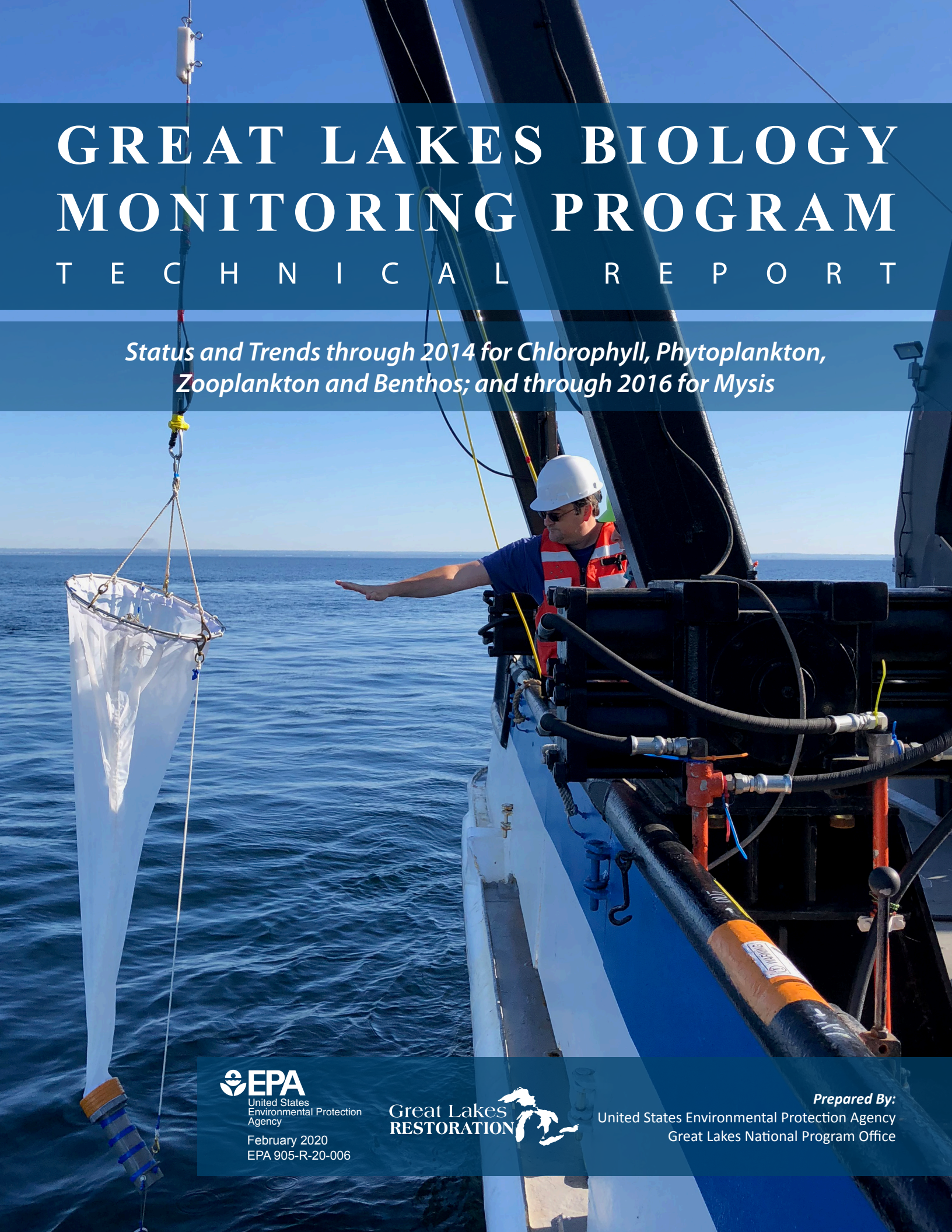


GREAT LAKES BIOLOGY MONITORING PROGRAM

T E C H N I C A L R E P O R T

*Status and Trends through 2014 for Chlorophyll, Phytoplankton,
Zooplankton and Benthos; and through 2016 for Mysis*




United States
Environmental Protection
Agency
February 2020
EPA 905-R-20-006

Great Lakes
RESTORATION 

Prepared By:
United States Environmental Protection Agency
Great Lakes National Program Office

ACKNOWLEDGMENTS

This work was supported 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.” We gratefully acknowledge the support of the following team members in the preparation of this Technical Report:

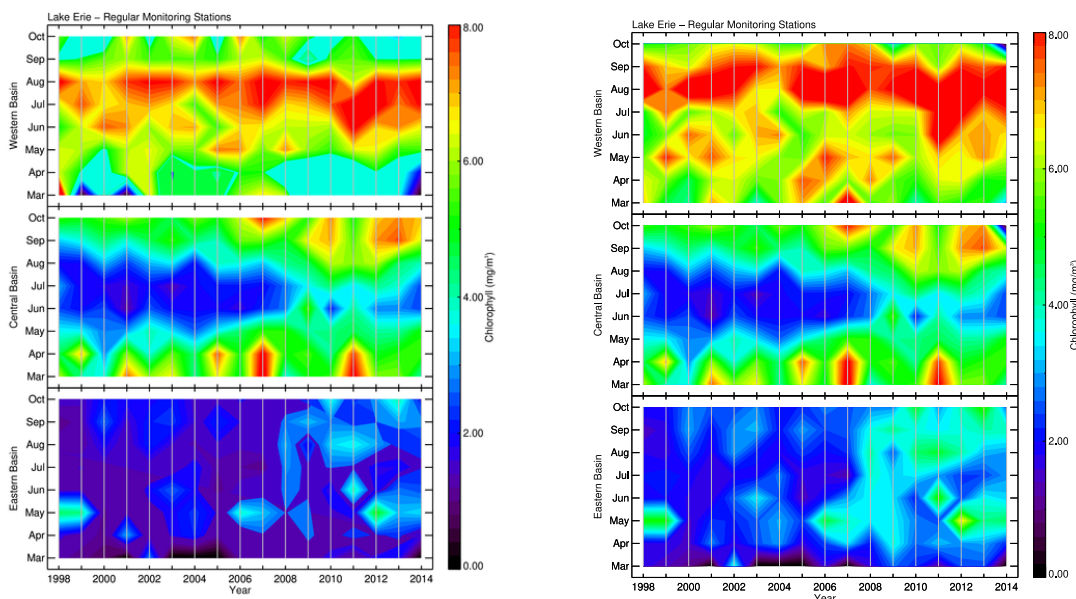
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Cover Photo Credit: Conrad DeBarros

Citation: U.S. EPA 2020. Great Lakes Biology Monitoring Program Technical Report: Status and Trends through 2014 for Chlorophyll, Phytoplankton, Zooplankton and Benthos; and through 2016 for *Mysis*. (EPA 905-R-20-006)

CORRIGENDUM

February 2020 update: Figure 3 (page 9) in the original version of this report (below at left) was incorrect. That figure has been corrected (reproduced below at right) in this version of the report. Errors in the code used to create the plot caused (a) the contours representing chlorophyll concentrations in western Lake Erie (top panel) to be based on twelve months (January–December) rather than on eight months (March–October) as intended and (b) an offset was added to the color table used to represent concentrations in the eastern basin (lower panel). The corrected plot is presented below at right.



The major consequence of error (a) is that the late summer chlorophyll peak in the western basin appeared to occur in July–August rather than in August–September. The consequence of error (b) is that concentrations in eastern basin appeared to be lower than they should have been, though the temporal patterns were unchanged. The interpretation of chlorophyll trends in Lake Erie as represented by Figure 3 also is unchanged.

Figures 19 (page 29) and 20 (page 30) in the original version of this report were incorrect. Erroneously high oligochaete values for Lake Erie in 1997 were presented in Figure 19, and erroneously low values for *Diporeia* in Lake Huron in 1997 were presented in Figure 20. Those figures have been corrected in this version of the report.

Figure 19 in the original version of this report (below at left) was incorrect. That figure has been corrected (reproduced below at the right) in this version of the report.

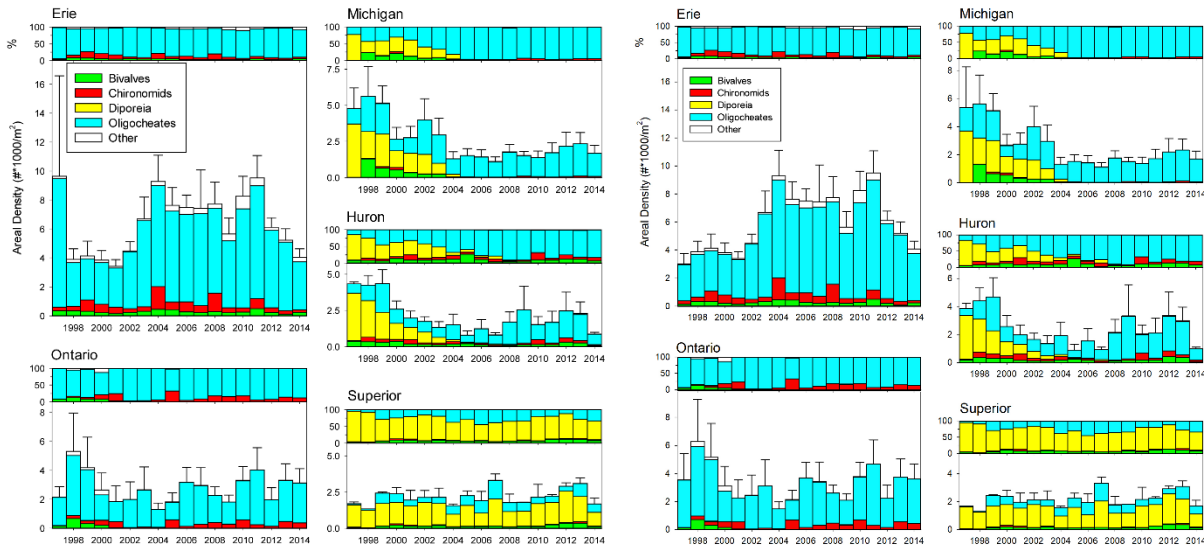


Figure 20 in the original version of this report (below at left) was incorrect. That figure has been corrected (reproduced below at the right) in this version of the report.

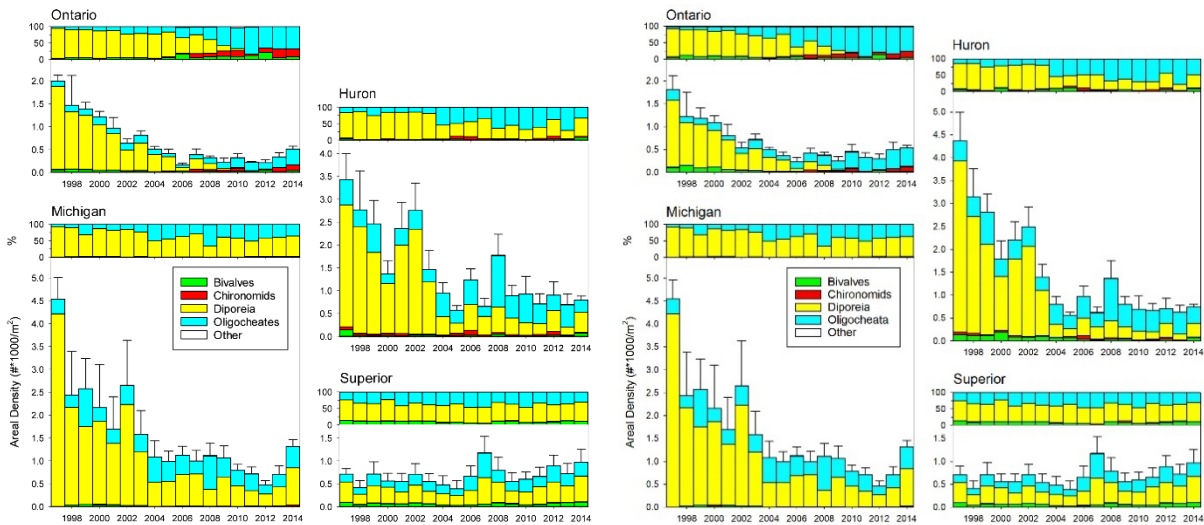


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1 EXECUTIVE SUMMARY

The United States Environmental Protection Agency (USEPA) Great Lakes National Program Office (GLNPO) Great Lakes Biology Monitoring Program (GLBMP) annually adds observations to the most comprehensive collection of consistent data describing the lower food web of the Great Lakes. The data generated by the GLBMP are essential for understanding the current status and recent trends of critical lower food web components of the Great Lakes' ecosystem. This report summarizes the GLBMP historical record of phytoplankton (2001–2014), zooplankton (1997–2014), *Mysis* (2006/2007–2016), and benthic (1997–2014) communities and estimates of remotely sensed chlorophyll (1998–2014) in all five Great Lakes.

LOWER FOOD WEB STATUS (2014)

- Chlorophyll-*a* concentrations in the surface waters estimated from satellite observations continue to be low overall compared to historical levels. Although highly variable in Lake Erie and Lake Ontario, annual average concentrations in lakes Michigan and Huron are at or near the lowest values observed by satellite (1998–2014) and have remained relatively stable in Lake Superior. This suggests an overall decline in primary production in the upper water column in some lakes, though compensating production may be occurring at depths below that sampled by the satellite sensors.
- Phytoplankton biovolumes are higher in the summer than in the spring in all lakes. Spring communities are dominated by diatoms, along with cryptophytes and dinoflagellates. Summer communities in the western and central basins of Lake Erie are dominated by cyanophytes, with diatoms continuing to dominate elsewhere. Low phytoplankton biovolumes relative to previous years in lakes Huron and Michigan are consistent with lower levels of primary production implied by the low chlorophyll-*a* concentrations.
- Zooplankton biomass is also higher in the summer than in the spring. In the summer, the zooplankton volumetric biomass follows the lakes' trophic gradient with highest values in western Lake Erie and lowest values in Lake Superior. Community composition also follows a trophic gradient with a reduction in cladoceran and cyclopoid biomass and an increase in calanoid biomass associated with decreasing productivity. Biomass and community composition are very similar in lakes Huron, Michigan, and Superior. A new (to the Great Lakes) zooplankter (*Thermocyclops crassus*, a small Eurasian cyclopoid copepod) was found in western Lake Erie in the 2014 sampling.
- Mysid shrimps are relatively large crustacean zooplankton, an important link between benthic and pelagic components of the food web, and an especially lipid-rich food source for fish. Mysids are found in all five lakes, though their abundance differs substantially among the lakes. In 2014, *Mysis* was most abundant in Lake Ontario and very rare in Lake Erie. Populations in Lake Huron were about 10% of those in lakes Michigan and Superior.
- The benthic communities in all lakes except Superior are dominated by the invasive quagga mussels. After mussels, oligochaetes are the second most abundant benthic organism in the shallower (< 70 meters) regions of all lakes except Superior. The previously abundant burrowing amphipod (*Diporeia*) has essentially disappeared from the shallow areas of all the lakes except Lake Superior, where they remain dominant. *Diporeia* are still present in the deeper areas of lakes Huron and Michigan, but they are virtually absent from the deeper areas of Lake Ontario.

LOWER FOOD WEB TRENDS

The structure of the lower food web in the Great Lakes has undergone dramatic changes since the GLBMP began consistent multi-trophic level monitoring in 1997. Because the several components of the lower food web are interconnected, analysis of each component is essential for developing an understanding of the different factors that may be responsible for the changes observed from 1997–2014/2016.

