos density and biomass is Lake Superior. Declines have also been seen in fingernail clam (Sphaeriidae) abundances, most notably at shallow sites in Lake Ontario and Lake Michigan and deep sites in Lake Huron. In contrast, chironomids and oligochaetes have shown no decline in these three lakes, but instead have increased in parts of lakes Ontario and Michigan.

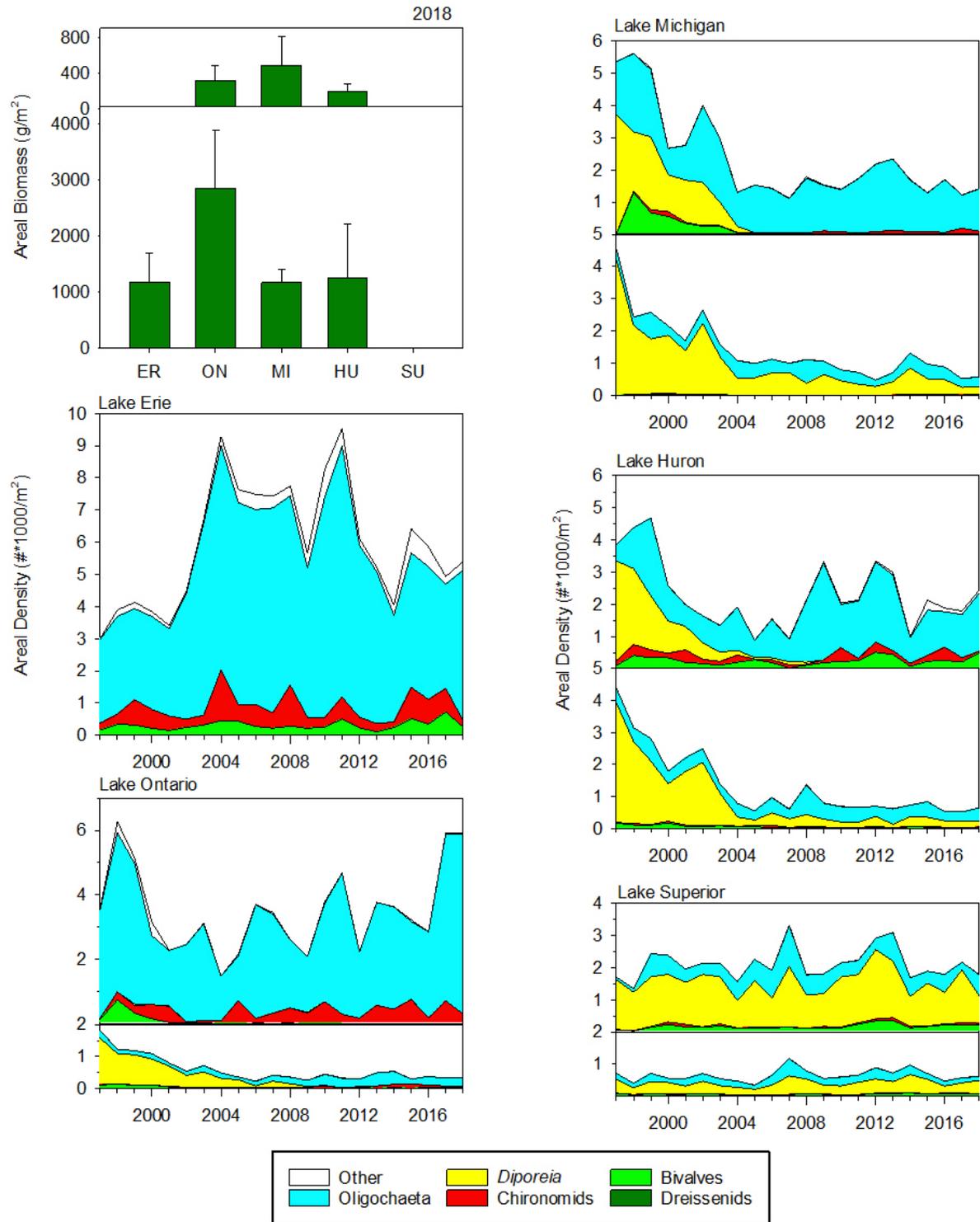
These changes have occurred during a period of increasing dreissenid densities in the lakes (Figure 8). Dreissenid mussels are known to increase habitat complexity and food supply, particularly in the

littoral and sublittoral zones (Higgins and Vander Zanden, 2010; Karatayev et al., 2015). While dreissenid populations have largely stabilized at our shallow sites, populations are still increasing in deep regions of lakes Ontario and Huron. The rapid increases seen in the early 2000s in Lake Michigan appear to have stabilized.

Overall, benthic communities in lakes Ontario, Michigan and Huron have shifted from dominance by *Diporeia* to dreissenids and oligochaetes during the time series; dreissenid populations continue to increase in Lake Huron and deep regions of Lake Ontario, but non-dreissenid populations have exhibited relative stability over the past decade.



**Figure 8.** Density (2003–2018) and biomass (2012–2018) of dreissenid mussels for shallow sites (< 70 m, top plots) and deep sites (> 70 m, bottom plots) in the Great Lakes. Dreissenid mussel populations are not established in Lake Superior.



**Figure 9.** Great Lakes total areal biomass (wet weight) by major taxonomic group for 2018 in all lakes (upper left plot) and areal density by major taxonomic group for 1997–2018, by individual lake. All plots are split into two panels, for data from stations < 70 meters depth (upper panel) and > 70 meters deep (lower panel). There are no deep stations in Lake Erie. Note that dreissenids are excluded from areal density plots.

## 4 CONCLUSIONS

Lake Erie is the only lake with consistently eutrophic conditions, and there is evidence of ongoing eutrophication in recent years. Spring blooms of diatoms and summer blooms of cyanophytes appear to be consistent features of the western and central basins, with summer/autumn chlorophyll and summer phytoplankton biovolume notably higher in the central and eastern basins in the 10-year period from 2008–2018. These increases in chlorophyll have not been accompanied by increases in spring TP, although concentrations in all three basins have consistently (western and central basin) or intermittently (eastern basin) exceeded GLWQA interim substance target levels. It should be noted that spring TP may not be the best indicator of potential productivity in this lake, since inflows of more highly bioavailable forms of phosphorus have been increasing in recent years despite constant TP loads ([Richards et al., 2010](#); [Scavia et al., 2014](#)). While other elements of the lower food web have exhibited marked inter-annual variability, particularly in the western and central basins, there has been no evidence of directional change in zooplankton or benthos communities during this period (2008–2018).

The dramatic declines in TP seen in the 1980s/90s in Lake Ontario were accompanied by declines in chlorophyll and increased transparency; any further changes in these variables during the 2000s have been subtle. Recent TP concentrations, transparencies, phytoplankton biovolume, and surface chlorophyll concentrations are characteristic of an oligotrophic system. TP concentrations are currently well below GLWQA interim target levels. Crustacean zooplankton communities have changed dramatically in recent years, with a shift away from species indicative of high planktivory (cyclopoids, bosminids, small daphnids, *Cercopagis*) towards calanoid copepods, larger daphnids and *Bythotrephes*. In addition, the amphipod *Diporeia*, already absent from our shallow sites by 1997, disappeared also from deep sites by 2011.

The rapid shifts in the lower food web experienced by Lake Huron and, to a lesser extent, Lake Michigan, in the early to mid-2000s are showing signs of moderation. Total phosphorus, spring chlorophyll, phytoplankton biovolume, crustacean zooplankton communities, and *Diporeia* populations have exhibited slight, if any, changes from 2008–2018. The offshore lower food webs of both lakes are currently characterized by greatly increased transparency, the lack of a pronounced spring chlorophyll maximum, and reduced spring phytoplankton (diatom) abundances. Summer crustacean zooplankton communities are dominated by calanoid copepods with relatively few cladocerans, and benthos are dominated by dreissenids, with residual populations of *Diporeia* found only in the deepest portions of the lakes. Measurements of TP, transparency, and chlorophyll indicate the trophic states of these lakes are at or below that of Lake Superior. The loss of prey items favored by forage fish, such as *Daphnia* and *Diporeia*, can have consequences for higher trophic levels, particularly in Lake Huron where *Mysis* biomass, another important prey item, is also low. Greater water clarity can have multiple consequences: deepening primary productivity, greater negative impacts of UV radiation, forcing zooplankton vulnerable to predation into less ideal environments deeper in the water column, and both increasing predation success of planktivores and increasing their susceptibility to visual predators.

Proliferation of *Dreissena* has been coincident with major food web changes in the Great Lakes, especially lakes Ontario, Michigan, and Huron. These mussels filter water, removing nutrients and phytoplankton from the lake and binding energy in benthic resources. Thus, they contribute to changes such as increased transparency and reduced nutrients and phytoplankton in offshore waters. Although there is still uncertainty about the mechanisms by which *Dreissena* impact water quality and the food web, there is a clear correlation between changing mussel abundances and trends in other components of the lower food web.

Lake Superior has exhibited less change than the other Great Lakes. Although no trends have been seen in chlorophyll or summer phytoplankton since 1998, both increasing spring phytoplankton biovolume and opposing trends in TP and Si suggest a slight long-term increase in productivity. Little evidence of directional change has been seen in crustacean zooplankton or benthos communities, although *Mysis* populations have increased. Benthic communities are also relatively unchanged, as *Dreissena* have not established significant populations in Lake Superior and *Diporeia* populations remain stable.

**Table 1.** Results of Spearman rank correlations on selected lower food web variables in the Great Lakes. Significant trends ( $\alpha = 0.05$ ) are indicated by red cells (negative trends) and green cells (positive cells). Note that analyses for benthos in Lake Erie were conducted on lake-wide averages. Phytoplankton trends were evaluated using Kendall rank tests, so ‘r’ values indicate average slope of the relationship ( $\mu\text{m}^3/\text{mL}/\text{y}$ ) for 2001–2018. Bivalve trends exclude dreissenid mussels.