- Analysis of satellite-derived estimates show a general increase in late summer chlorophyll-*a* concentrations in western Lake Erie. Concentrations in the central basin of Lake Erie also tended to increase over the years primarily due to a reduction in the duration of the period of post-spring bloom minima. Although much lower than in the west and central basins of Erie, average concentrations in the eastern basin of Lake Erie and in Lake Ontario have been increasing as well. In contrast, the spring bloom in lakes Huron and Michigan have disappeared, being last clearly discernable in Huron in 2004 and Michigan in 2005. These rapid declines may be due to nutrient sequestration and direct consumption of phytoplankton by *Dreissena* mussels (hereafter *Dreissena*) as well as other potential causes. Spring chlorophyll concentrations in Lake Superior also appeared to decline after 2004, though this decline is relatively small and, in the absence of *Dreissena* in that lake, the mechanism for the decline is unclear. In recent years, highest chlorophyll concentrations appear to occur in the autumn in all lakes except Erie.
- In accordance with the chlorophyll-*a* estimates, summer phytoplankton biovolume measurements are variable in both lakes Erie and Ontario. The abundance of cyanophytes has increased during the summer in these lakes, while spring diatom abundances are dominated by centric diatoms. Spring diatom abundances have dropped significantly in lakes Michigan and Huron in fairly close correspondence with the declines in chlorophyll-*a*. In contrast to the other lakes, phytoplankton biovolume estimates for Lake Superior suggest an increase in spring and decrease in summer.
- Summer crustacean communities in Lake Erie are variable with no overall trend. In Lake Ontario, however, the community began a clear shift from cyclopoid dominance to calanoid dominance around 2004. A further shift was noted from 2008–2011 marked by increased biomass of *Leptodiamptomus sicilis*, *Bythotrephes longimanus*, and *Daphnia mendotae*. Both lakes Michigan and Huron showed substantial losses of crustacean biomass again occurring at approximately the same time as the reductions in chlorophyll-*a* and phytoplankton. These reductions were primarily due to declines in cladoceran biomass. Zooplankton populations in Lake Superior have been relatively stable and dominated by calanoid copepods.
- *Mysis* biomass remains low in Lake Erie, where they are only found in the deeper portions of the eastern basin, and remains high in lakes Ontario (where the populations do vary annually but without clear pattern), Michigan and Huron. *Mysis* abundance in Lake Superior, however, has increased since 2007. Populations in Lake Huron are about 10% of those in lakes Michigan and Superior.
- *Dreissena*, in particular quagga mussels, now dominate the benthic communities in all lakes except Superior. The increase in *Dreissena* has been accompanied by the disappearance of *Diporeia* while oligochaete abundances have remained stable. Because of the decline in *Diporeia*, *Dreissena*, and oligochaetes now dominate the benthic community in lakes Erie, Ontario, Michigan, and Huron.

2 INTRODUCTION

In this report we present the biological data collected as part of the United States Environmental Protection Agency (USEPA) Great Lakes National Program Office (GLNPO) Great Lakes Biology Monitoring Program (GLBMP). Data from 2014 are presented in the context of historical data from consistent time series for phytoplankton (2001–2014), zooplankton (1997–2014), mysids (2006/7–2016) and benthos (1997/1998–2014). In addition, chlorophyll-*a* concentrations estimated from remote sensing data, validated with extracted chlorophyll generated from the GLNPO monitoring program ([Lesht et al. 2013](#)), are presented from 1998 to 2014. Our goal is to provide a brief general description of the status of the lower food web of all five Great Lakes in 2014, and to highlight the most important trends in chlorophyll-*a*, phytoplankton, zooplankton and benthos. Community trend results are generally presented in the order to span the trophic gradient: Erie, Ontario, Michigan, Huron, and Superior.

USEPA GLNPO has conducted regular monitoring of the Great Lakes since 1983. This GLBMP helps EPA to satisfy our statutory requirements under section 118 of the Clean Water Act to establish a Great Lakes system-wide surveillance network to monitor the water quality of the Great Lakes. It also helps satisfy our obligations under the [Great Lakes Water Quality Agreement](#) to “monitor

environmental conditions so that the Parties may determine the extent to which General Objectives, Lake Ecosystem Objectives and Substance Objective are being achieved,” and “undertake monitoring and surveillance to anticipate the need for further science activities and to address emerging environmental concerns.” Further, this program allows EPA to meet commitments in the GLRI Action Plan II to “assess the overall health of the Great Lakes.” The monitoring effort is designed to track whole-lake responses to changes in environmental stressors, so sampling is largely restricted to the relatively homogeneous offshore waters of each lake. As the initial focus of the surveys was on chemical eutrophication and the response of the lakes to changes in phosphorus loading, spring surveys were originally initiated to provide data to establish whole-lake nutrient concentrations, while summer surveys were aimed at determining epilimnetic depletion and hypolimnetic enrichment of nutrients. GLNPO also uses the spring and summer surveys to collect lower food web data that are important for fisheries management and non-native species detection. Because of the logistical challenges of sampling a waterbody as large as the Great Lakes, temporal resolution is currently limited to two well-defined periods during the year: the spring isothermal period (March/April/May depending on ice cover), and the stable, stratified summer period (August). More context on the development of the GLNPO surveys is provided in Barbiero *et al.* (2018a) and Burlakova *et al.* (2018b).

3 HISTORICAL SAMPLING CONTEXT

GLNPO's monitoring of the Great Lakes began in 1983 in lakes Michigan, Huron and Erie. Sampling was extended to include Lake Ontario in 1986 and Lake Superior in 1992. In addition to a wide range of physical and chemical parameters, the lakes have been sampled for phytoplankton and zooplankton since the inception of the program. However, inconsistent data collection over the years has resulted in truncated time series for these two variables. Inconsistencies in phytoplankton taxonomic identification have led to a break in comparability between older and more recent data; thus, in this report we present phytoplankton data from only 2001–2014, which represents years for which a consistent time series exists. From 1983–1996, zooplankton tows were collected primarily from a depth of 20 meters. Such samples do not cover all depths inhabited by zooplankton, and show large differences between samples collected day and night; therefore, they represent an incomplete picture of the zooplankton community. Tows to a depth of 100 meters were added to the monitoring program in 1997. Data from these deeper tows are reported here, as they are more representative of the total zooplankton community. Sampling for *Mysis diluviana*, a key zooplankton species in the offshore food web, was initiated in 2006 in lakes Michigan and Huron and in 2007 in the other three lakes. While historically enumerated in GLBMP zooplankton samples, this crustacean species is not effectively sampled with the standard 100-meter zooplankton tows. A benthic invertebrate biomonitoring program was initiated in summer of 1997. *Dreissena* spp. (the zebra mussel *D. polymorpha*, and the quagga mussel *D. rostriformis bugensis*) were first enumerated in 2003. A remote sensing component was added to the program in 2010 making it possible to fill the temporal and spatial gaps for chlorophyll-*a* in the field survey data and assess spatial variability on kilometer scales back to 1998.

4 DESCRIPTION OF SAMPLING METHODS

During the annual surveys, samples for nutrients, phytoplankton, and zooplankton are collected from 72 regular open water stations (Appendix A provides a complete list of standard operating procedures). Mysis samples are taken when a station is visited at night. Benthos samples are taken from 33 of these “plankton” stations, as well as from an additional 25 exclusively benthos stations (Figure 1) during the August survey. In 2014, spring sampling was undertaken on lakes Michigan, Huron, Erie and Ontario between April 17 and April 26, and on Lake Superior between May 15 and May 18. Extensive ice cover in the winter of 2013–14 delayed spring sampling in all lakes, which usually commences the last week of March or the first week of April. Summer sampling occurred between August 6 and August 28.

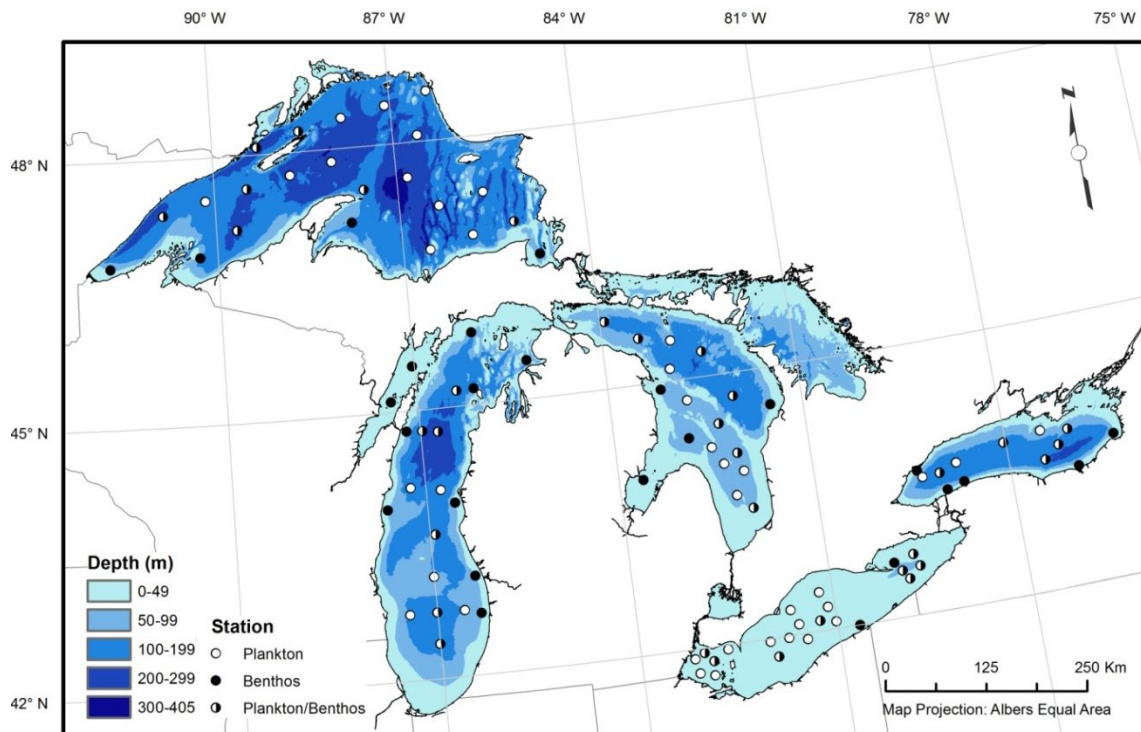


Figure 1. Map of GLNPO long-term monitoring stations for annual spring and summer nutrients and plankton sampling (includes phytoplankton, zooplankton, *Mysis*) and summer benthos sampling.

4.1 PHYTOPLANKTON

At each station, integrated samples for phytoplankton enumeration were created from a composite of water samples taken at discrete depths (spring integrated sample: surface, 5 meters, 10 meters, and 20 meters; summer integrated sample: 2 to 4 depths in the epilimnion; summer deep chlorophyll layer also sampled when present) with Niskin bottles mounted on a SeaBird Carousel Water Sampler. Samples were preserved in the field with Lugol's solution, and with formalin upon return to the laboratory. From 2001–2006, phytoplankton were analyzed from a limited number of stations.

4.2 ZOOPLANKTON AND MYSIDS

Two vertical net tows (one 20-meter depth tow and one 100-meter tow) were performed at each site for zooplankton sample collection, except in Lake Superior where duplicate net tows are collected, using a 0.5-meter diameter conical net

equipped with a TSK (Tsurumi Seiki Co., Ltd.) flowmeter. The first tow was taken from 20 meters below the water surface or 2 meters above the bottom, whichever was less, using a 64- μ m mesh net, and the second tow was taken from 100 meters below the water surface or from 2 meters above the bottom, whichever was less, using a 153- μ m mesh net. Only data from 153- μ m mesh net tows are reported here.

A larger 1-meter diameter net towed vertically from 2 to 5 meters from the bottom to the surface at night was used to measure mysid abundance. Replicate tows were performed at stations visited at night from 1 hour after sunset to one hour before sunrise with all lights except navigation lights on the research vessel turned off. Only red light that is not visible to mysids ([Gal et al. 1999](#)) was used during these tows. Stations shallower than 30 meters are typically not sampled for mysids. Mysids avoid even very low light levels ([Gal et al. 1999](#); [Boscarino et al. 2010](#)) and can avoid smaller-sized nets.

4.3 BENTHOS

During the summer survey, quantitative samples for benthic invertebrate analysis were collected from selected stations using a Ponar grab sampler (surface area 0.0523 m²). Samples were taken in triplicate, and material sieved through a 500- μ m mesh net. Samples were preserved with buffered formaldehyde with Rose Bengal to a final concentration of 5–10% formaldehyde.

5 LABORATORY METHODS

5.1 PHYTOPLANKTON

Phytoplankton were identified and abundances were estimated using the Utermöhl technique (Lund et al. 1958) at a magnification of 500x, with diatoms other than *Rhizosolenia* identified as either centrics or pennates. Diatoms were identified, and relative abundances determined, from permanent slide mounts at 1250x. Relative proportions of each taxon of centrics and pennates were then multiplied by the appropriate Utermöhl quantitative counts. At least 10 individuals of each taxon were measured per sample, and cell volumes computed using appropriate geometrical formulae listed in EPA SOP LG401 (rev 5, 2010). Primary taxonomic keys used were Prescott (1962), Krammer and Lange-Bertalot (1986, 1991, 1997), Patrick and Reimer (1966, 1975) and Germain (1981).

5.2 ZOOPLANKTON AND MYSIDS

Samples for zooplankton analysis were split in the lab using a Folsom plankton splitter, and four stratified aliquots examined per sample using a stereoscopic (crustaceans) or compound (rotifers) microscope. Two subsamples of 200–300 crustaceans were identified to the lowest practical taxonomic group (mostly species). Rarer species were enumerated in additional subsamples. *Mysis*, *Cercopagis* and *Bythotrephes* were identified in the whole sample. Copepods were identified as immature, mature males or mature females. Nauplii, veligers and rotifers were not counted in the 100-m tows and therefore not reported here. Primary taxonomic keys used were Balcer *et al.* (1984), Hudson *et al.* (1998), Brooks (1957),

Evans (1985), Edmondson (1959) and Rivier (1998). Length measurements were made on the first twenty individuals of each species encountered per sample and dry mass calculated from length-weight regressions (listed in EPA SOP LG403, rev 8, 2017). Because constants for length-weight regressions were updated in 2017, the data presented here deviate somewhat from earlier publications. All data since the initiation of the 100-meter deep tows in summer 1997 are presented except for spring 2000, which has not yet been analyzed. Data are presented as volumetric biomass (mg DW/m³). Comparisons of volumetric density in the water column across lakes with different maximum depths is problematic because individuals are not evenly distributed throughout the water column. As a result, low zooplankton densities in deep water will dilute average water column biomass estimates in deep lakes. However, comparisons among the deeper lakes is appropriate because the depths sampled are similar. Comparisons across time are the same regardless of whether whole water column summed values (areal) or average values per m³ are used since the same stations are visited each year.

Mysids were counted from the mysid net sample and the first 100 individuals were photographed and measured (tip of rostrum to end of abdomen) following EPA SOP LG408 (rev 2, 2017). Lengths were converted to dry biomass using Johannsson (1995) length-weight regression as modified by Rudstam *et al.* (2008).

5.3 BENTHOS

Benthic organisms were picked out of samples in the laboratory using a dissecting microscope following EPA SOP LG 407 (rev 9, 2015). Enumeration of *Dreissena* at each station began in 2003; measurements of shell length commenced in 2007; and measurements of total wet weight (with shell) commenced in 2012. Other major taxonomic groups (amphipods, chironomids, oligochaetes, mollusks) were identified, counted and weighed after being blotted dry. After counting and weighing by size category, chironomids and

oligochaetes were mounted on slides for identification. *Dreissena* were identified to species, and then divided, counted and weighed by 5-mm size fractions to the nearest 0.0001 gram after being blotted dry on absorbent paper. Adult oligochaetes were identified to species; immatures were taken to the lowest taxonomic level possible, usually family. Oligochaete fragments, though counted, were excluded from density but used for biomass estimates. Chironomids were identified to the lowest practical taxonomic level, usually genus. Other invertebrates were identified to species, when possible. All unmounted specimens after identification and weighting were preserved in a mixture of ethanol (85%), water (10%) and glycerin (5%).

6 REMOTE SENSING OF SURFACE CHLOROPHYLL

6.1 DESCRIPTION OF ANALYSIS

In situ measurements of chlorophyll-*a* concentration made during the regular surveys (to be reported separately) were supplemented by estimates of chlorophyll-*a* concentration in the surface waters derived from satellite observations. Although limited to the surface waters and subject to interference by clouds, the satellite-derived estimates provide frequent (as often as daily) and high spatial resolution (approximately 1 kilometer) observations throughout the year, making it possible to discern both spatial and annual temporal patterns. The satellite-derived estimates we report here are based on a band-ratio retrieval algorithm developed using GLNPO monitoring data (Lesht et al. 2013; 2016) applied to data from the Sea-viewing Wide Field-of-view (SeaWiFS, 1998–2007) and Moderate resolution imaging spectroradiometer (MODIS, 2002–present) ocean color sensors.

6.2 2014 SURFACE CHLOROPHYLL

Monthly averages of the satellite-estimated surface chlorophyll concentration in each lake are shown in [Figure 2](#). The images in the upper panels are based on the by-pixel means of all the satellite (MODIS) scenes collected during the indicated month. For lakes Huron, Ontario, Michigan and Superior, the values plotted in the lower panel line plot are the monthly averages of chlorophyll concentration in those main-lake pixels in water depths exceeding 30 meters. These averages do not include the major embayments of Saginaw Bay, Georgian Bay and the North Channel in Lake Huron and Green Bay in Lake Michigan. The Lake Erie basin averages include all the pixels from all depths in each of the three basins but excluding Lake St. Clair. Black areas in March and April are regions where no satellite data were recovered due to ice cover.

In 2014 March–October average surface chlorophyll-*a* concentrations in the lower lakes decreased following the general trophic gradient from western Lake Erie (9.4 mg/m³) through Lake Ontario (4.1 mg/m³). In the upper lakes, surface chlorophyll-*a* concentration was highest in Lake Superior (1.3 mg/m³) followed by lakes Michigan (1.0 mg/m³) and Huron (0.8 mg/m³). The spatial distributions of chlorophyll-*a* in the lakes during the year varied, with the highest values generally occurring in the late summer through fall. In Lake Erie, high values were observed in the western basin beginning in July that persisted and spread through the central basin in the following months. In Lake Ontario, high values began appearing along the northern and southern coasts in August but concentrations decreased in October. Flux of high chlorophyll-*a* concentrations typical of the major embayments in lakes Michigan and Huron began to influence the main lake basins of those lakes in late Summer. In Lake Superior, higher concentrations in the western sections of the lake beginning in September and October account for increases in lake average concentration late in the year.

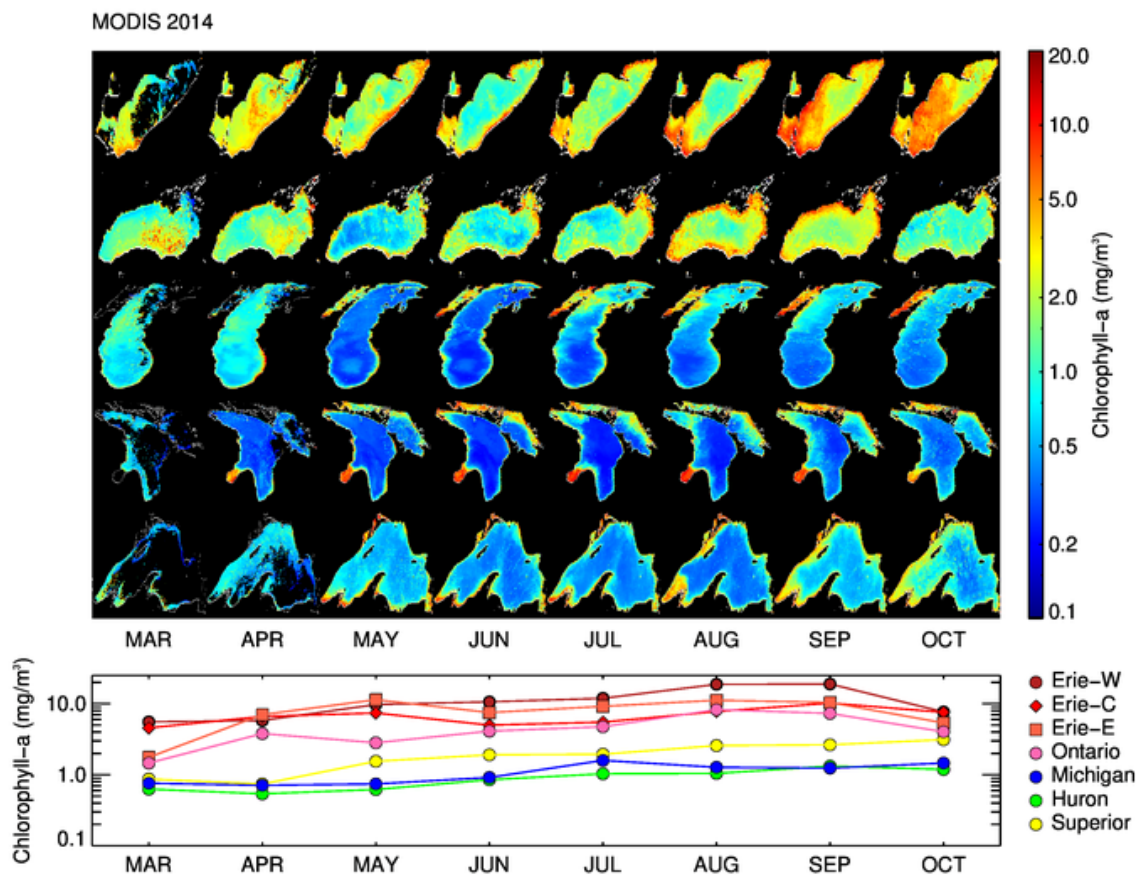


Figure 2. Monthly average surface chlorophyll-*a* concentrations estimated from satellite observations. Upper panels are by-pixel averages of all satellite images collected during the month. The lower panel shows the average concentrations in the three basins of Lake Erie and in the main basins (excluding major embayments) of each of the other lakes. Note that the chlorophyll-*a* concentrations in both the images and the line plot are depicted on a log scale. Areas shown in black during the spring months are regions where ice-cover interfered with the chlorophyll-*a* retrieval. Lake images are not projected nor drawn to scale.

6.3 SURFACE CHLOROPHYLL TRENDS FROM 1998 TO 2014

Reliable estimates of surface chlorophyll concentration based on observations made by satellites date from 1998. Figures 3–7 illustrate how the monthly average chlorophyll-*a* concentration in each of the lakes (each basin for Lake Erie) has changed from 1998 to 2014. For each satellite image collected in every month-year combination, we extracted the satellite chlorophyll-*a* estimates from the pixels nearest to the sampling stations (see [Figure 1](#) for station locations) and averaged these values. We used the

satellite estimates extracted from the station locations because they are the closest match to the other datasets reported here that arise from ship-borne sampling. Although these average values are not samples from a continuous function in month-year space as would be mathematically required for contour analysis, displaying them in a contour or isopleth plots helps to visualize changes in the phytoplankton cycle both during and across years.

LAKE ERIE

The satellite observations reveal some changes in the annual surface chlorophyll-*a* concentration pattern across the years in Lake Erie ([Figure 3](#)). In

the western basin, increases in chlorophyll-*a* concentration in the late summer, possibly associated with harmful algal blooms have generally intensified in the years since 2006. Average concentrations in the spring also have tended to increase in this time period. In the central basin, the most prominent change is the narrowing

(in time) and ultimate absence of a summer concentration minimum between 2008 and 2013 thus creating a single summer peak in chlorophyll rather than separate peaks in the spring and autumn. Concentrations in the eastern basin are lower than in the other two basins but also show an increasing tendency since 2006, especially in late summer.

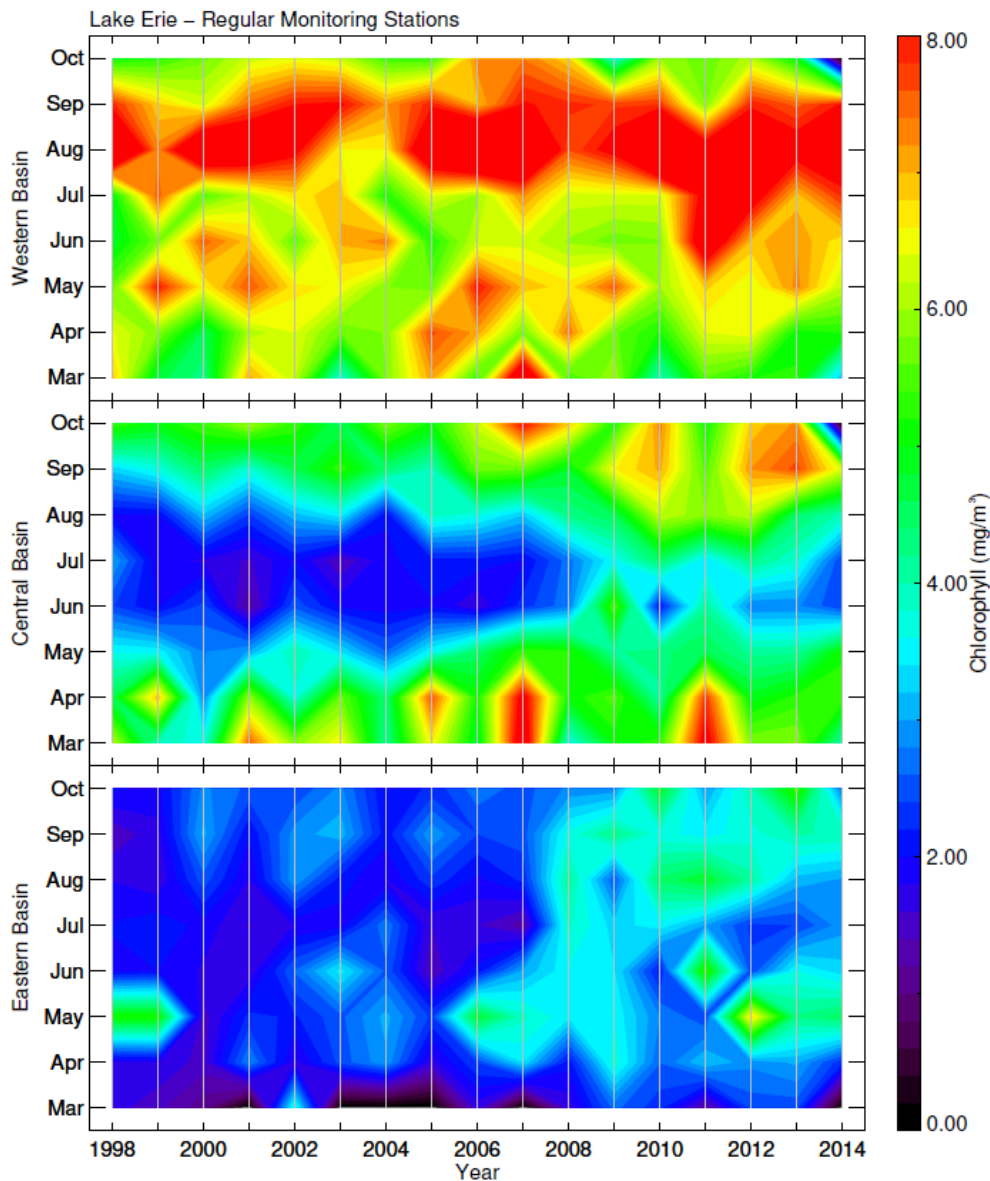


Figure 3. Monthly averaged (March–October) surface chlorophyll-*a* concentrations at station locations in Lake Erie for the period 1998–2014. The top panel is based on the western basin stations, the middle panel on the central basin stations, and the bottom panel on the eastern basin stations.

LAKE ONTARIO

The seasonal trend in Lake Ontario annual chlorophyll is generally bi-modal with both late spring and early autumn peaks separated by a summer minimum. The magnitudes of the peaks and the length of the summer minimum has been variable, but appear to have been increasing since 2007 ([Figure 4](#)).

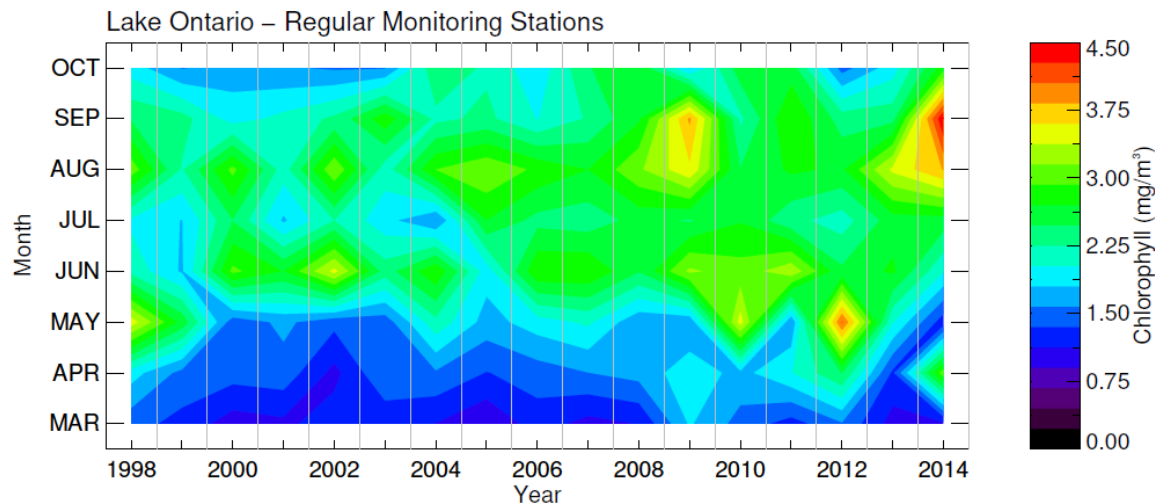


Figure 4. Monthly averaged (March–October) surface chlorophyll-*a* concentrations at station locations in Lake Ontario for the period 1998–2014.

LAKE MICHIGAN

Seasonal trends in Lake Michigan phytoplankton as measured by surface chlorophyll-*a* concentration have changed dramatically over the period of observation ([Figure 5](#)). Before 2005, chlorophyll-*a* peaked during the spring bloom period. Since about 2005, however, the spring chlorophyll-*a* peak has been absent and the annual average concentration has steadily declined. First reported by Lesht and Wortman ([2007](#)), the absence of the spring bloom has been most often attributed to direct filtration by dreissenid mussels ([Kerfoot et al. 2010](#)), although subsequent research has suggested the potential importance of other factors such as nutrient interception by nearshore populations of dreissenid mussels and meteorological influence on phosphorus dynamics ([Barbiero et al. 2018b](#)).