Variable	Season	ER W		ERC		ERE		ON		MI		HU		SU	
		r	P	R	P	r	P	r	P	r	P	r	P	r	P
TP*	Spring	0.35	0.047	0.21	0.231	-0.25	0.159	-0.80	0.000	-0.87	0.000	-0.68	0.000	0.41	0.044
Si*	Spring	0.75	0.000	0.13	0.460	0.27	0.135	0.83	0.000	0.96	0.000	0.76	0.000	-0.47	0.017
Secchi†	Spring	-0.37	0.049	-0.33	0.056	0.48	0.011	0.84	0.000	0.69	0.000	0.74	0.000	0.34	0.085
Secchi†	Summer	-0.10	0.587	-0.33	0.065	0.01	0.953	0.62	0.000	0.66	0.000	0.44	0.014	-0.02	0.908
Chlorophyll§	Spring	-0.32	0.157	0.36	0.105	0.23	0.314	0.27	0.228	-0.95	0.000	-0.95	0.000	-0.28	0.223
Chlorophyll§	Summer	0.24	0.284	0.77	0.000	0.44	0.048	0.20	0.373	-0.66	0.001	-0.41	0.063	0.29	0.193
Chlorophyll§	Autumn	-0.24	0.284	0.87	0.000	0.81	0.000	0.43	0.051	0.21	0.355	-0.16	0.491	0.35	0.115
Phytoplankton‡	Spring	-31313	0.345	-85107	0.009	-30275	0.249	8606	0.047	-767	0.048	-5324	0.000	1940	0.000
Phytoplankton‡	Summer	154452	0.047	42134	0.013	29929	0.178	22403	0.007	6151	0.151	6427	0.047	-62	0.163
Zooplankton**	Summer	0.26	0.232	-0.25	0.255	-0.10	0.661	-0.60	0.003	-0.75	0.000	-0.80	0.000	-0.04	0.856
Mysis††	Spring					0.22	0.683	0.26	0.416	-0.62	0.039	-0.72	0.011	0.83	0.000
Mysis††	Summer					-0.06	0.839	-0.21	0.520	0.03	0.924	-0.52	0.095	0.53	0.082
<b>Shallow</b>															
Bivalves**	Summer					0.11	0.635	-0.84	0.000	-0.55	0.009	0.04	0.868	0.54	0.010
Chironomids**	Summer					-0.01	0.948	0.42	0.050	0.51	0.015	0.05	0.821	0.29	0.181
Diporeia**	Summer					0.02	0.936	-0.41	0.055	-0.84	0.000	-0.94	0.000	-0.08	0.736
Oligochaetes**	Summer					0.04	0.844	0.19	0.397	-0.19	0.388	0.39	0.073	0.13	0.554
Other**	Summer					0.52	0.013	-0.32	0.147	0.31	0.153	0.89	0.000	0.47	0.026
<b>Deep</b>															
Bivalves**	Summer							-0.48	0.023	-0.44	0.040	-0.77	0.000	0.31	0.159
Chironomids**	Summer							0.77	0.000	0.62	0.002	-0.38	0.083	0.20	0.363
Diporeia**	Summer							-0.94	0.000	-0.84	0.000	-0.78	0.000	0.25	0.266
Oligochates**	Summer							0.69	0.000	-0.11	0.635	-0.24	0.278	0.05	0.813
Other**	Summer							-0.28	0.199	-0.12	0.593	0.13	0.572	0.15	0.508

Years included: \*1983–2018 †1983–2019 §1998–2018 ‡2001–2018 \*\*1997–2018 ††2006–2016

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## APPENDIX A – LIST OF THE SAMPLING AND ANALYTICAL STANDARD OPERATING PROCEDURES

The table below provides a list of the current version of the sampling and analytical standard operating procedures supporting the variables highlighted in this report.

### Sampling and Analytical Standard Operating Procedures

GLNPO Method	Title of the Standard Operating Procedure	Version Number, Date
LG205	Standard Operating Procedure for Chloride and Silica in Lake Water (Lachat Method) (FOH)	Revision 01, March 2018
LG209	Standard Operating Procedure for Particulate-Phase Total Phosphorus by Persulfate Oxidation Digestion (Lachat Method) (FOH)	Revision 02, March 2018
LG402	Standard Operating Procedure for Zooplankton Sample Collection and Preservation and Secchi Depth Measurement Field Procedures	Revision 12, February 2017
LG403	Standard Operating Procedure for Zooplankton Analysis	Revision 08.01, February 2017, Updated July 2019
LG406	Standard Operating Procedure for Benthic Invertebrate Field Sampling Procedures	Revision 13, July 2019, Effective March 2019
LG407	Standard Operating Procedure for Benthic Invertebrate Laboratory Analysis	Revision 09, April 2015
LG408	Standard Operating Procedure for Mysid Analysis	Revision 03, July 2019
LG409	Standard Operating Procedure for <i>Mysis</i> Sample Collection and Preservation	Revision 03, July 2019