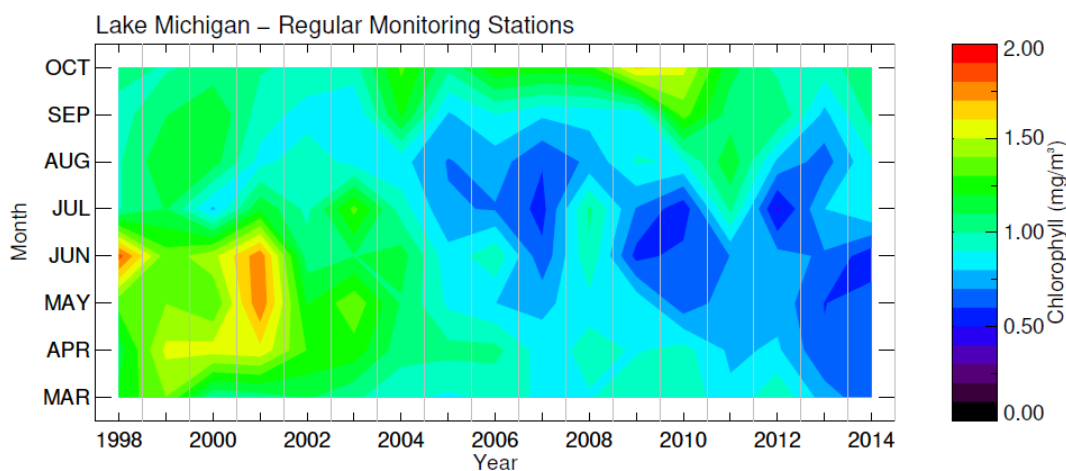


Figure 5. Monthly averaged (March–October) surface chlorophyll-*a* concentrations at station locations in Lake Michigan for the period 1998–2014.

LAKE HURON

The change in the seasonal chlorophyll-*a* pattern in Lake Huron ([Figure 6](#)) is very similar to that observed in Lake Michigan. The well-defined spring peak in surface chlorophyll-*a* concentration found prior to 2004 is absent in subsequent years. The similarity between the changes in lakes Huron and Michigan is of particular interest because the population of dreissenid mussels in Lake Huron is much lower than in Lake Michigan suggesting that the decline in the spring bloom in Lake Huron may result from different or from a combination of causes ([Barbiero et al. 2018b](#)). Of all the Great Lakes, Lake Huron has the lowest overall chlorophyll concentration.

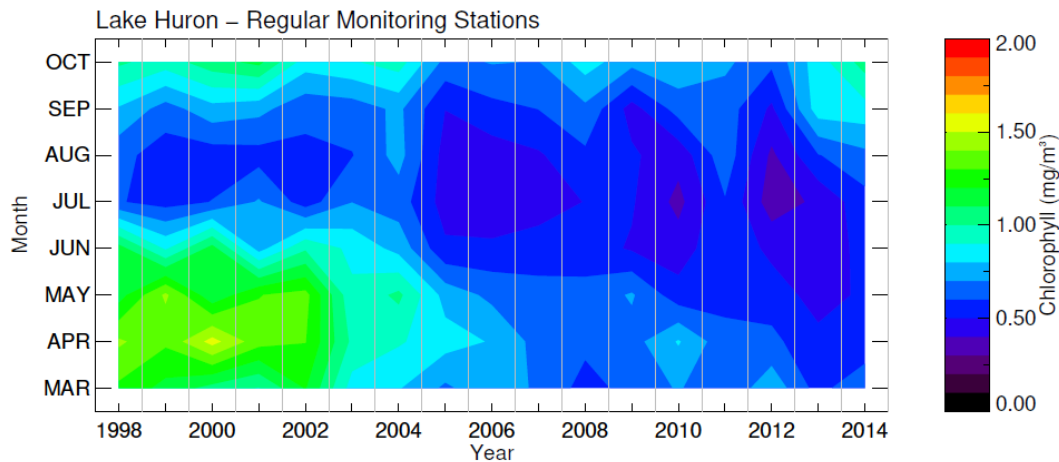


Figure 6. Monthly averaged (March–October) surface chlorophyll-*a* concentrations at station locations in Lake Huron for the period 1998–2014.

LAKE SUPERIOR

Although not as dramatic as the changes in lakes Huron and Michigan, Lake Superior also appears to have experienced a decline in spring peak chlorophyll-*a* since 2005 ([Figure 7](#)). Lake Superior chlorophyll-*a* concentrations peaked regularly during April–May prior to 2005, but since then the highest concentrations have been observed during the fall. Because dreissenid mussels have not colonized Lake Superior (except for some isolated coastal areas) this apparent chlorophyll-*a* decline must result from some other mechanism.

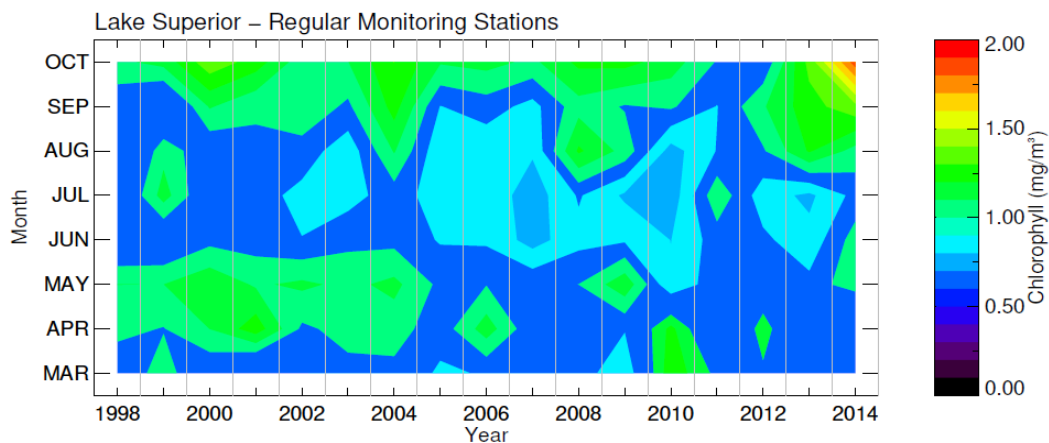


Figure 7. Monthly averaged (March–October) surface chlorophyll-*a* concentrations at station locations in Lake Superior for the period 1998–2014.

7 PHYTOPLANKTON

7.1 COMMUNITY COMPOSITION IN 2014

SPRING

During spring, a total of 198 phytoplankton taxa was found. Total phytoplankton sample biovolumes across the lakes ranged from approximately $5 \times 10^4 \mu\text{m}^3/\text{mL}$ in Lake Superior to approximately $1 \times 10^6 \mu\text{m}^3/\text{mL}$ in the central basin of Lake Erie ([Figure 8](#)). Lakes Superior, Michigan and Huron phytoplankton communities consisted mainly of centric and pennate diatoms, cryptophytes and dinoflagellates in spring, although the proportions of each group varied among the lakes. In Lake Erie, the western basin of Lake Erie phytoplankton community was dominated by centric and pennate diatoms in spring. The central basin and eastern basin phytoplankton communities had high levels of centric diatoms and dinoflagellates in spring. Lake Ontario's spring phytoplankton community was dominated by centric diatoms, dinoflagellates and cryptophytes.

SUMMER

During summer, a total of 223 phytoplankton taxa was found. Summer phytoplankton communities in lakes Superior, Michigan and Huron consisted mainly of centric and pennate diatoms, dinoflagellates and cryptophytes (particularly in Lake Huron) ([Figure 12](#)). The western and central basin of Lake Erie phytoplankton communities were dominated by cyanobacteria in summer, while the eastern basin had high pennate diatom biovolumes. Lake Ontario's phytoplankton community was dominated by pennate diatoms, cryptophytes and dinoflagellates in summer.

7.2 COMMUNITY COMPOSITION FROM 2001 TO 2014

Hundreds of unique taxa were encountered in the 2001–2014 phytoplankton dataset. The assemblages comprised centric diatoms, pennate diatoms, chrysophytes, chlorophytes, cryptomonads, cyanophytes, euglenoids, dinoflagellates and rare, unknown entities. Spring biovolumes were highest in Lake Erie ([Figure 8](#)), and dominated by the centric diatom ([Figure 9](#)) *Aulacoseira islandica*, consistent with recent findings of blooms of this taxon ([Reavie et al. 2016](#); [Barbiero et al. 2006](#)). Summer biovolume tended to be highest for the cyanophyte *Microcystis aeruginosa* in Lake Erie's western basin, but there were also some high abundances of diatoms, dinoflagellates and cryptophytes. These data illustrate how some taxa with low numeric abundance and large cell size (e.g., the dinoflagellate *Peridinium* in spring Lake Ontario) can comprise an important component of lake productivity.

Overall, the dominant phytoplankton in spring tended to be opportunistic diatom taxa (*Aulacoseira*, *Stephanodiscus*) which make use of abundant nutrients such as phosphorus and silica before declining due to nutrient limitation later in the year. Lake Erie had the highest biovolume of dominant taxa; algal biovolume overall was relatively low in the upper lakes (Superior, Huron, Michigan; [Figure 8](#)). In the summer, the upper lakes were dominated by diatoms such as *Synedra* and *Cyclotella* and in Huron by large-celled dinoflagellates.

7.3 COMMUNITY TRENDS FROM 2001 TO 2014

Temporal changes in phytoplankton abundance are shown through histograms that summarize within-lake and sometimes within-basin averages (Figures 9–12). In the 14 years of data presented, certain phytoplankton taxa in certain lake basins have flourished and other taxa have declined. These changes are attributed to food web shifts and changes in water quality. Likely reasons for these changes include selective grazing by herbivores, changes in nutrient concentrations and availability (e.g., Lake Erie) and climate-related changes in physical properties of the lakes such as extended ice-free seasons and enhanced summer stratification. These mechanisms are discussed in greater detail in Reavie *et al.* (2014, 2017).

LAKE ERIE (Figures 9, 11)

Lake Erie's western basin was typically dominated by centric diatoms in the spring (e.g., *Diatoma*, *Aulacoseira*) although recently large-celled pennate diatoms (*Surirella*) and euglenoids (*Phacus*) have also comprised a significant portion of the assemblage. The last decade exhibited large fluctuations in algal abundance and composition in the spring, but summer has seen a persistent increase in cyanophytes (dominated by *Aphanocapsa* and *Microcystis*). There is evidence that summer algal biovolume is increasing, but year-to-year fluctuations are unpredictable with especially high abundance in 2011.

Spring in Lake Erie's central basin was overwhelmingly dominated by the filamentous centric diatom *A. islandica*. Spring diatom abundances remain high in the basin, but data suggest a decline since the 2006 peak. Summer assemblages reveal increases in algal density and biovolume, particularly for cyanophytes (e.g., *Aphanocapsa* and *Aphanizomenon*) and a periodic high abundance of pennate diatoms (*Fragilaria crotonensis*).

Lake Erie's eastern basin was similarly dominated by *A. islandica* in the spring, but little change was observed for the last 10 years. Summer data indicated an increase in biovolume

in 2008 and 2009, particularly by cyanophytes (e.g., *Aphanocapsa*) and pennate diatoms (*Fragilaria crotonensis*).

LAKE ONTARIO (Figures 10, 12)

While not easily apparent in the histogram, overall Lake Ontario phytoplankton density and biovolume increased over the last 14 years, as detected by Kendall rank correlation testing ($P < 0.05$). During that time, the relative density of dinoflagellates (*Peridinium*) increased in the spring. Summer cyanophytes (largely *Aphanocapsa*) increased in number but the assemblage is dominated by pennate diatoms (e.g., *Fragilaria crotonensis*), cryptophytes (*Cryptomonas*) and dinoflagellates (*Ceratium hirundinella*).

LAKE MICHIGAN (Figures 10, 12)

Cell density in Lake Michigan is dominated by cyanobacteria, but in terms of biovolume, spring in the northern basin is dominated by dinoflagellates (e.g., *Gymnodinium helveticum*) and centric diatoms while the southern basin has large amounts of cryptophytes. In the summer, Lake Michigan is dominated by diatoms (e.g., *Cyclotella comta*, *Fragilaria crotonensis*). There has been a notable decline in spring biovolume in the southern basin since 2001 and since approximately 2008 there has been a greater relative dominance by cryptophytes (*Cryptomonas* and *Rhodomonas*). The major period of algal decline occurred in spring 2002 and 2003 in the northern basin and 2005 in the southern basin. A similar decline has not been observed for summer phytoplankton; summer algal biovolume has been variable.

LAKE HURON (Figures 10, 12)

Cyanophytes (e.g., *Aphanizomenon*, *Aphanocapsa*) dominate Lake Huron's phytoplankton in terms of cell densities, but in terms of biovolume Lake Huron is dominated by diatoms (e.g., *Cyclotella*), cryptophytes and chrysophytes in the spring, and by diatoms (e.g., *Tabellaria*, *Cyclotella*), chrysophytes and dinoflagellates (e.g., *Peridinium*) in the summer. Since 2001, Lake Huron has seen a decline in spring biovolume with the major

transition occurring from 2002 to 2003 with a significant drop in diatom abundance. Summer data reveal a similar, less dramatic decadal decline with the main drop occurring from 2001 to 2002, overall suggesting that the major shift in Lake Huron's phytoplankton community occurred predominantly between the spring and summer sampling seasons in 2002. Since approximately 2003, the data suggest some recovery in algal abundance in the northern basin and in the spring in the southern basin.

LAKE SUPERIOR (Figures 10, 12)

Phytoplankton biovolume in Lake Superior is dominated by diatoms, chrysophytes, cryptophytes and dinoflagellates in the spring, and more so by diatoms in the summer. Over the 14 years, little overall change in algal abundance and composition is evident in the histograms, although trend analysis (Kruskal-Wallis, $P < 0.05$) detected significant increases in overall abundance in the spring and a decrease in summer abundance.

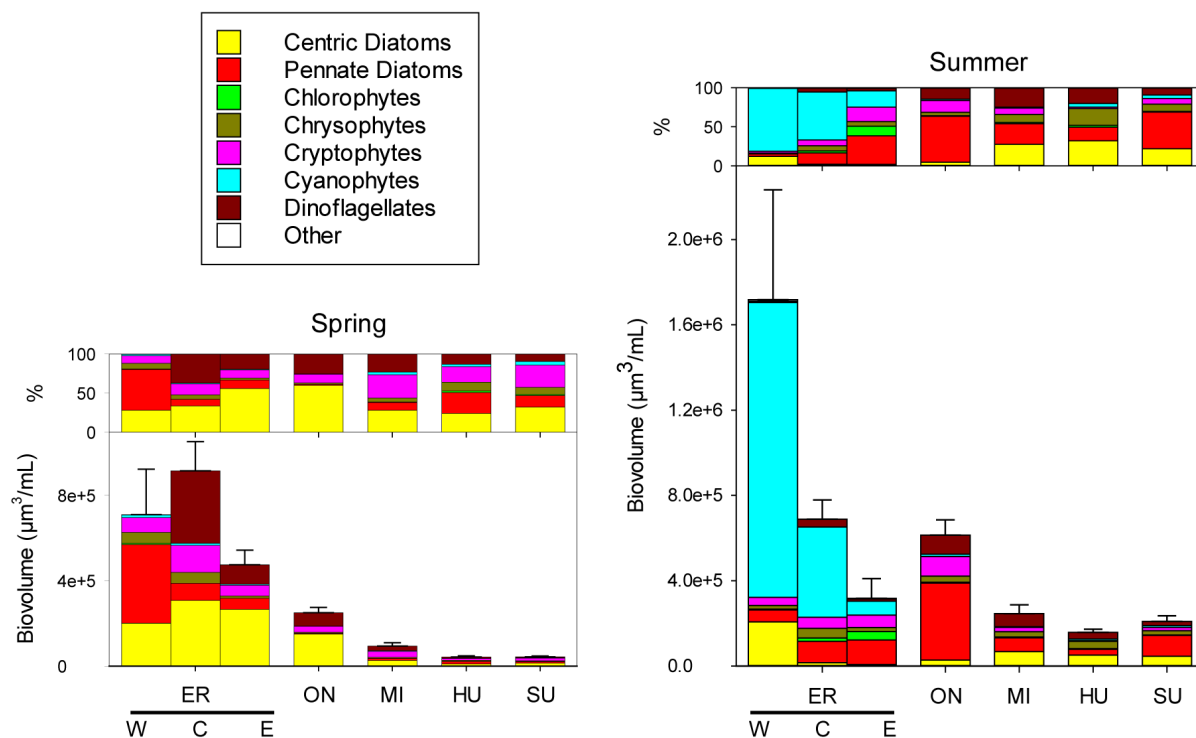


Figure 8. Phytoplankton biovolume (bottom panels) and percent biovolume (top panels), by major taxonomic group, for spring and summer, 2014.

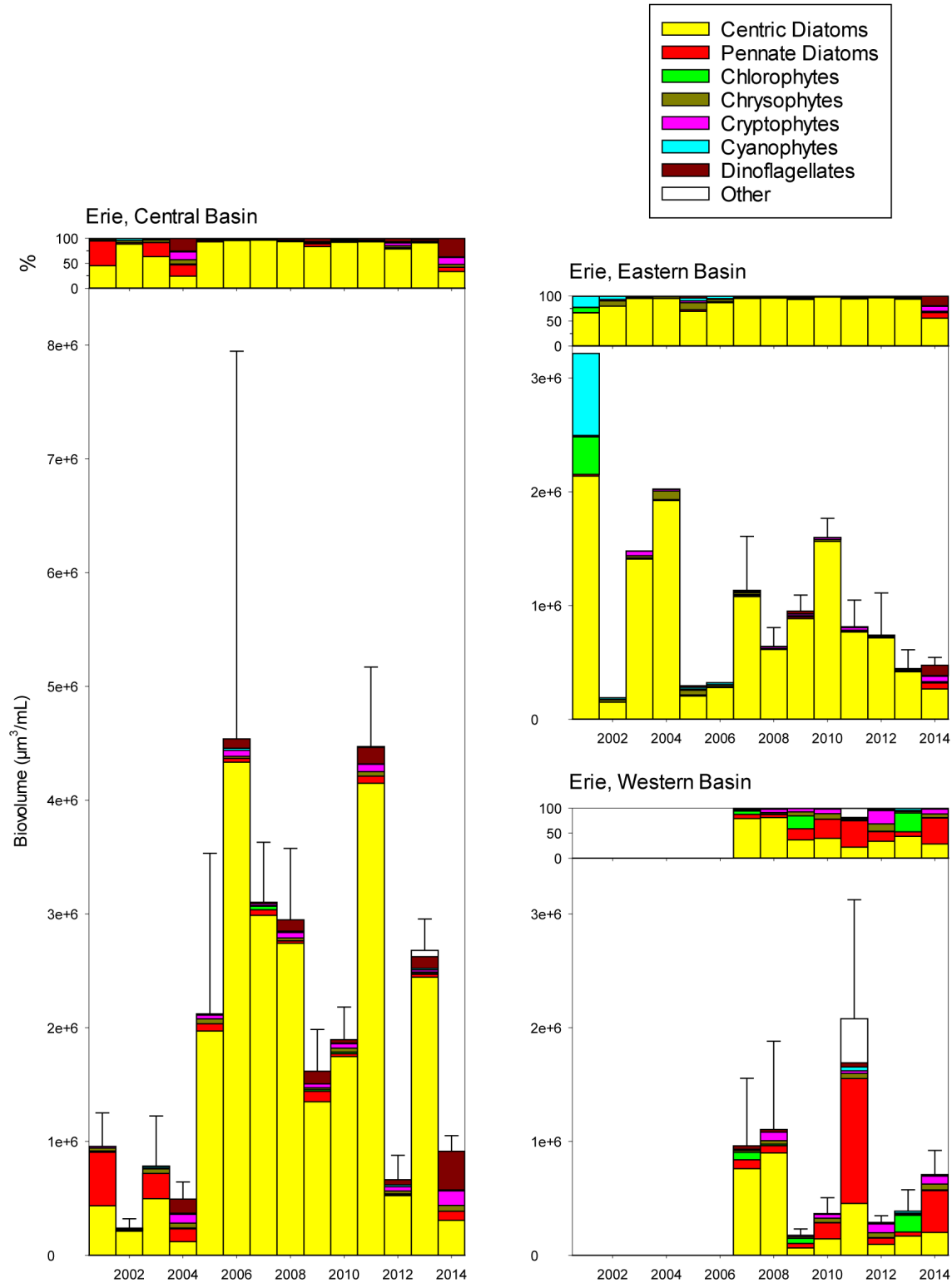


Figure 9. Phytoplankton biovolume (bottom panels) and percent biovolume (top panels), by major taxonomic group, in Lake Erie for spring 2001–2014. Error bars represent one standard error.

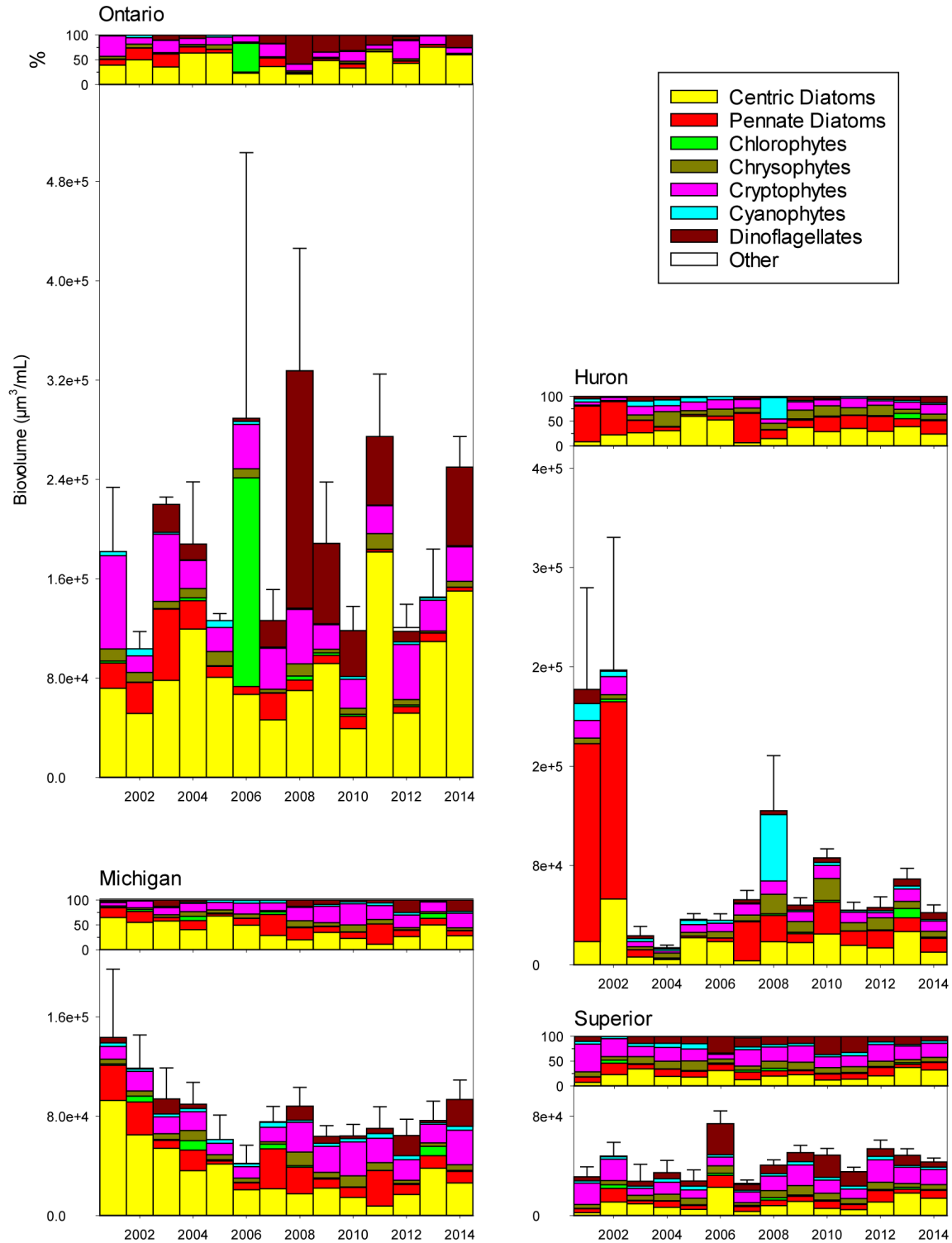


Figure 10. Phytoplankton biovolume (bottom panels) and percent biovolume (top panels), by major taxonomic group, in lakes Ontario, Huron, Michigan and Superior for spring 2001–2014. Error bars represent one standard error.

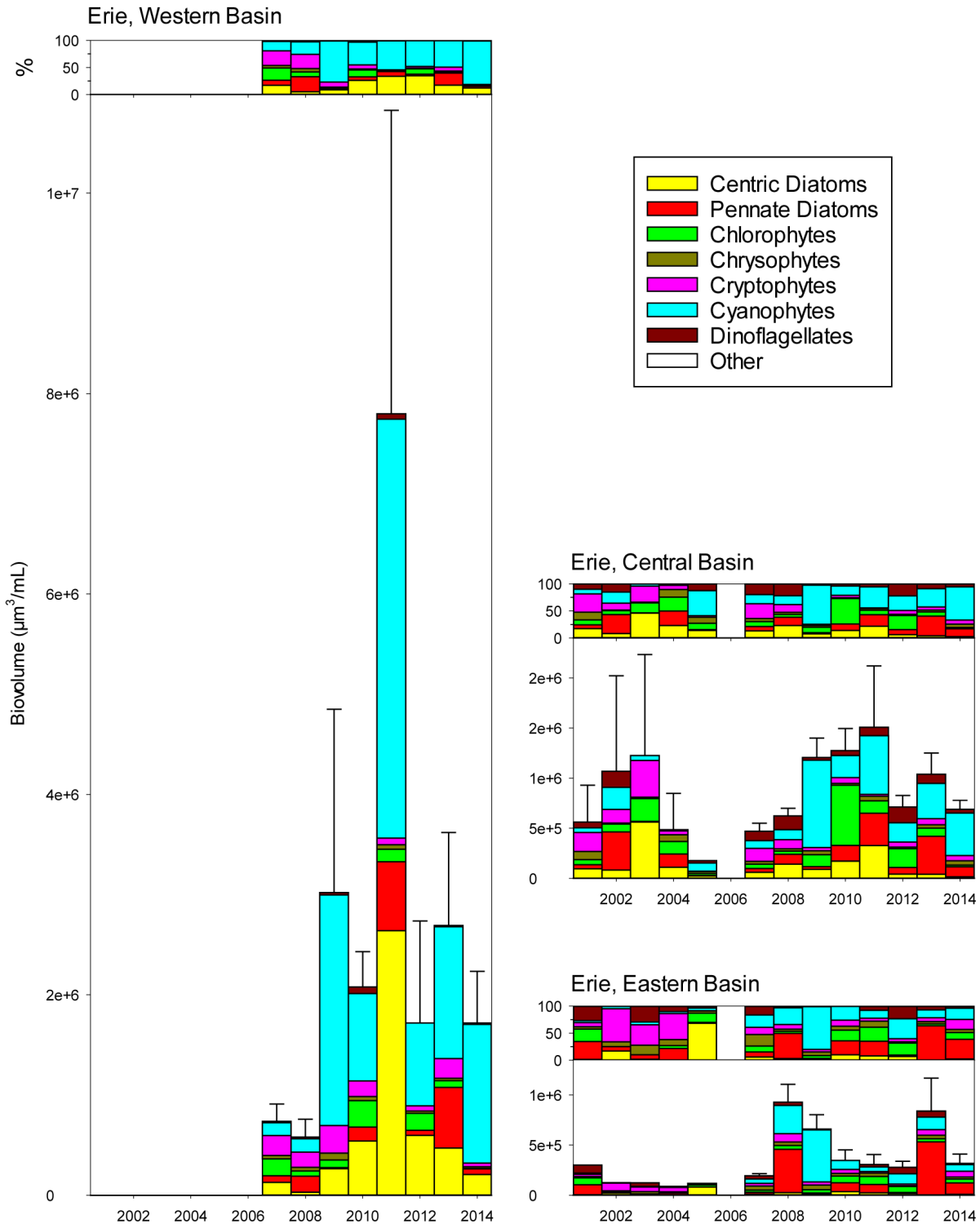


Figure 11. Phytoplankton biovolume (bottom panels) and percent biovolume (top panels), by major taxonomic group, in Lake Erie for summer 2001–2014. Error bars represent one standard error.

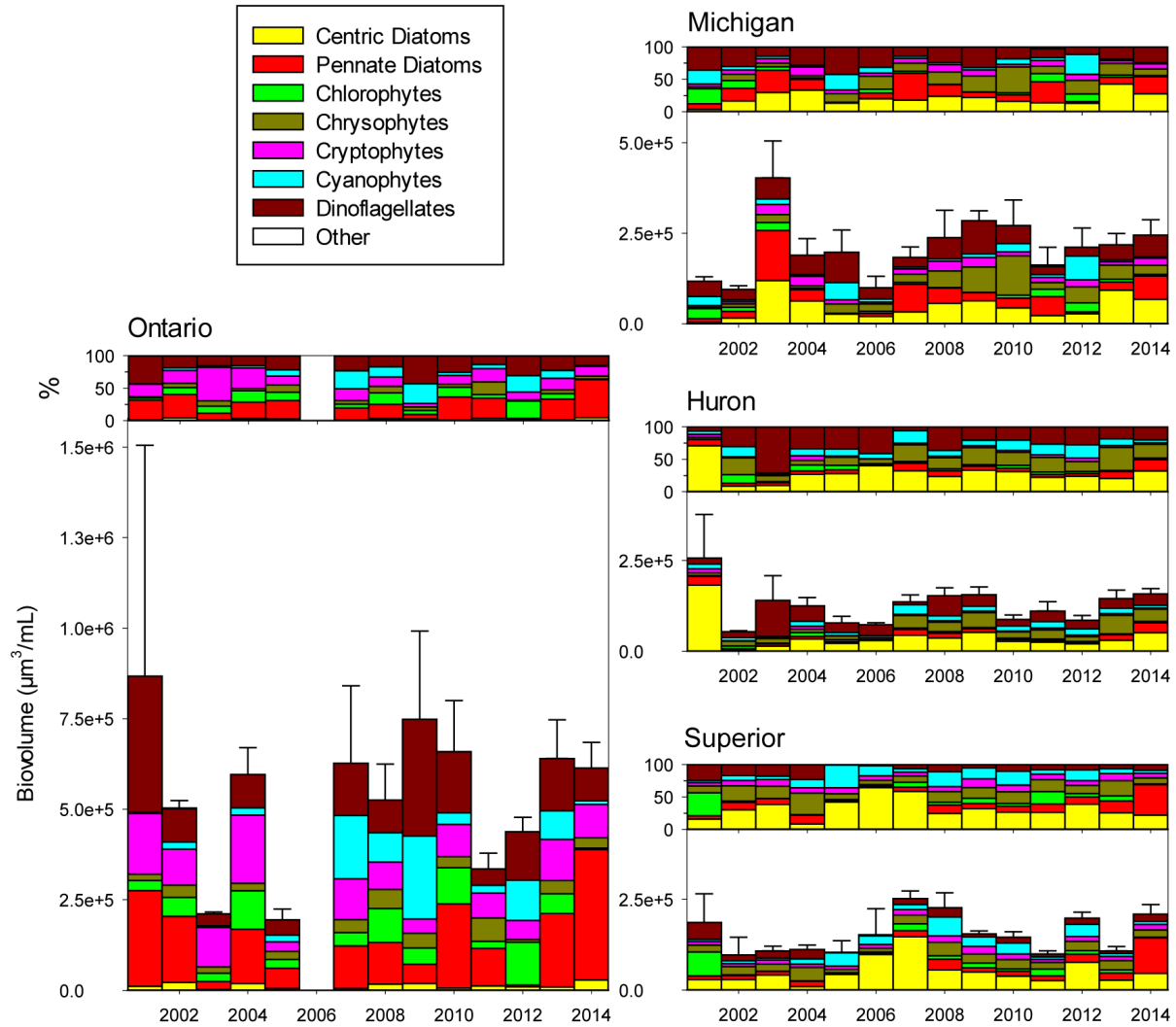


Figure 12. Phytoplankton biovolume (bottom panels) and percent biovolume (top panels), by major taxonomic group, in lakes Ontario, Huron, Michigan and Superior for summer 2001–2014. Error bars represent one standard error. No samples were analyzed for Lake Ontario in 2006.

8 ZOOPLANKTON

8.1 COMMUNITY COMPOSITION IN 2014

Zooplankton communities in 2014 differed from lake to lake, in size and composition, with differences most pronounced in summer ([Figure 13](#)).

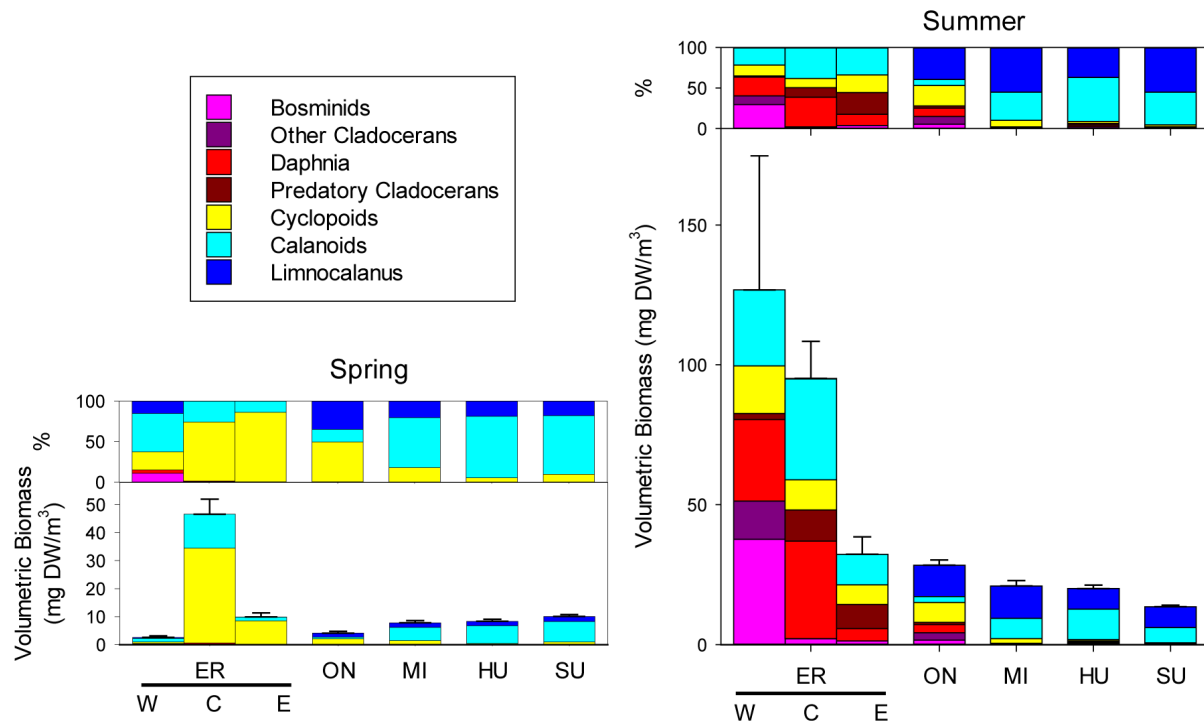


Figure 13. Crustacean volumetric biomass (bottom panels) and percent volumetric biomass (top panels), by major taxonomic group, for spring and summer, 2014.

SPRING

Spring communities in lakes Superior, Michigan and Huron were dominated by calanoid copepods, while cyclopoid copepods and copepodites contributed a larger proportion of the biomass in lakes Erie and Ontario. Cladocerans were limited for the most part to the western basin of Lake Erie. Total crustacean biomass (excluding *Mysis*) was lower in the spring than in the summer.

SUMMER

Broadly correlated with lake productivity, summer zooplankton volumetric biomass was highest in the western and central basins of Lake Erie, followed by the eastern basin of Lake Erie and Lake Ontario, with the lowest volumetric biomass

seen in Lake Superior. Cladocerans and cycloids were more common in the more productive lakes Erie and Ontario whereas calanoids dominated in lakes Michigan, Huron and Superior, consistent with a greater prevalence of cladocerans and cycloids in more productive systems. Seasonal differences in biomass between April and August also followed this pattern, with the greatest increases in biomass between the two sampling dates being seen in lakes Erie and Ontario. Communities in lakes Huron and Michigan were very similar, and exhibited somewhat higher levels of volumetric biomass as well as a greater contribution from non-*Limnocalanus* calanoid copepods than was seen in Lake Superior.

NEW INTRODUCED SPECIES

A new zooplankton introduction was detected in the Great Lakes in a sample collected in Lake Erie in 2014 ([Connolly et al. 2017](#)), marking the first established population of a non-indigenous zooplankton species in the Great Lakes since *Hemimysis anomala* was found in lakes Michigan and Ontario in 2006 ([Pothoven et al. 2007](#); [Walsh et al. 2010](#)). The zooplankton, *Thermocyclops crassus*, is a small Eurasian cyclopoid copepod which was found in the western basin of Lake Erie near the entry of the Detroit River into Lake Erie – a shallow, warm, and eutrophic habitat, similar to its reported native habitats ([Connolly et al. 2017](#)). Its abundance is extremely low relative to the most similar native copepod species *Mesocyclops edax* ($1/m^3$, compared to $1,000/m^3$). *Thermocyclops crassus* had previously been reported from Lake Champlain in 1991, in the shallow, eutrophic Missisquoi Bay ([Duchovnay et al. 1992](#)). The vector for this new introduction has not been determined. According to the U.S. Fish and Wildlife Service, the ecosystem risk from *Thermocyclops crassus* is uncertain because past introductions have not been studied to determine whether impacts occurred ([U.S. FWS 2016](#)).

8.2 COMMUNITY COMPOSITION TRENDS FROM 1997 TO 2014

SPRING

Little interannual difference in spring volumetric biomass was seen in Lake Superior, where calanoids dominated in all years ([Figure 14](#)). Cyclopoid copepods contributed less volumetric biomass in lakes Michigan and Huron than in lakes Erie and Ontario, and were more prevalent in the early years of the time series, with some exceptions (2011 and 2013 in Lake Michigan, 2013 in Lake Huron). As noted, a distinct reduction in biomass was seen in Lake Huron in 2004; a general but less pronounced trend of decreasing biomass was also seen in Lake Michigan. In general, communities in these two lakes exhibited substantial similarities ([Barbiero et al. 2018b](#)).

Spring biomass in the western basin of Lake Erie exhibited a notable decrease in 2004 ([Figure 14](#)). This corresponded with a coincident decrease in Lake Huron, and most likely represented a reduction in zooplankters washing into the western basin of Lake Erie from the upstream Lake Huron. The central basin of Lake Erie exhibited somewhat increased biomass in the later years of the time series, with cladocerans contributing an increased proportion of the biomass during this period. While volumetric biomass levels in the eastern basin were substantially lower than those seen in the central basin, interannual trends were similar in the two basins.

Lake Ontario exhibited an increase in calanoid volumetric biomass over time, especially in the 2005–2011 time period. A return to more cyclopoid biomass is seen in recent years.

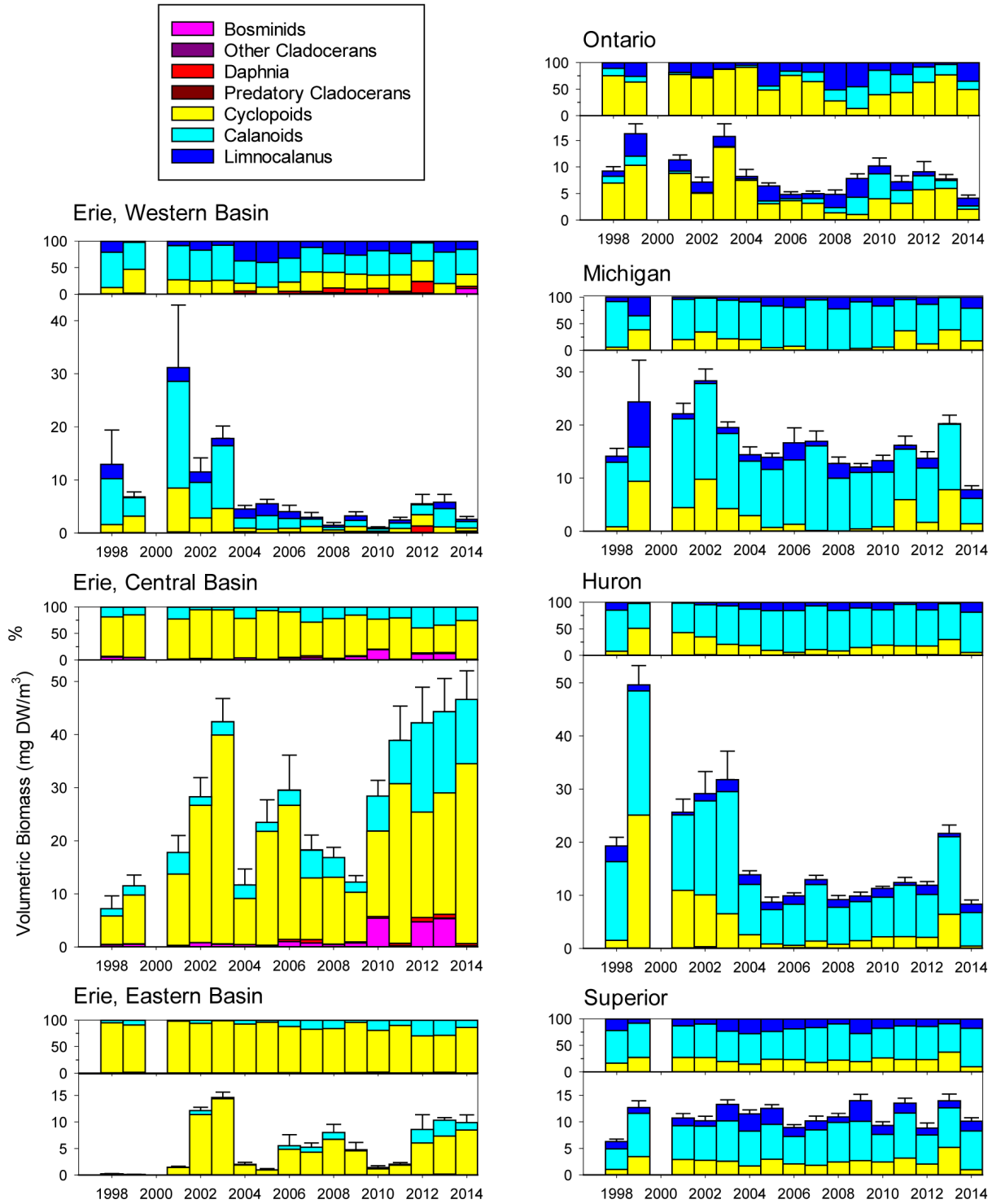


Figure 14. Crustacean volumetric biomass (bottom panels) and percent volumetric biomass (top panels), by major taxonomic group, for spring 1998–2014. Error bars represent one standard error. No samples were analyzed for spring in 2000.

SUMMER

Summer Lake Superior communities have been dominated by calanoid copepods, notably *Limnocalanus*, with little evidence of change over time ([Figure 15](#)). Summer crustacean communities in lakes Michigan and Huron have exhibited reductions in cladoceran biomass and shifts towards greater dominance by calanoid copepods, with strong similarities between the two lakes ([Barbiero et al. 2009, 2013, 2018b](#)). This trend has continued through 2014. Total volumetric biomass in Lake Huron has been notably consistent since 2005, with 2010 and 2012 being anomalous years of relatively high cladoceran biomass. While the reduction in cladocerans has not been as pronounced in Lake Michigan, an increase in *Limnocalanus* biomass, seen most consistently in the northern basin, has contributed to the relative shift towards greater calanoid dominance.

Summer crustacean communities in the western basin of Lake Erie showed a high degree of interannual variability, with no overall trend ([Figure 15](#)). While volumetric biomass tended to be higher than in other areas of the Great Lakes, the lowest volumetric biomass recorded in our time series (2001) was also found in the western basin. Substantial interannual variability was also found in the other basins of Lake Erie, although not to the extent seen in the western basin. Calanoid copepods contributed a higher proportion of biomass to the central and eastern basins, while

Bythotrephes volumetric biomass in these basins tended to be substantially higher than in both the western basin and the other lakes.

Beginning in 2004, communities in Lake Ontario showed a clear shift towards proportionally less cyclopoid biomass and more calanoid biomass. This represents a shift in the Lake Ontario summer crustacean community from an assemblage dominated by *Diacyclops thomasi*, *Daphnia retrocurva* and bosminids, and with *Cercopagis pengoi* (which invaded the lake in 1998, [Makarewicz et al. 2001](#)) the dominant predatory cladoceran, to one characterized by reduced cyclopoid biomass, a more varied predatory cladoceran community, and increased biomass of calanoid copepods ([Barbiero et al. 2014; Rudstam et al. 2015](#)). A further shift from 2008–2011 towards increased biomass of *Leptodiptomus sicilis*, *Bythotrephes longimanus* and *Daphnia mendotae* was also noted. More recent years have seen a reversion towards the *Cercopagis*, *D. retrocurva*, *D. thomasi* community. Vertebrate predation may be a main driver in structuring this crustacean community, with lower predation permitting the development of *Bythotrephes* populations, which in turn suppressed *D. retrocurva* and promoted *D. mendotae* ([Barbiero et al. 2014; Rudstam et al. 2015](#)). If so, then current levels of vertebrate predation pressure could be oscillating around the alewife abundance that can suppress *Bythotrephes* populations, resulting in interannual shifts between the two community types.

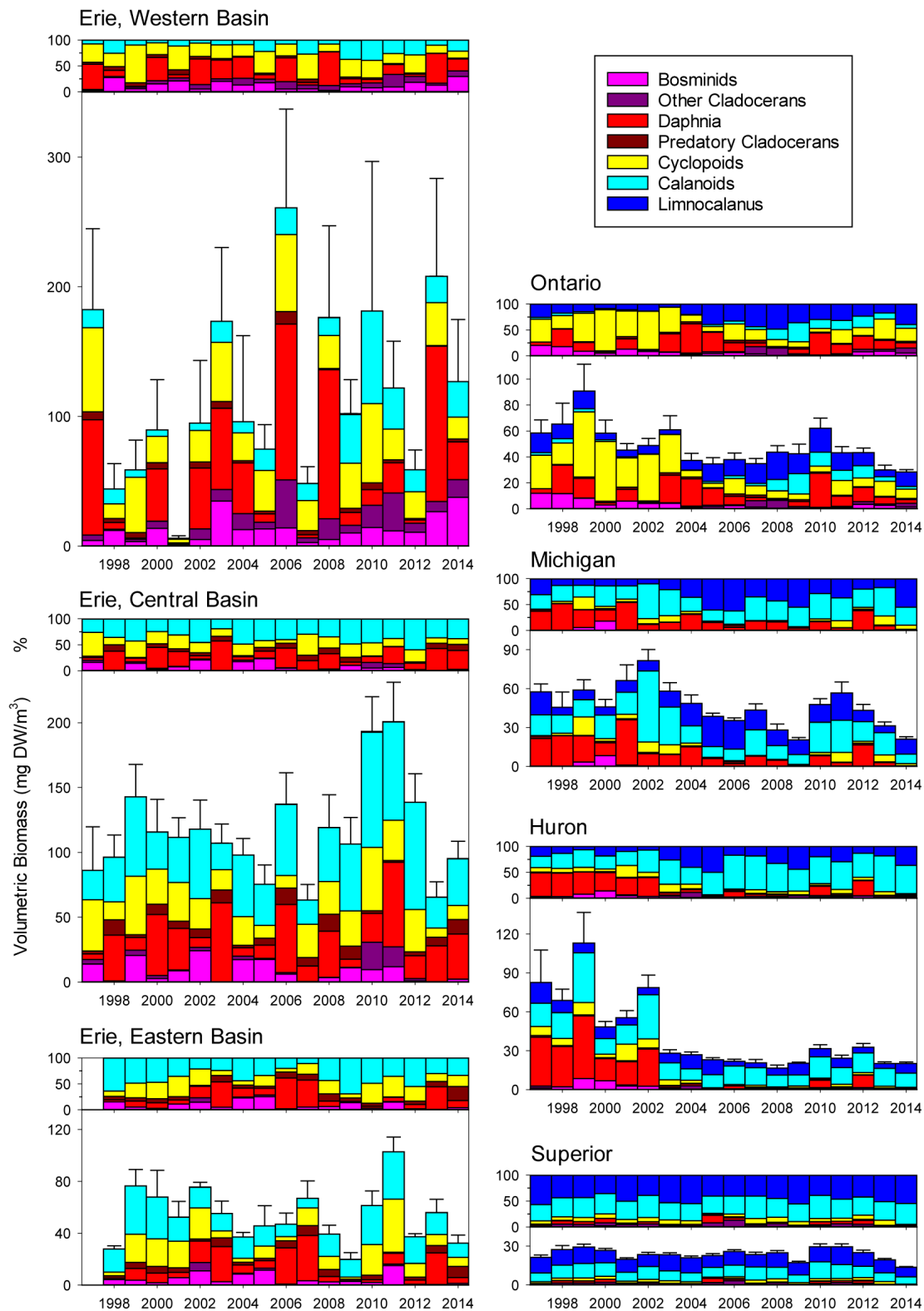


Figure 15. Crustacean volumetric biomass (bottom panels) and percent volumetric biomass (top panels), by major taxonomic group, for summer 1997–2014. Error bars represent one standard error.

9 MYSIS

9.1 ABUNDANCE IN 2014

Mysis diluviana occurs in all five of the Great Lakes but densities vary substantially among lakes. *Mysis* is a long-lived crustacean zooplankton species that reproduces after two years and areal density ($\#/m^2$) is therefore fairly similar in spring and summer. In Lake Erie, the species is rare and was only found in the deeper Eastern basin in the spring. In the other lakes, densities ranged from around $40/m^2$ (Huron), 140 to $200/m^2$ in lakes Michigan and Superior and 350 to $450/m^2$ in Lake Ontario. Areal biomass (spring–summer) was also lower in Lake Huron (14–59 g DW/ m^2) than in the other three lakes (Michigan 179–348 g DW/ m^2 , Superior 350–416 g DW/ m^2 , Ontario 361–724 g DW/ m^2). The number of stations sampled per lake ranged from 1 to 8 in spring and from 1 to 9 in summer.

In 2014, mysid biomass was <1% of the total crustacean biomass in Lake Erie, <4% in Lake Huron, 14–18% in Lake Michigan, 17–25% in Lake Superior and 21–48% in Lake Ontario, with the higher values representing spring conditions.

9.2 POPULATION TRENDS FROM 2006 TO 2016

Annual trends are presented for both spring and summer in the four deeper lakes ([Figure 16](#)). Because mysid biomass is depth-dependent (fewer mysids present in water shallower than 100 meters), and spring values tend to be lower than summer values, we analyzed time trends including station depth and season as covariates. This analysis has been completed for the time period 2006/2007 to 2016 ([Jude et al. 2018](#)). Sampling began in 2006 in lakes Huron, Michigan and Ontario and in 2007 in lakes Superior and Erie. Mysid areal biomass showed no significant time trends in lakes Huron, Michigan and Ontario although it did increase significantly during this time period in Lake Superior. Over the whole time period 2006/2007 to 2016, mysid biomass was significantly lower in Lake Huron than the other three deep lakes, significantly lower in Michigan than in Ontario with Superior not significantly different from either Michigan or Ontario ([Figure 17](#)). The proportion of crustacean biomass represented by mysids was on average for these years 12–18% in Lake Michigan, 14–18% in Lake Superior, 13–30% in Lake Ontario and <3% in lakes Huron and Erie. Lake Erie has shown consistently low mysid biomass throughout the time period.

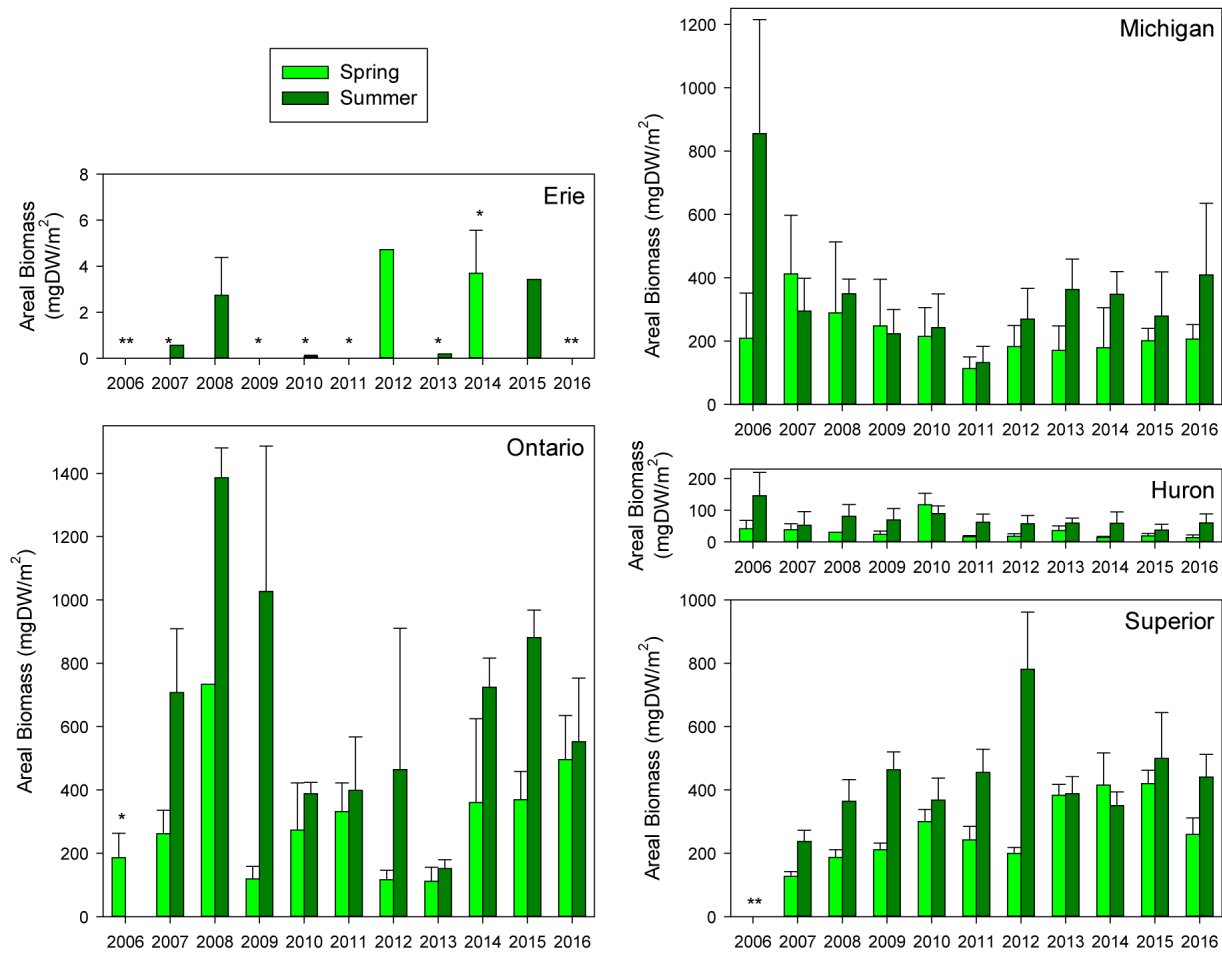


Figure 16. *Mysis diluviana* areal density (mg DW/m²) trends from 2006–2016. Averages are based on stations deeper than 30 meters. (*) signifies years where *Mysis* were not sampled during one season: Lake Erie (spring 2007, 2009, 2010 and 2013; summer 2011 and 2014) and Lake Ontario (summer 2006). (**) signifies years where *Mysis* were not sampled during either season: Lake Erie (2006, 2016) and Lake Superior (2006). Error bars represent one standard error. Y-axis scales are consistent across graphs with the exception of Lake Erie.

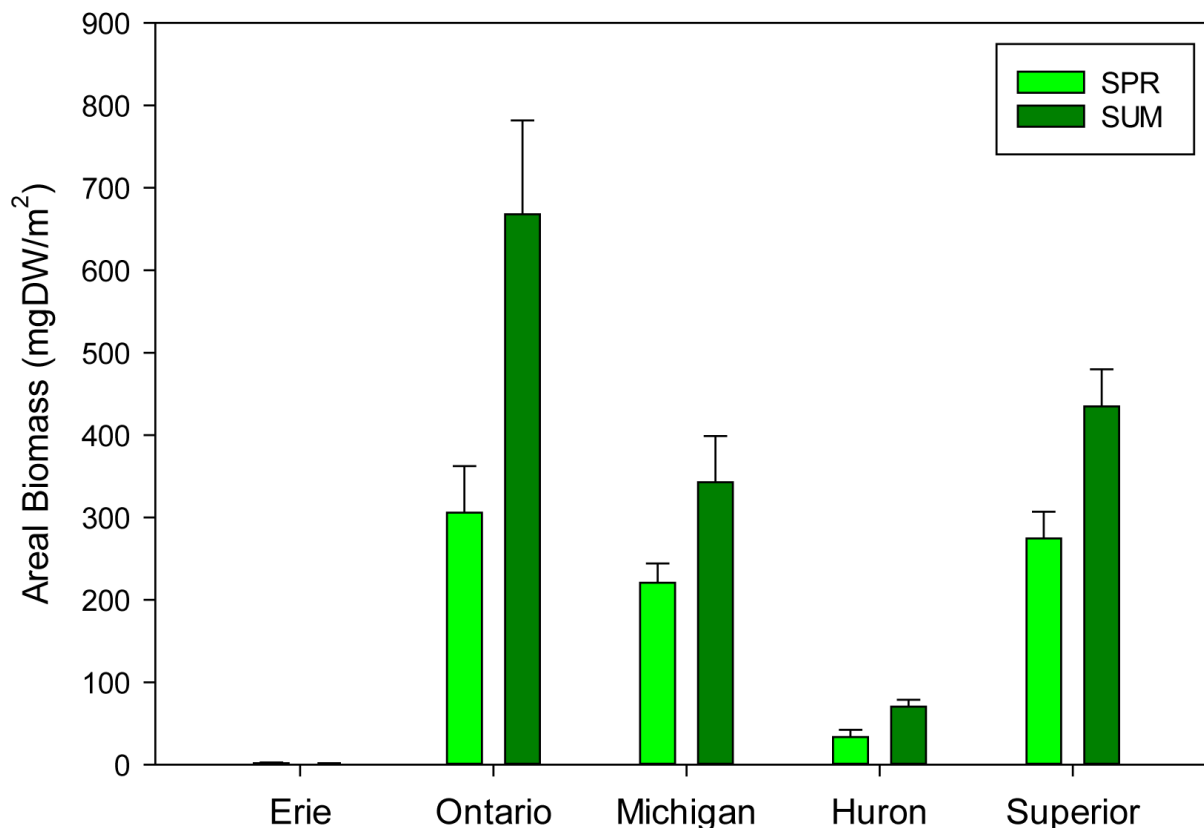


Figure 17. *Mysis diluviana* areal biomass (mg DW/m²) for stations deeper than 30 meters, averaged across years for the spring and summer surveys (2006/7–2016). Error bars represent one standard error.

Although the number of stations sampled is small in some years, these patterns are generally similar to the more extensive surveys available. For example, more extensive surveys of Lake Ontario mysids in 2013 by Cornell, USEPA, and the Department of Fisheries and Oceans – Canada (DFO) also shows a strong decline in mysids in 2013 and an increase in 2014 (Holda et al. 2019). However, the peak in Lake Ontario in 2008 is likely an artifact of the small sample size as 2008 had only marginally higher average biomass than surrounding years in the DFO data (Johannsson et

al. 2011). Reported mysid densities from Lake Michigan for this time period is limited. For two stations in southeastern Lake Michigan, data from National Oceanic and Atmospheric Administration’s Great Lakes Environmental Research Laboratory show densities of 100–150/m² (Pothoven and Vanderploeg 2017) which is similar to averages in the GLNPO data (104/m² – spring, 146/m² – summer, Jude et al. 2018).

10 BENTHOS

10.1 COMMUNITY COMPOSITION IN 2014

The composition of benthic communities in summer 2014 changed along a productivity/depth gradient, from shallow and productive Lake Erie, Green Bay, and Saginaw Bay, characterized by a high percentage of oligochaetes, high abundance of *Dreissena* (zebra and quagga mussels) and no *Diporeia*, to deep Lake Superior characterized by low densities of oligochaete species intolerant to organic pollution, abundant *Diporeia*, and absence of *Dreissena*.

The highest total wet biomass of benthos in 2014 was found in Lake Ontario, followed by, in order of decreasing biomass, Lake Erie, Michigan, Huron and Superior. The largest contributor of biomass in all lakes except Superior in 2014 was the quagga mussel (wet weight with shells); the highest lakewide average biomass of quagga

mussels was found in Lake Ontario (1008 g/m², 83.8% of total benthos biomass), followed by lakes Erie (784 g/m², 98.7%) and Michigan (656 g/m², 99.3%). The lowest biomass of *Dreissena* was found in Lake Huron (125 g/m², 98.7%). Excluding *Dreissena*, the highest areal benthos biomass was found in Lake Erie. In all lakes, non-dreissenid communities were dominated by oligochaetes ([Figure 18](#)) except for Lake Superior where *Diporeia* dominated benthos density and biomass in both shallow (< 70 meter) and deep (> 70 meter) zones. *Diporeia* was also a co-dominant species in the deep offshore sediments of lakes Michigan and Huron. In Lake Erie, the burrowing mayfly *Hexagenia* spp. was found only in the western basin but comprised 12% of total non-dreissenid biomass in that basin.

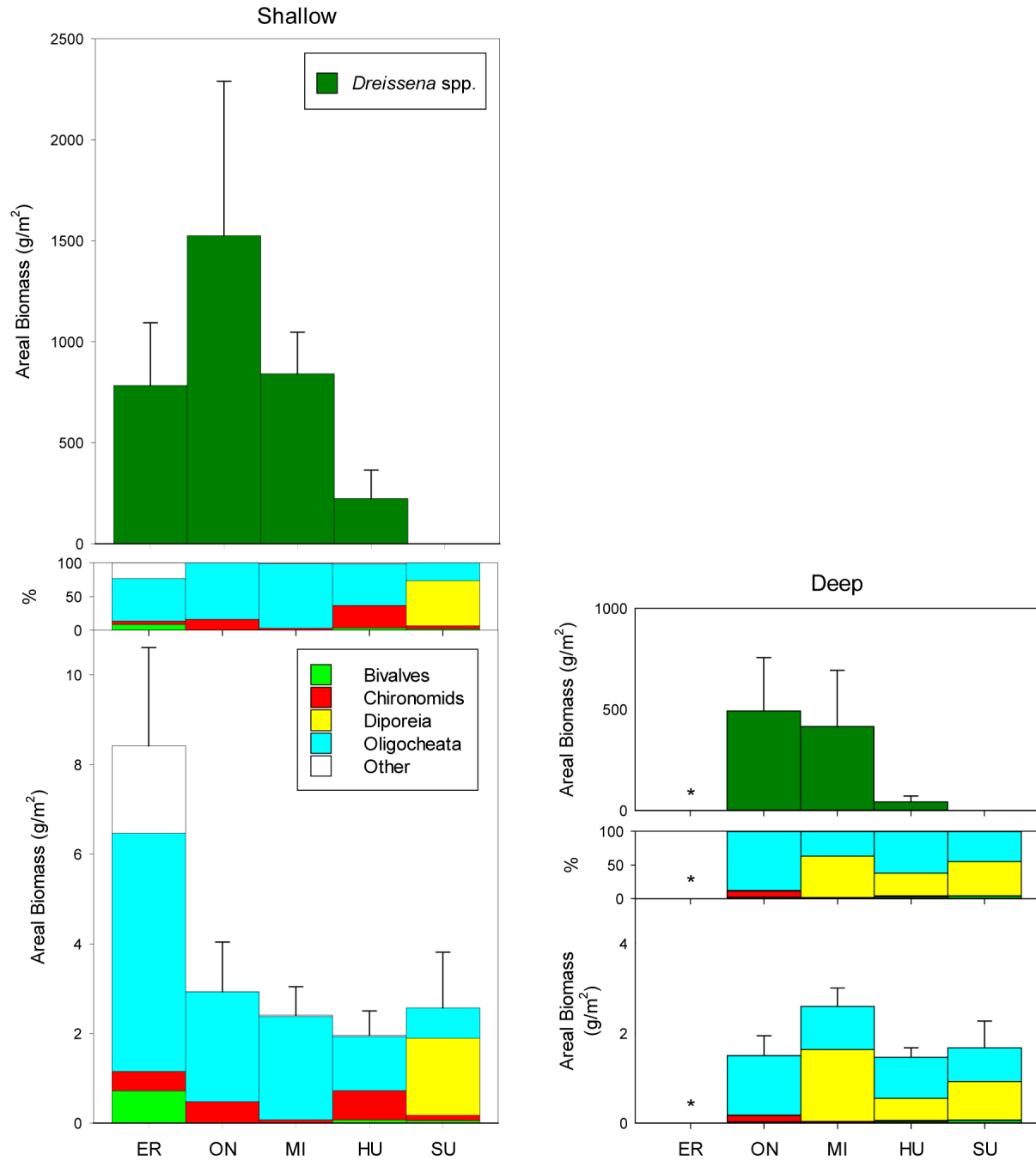


Figure 18. Absolute and percent areal biomass of benthos by major taxonomic group excluding *Dreissena* spp. (bottom and middle panels) and areal biomass of *Dreissena* spp. (top panels) at shallow (< 70 meters) and deep (> 70 meters) stations in 2014. The asterisk (*) indicates that Lake Erie has no deep stations. Error bars represent one standard error.

10.2 COMMUNITY COMPOSITION TRENDS FROM 1997 TO 2014

Trends in benthos communities from 1997 to 2014 are presented in [Figures 19](#) and [20](#). The largest changes over the last 17 years were found in the profundal communities (> 70 meters) of lakes invaded by quagga mussels (all lakes except for Lake Superior): profundal species, excluding quagga mussels, decreased in abundance, and their depth distribution shifted deeper compared to the beginning of the time series. *Diporeia*, formerly

dominant in lakes Michigan, Huron and Ontario, has largely disappeared from stations < 70 meters and is now replaced by quagga mussels. A large decline was also found in Sphaeriidae. From 1997–2014, the abundance of littoral and sublittoral groups (especially Naididae and Turbellaria) increased, and quagga mussel density and depth distribution increased significantly in all invaded lakes ([Burlakova et al. 2018a](#)).

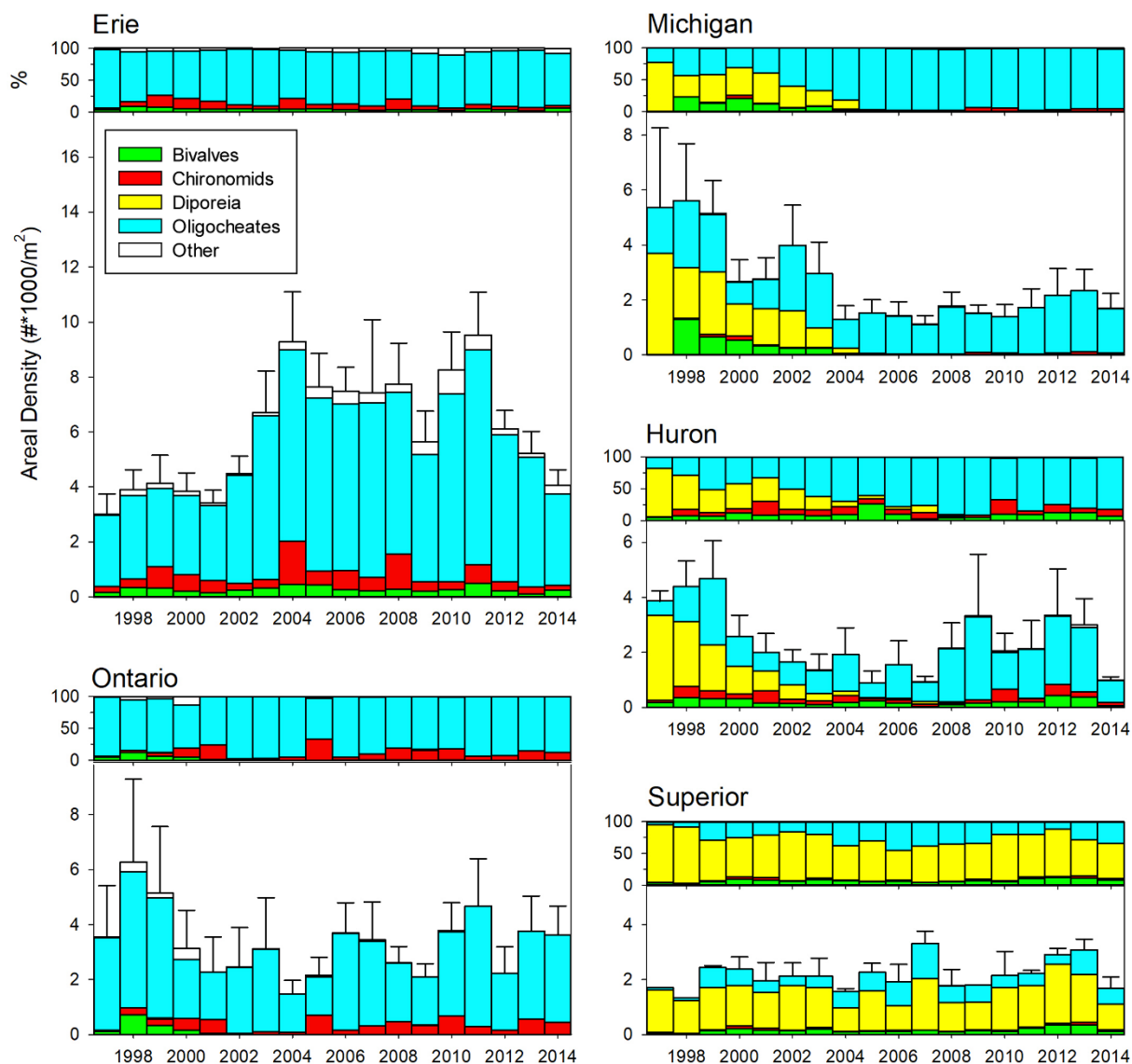


Figure 19. Trends in benthos areal density (bottom panels) and percent areal density (top panels) of major taxonomic groups in Great Lakes (1997–2014) < 70 meters depth. These values exclude *Dreissena* spp. Error bars represent one standard error.

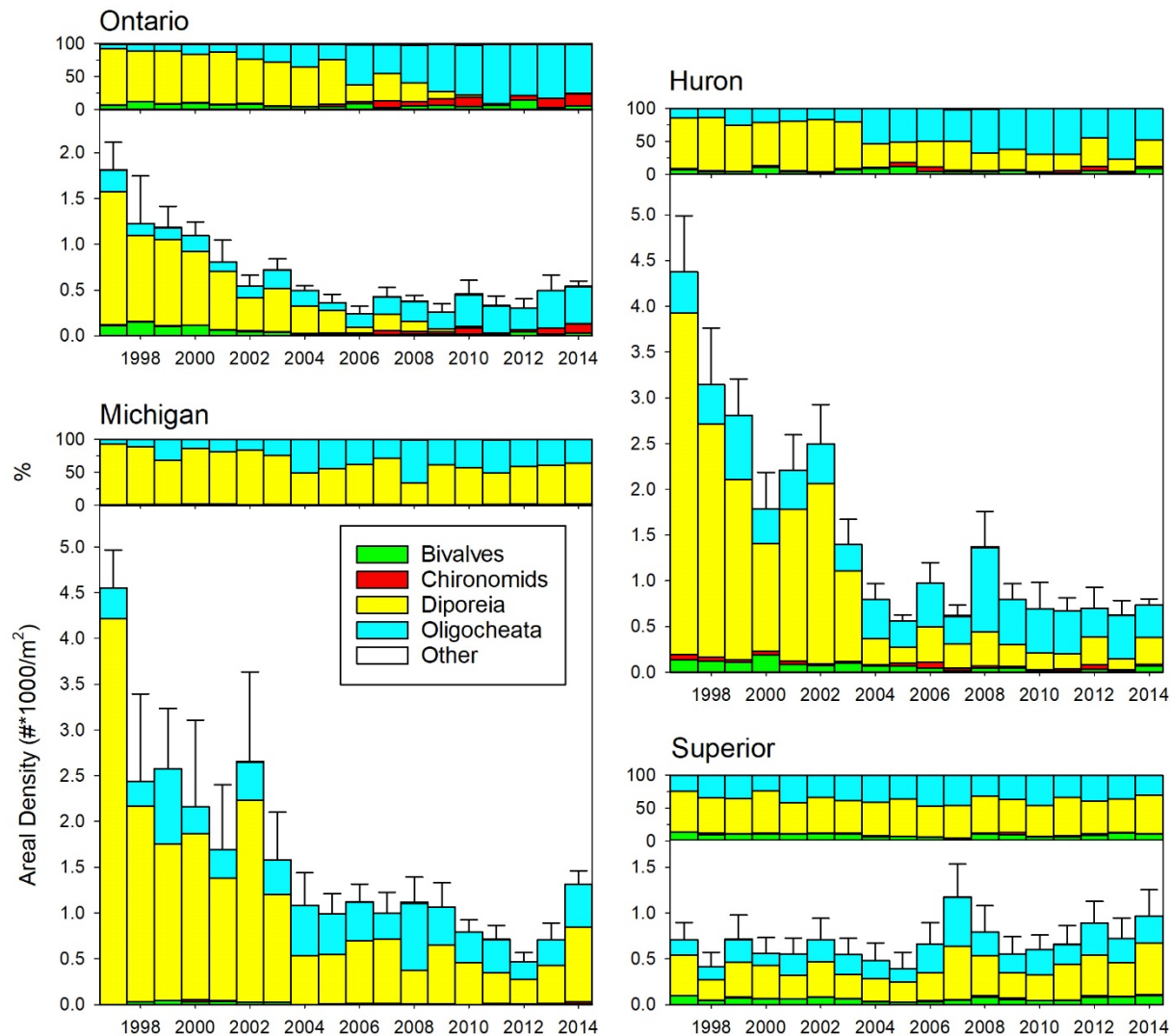


Figure 20. Trends in benthos areal density (bottom panels) and percent areal density (top panels) of major taxonomic groups in Great Lakes (1997–2014) > 70 meters depth. These values exclude *Dreissena* spp. Error bars represent one standard error.

LAKE ERIE

The total benthic density increased between 2000 and 2010, mainly due to increased *Dreissena* and Oligochaeta abundances, and then declined, returning to total densities observed in the late 1990s. Among Oligochaeta, the density of organic pollution-intolerant Lumbriculidae decreased in the eastern basin, while pollution-tolerant Tubificidae and Naididae were increasing lakewide. As a result, total Oligochaeta density increased at most stations, with the strongest trends observed in western and central basins. Abundance of Hirudinea and Turbellaria

increased, but no significant lakewide trends were found for Chironomidae, Trichoptera, Amphipoda, Isopoda, and Sphaeriidae. No *Diporeia* have been collected in the lake since the beginning of the monitoring program in 1997.

LAKE ONTARIO

Densities of Oligochaeta increased in the profundal zone, largely due to an increase in Lumbriculidae. Observed declines in *Diporeia* were most dramatic in the profundal zone, as their decline at shallower depths had begun before initiation of our benthic sampling program in 1997

([Watkins et al. 2013](#)). *Diporeia* densities in the profundal zone declined more than 100-fold and the species almost disappeared from monitoring stations. Sphaeriidae decreased lakewide, and particularly at shallow depths. Densities of quagga mussels increased at all depths, but most dramatically in the profundal zone. Due to the decline in *Diporeia*, total profundal benthos decreased; however, when both quagga mussels and *Diporeia* were excluded from the analysis, the trend was positive due to increases in Oligochaeta.

LAKE MICHIGAN

Densities of *Diporeia* declined dramatically lakewide from 1997–2014. The most abrupt declines were recorded between 30 and 60 meter depths where *Diporeia* densities have plummeted from the end of 1990s to mid-2000s ([Figures 19, 20](#)). In 2014, *Diporeia* were not present at any of the < 70 meter stations; however, densities at the profundal zone stations have remained relatively stable from 2004 to 2014. Sphaeriidae densities declined lakewide, with the largest losses at shallow (< 70 meter) depths. Similar declines were found in *Heterotrissocladus* spp., particularly at shallow depths (< 70 meters). Quagga mussel densities increased lakewide including at the deepest stations (128–250 meters) where they were first recorded in 2008. Only one station in the southern basin (MI18M, 160 meters) had yet to be invaded by *Dreissena* in 2014. The highest densities of *Dreissena* (up to 50,000/m²) were observed between 40–120 meters, with low abundance deeper than 120 meters. Following the large declines in *Diporeia* (from 52% to 3% of total density), the benthic community of Lake Michigan is currently dominated by quagga mussels (80% of total density). Total lakewide benthic densities increased at depths < 70 meters, but non-dreissenid benthos decreased significantly overall and progressively so with increasing depths, mostly due to the large declines in previously dominant *Diporeia* and declines in Sphaeriidae ([Figures 19, 20](#)).

LAKE HURON

The percent of Oligochaeta comprising the total benthos abundance increased lakewide ([Figures 18, 19](#)). In 2014, quagga mussel densities were still increasing and were found at 8 of 11 stations; the three long-term monitoring stations not yet invaded are all > 70 meters deep. The proportion of *Diporeia* densities that comprised the total benthos density declined from 58% in 1998–2002 to 5% in 2010–2014 and was replaced by quagga mussels (36% of total benthos density in 2010–2014) and Tubificidae (30% of total benthos density in 2010–2014). Sphaeriidae densities declined lakewide, especially at stations < 70 meters deep. Among Chironomidae, there was a significant loss in the formerly dominant deepwater species *Heterotrissocladus* spp. Due to the significant decrease in *Diporeia*, densities of native profundal benthos declined ([Figure 20](#)).

LAKE SUPERIOR

While there was a significant increase in densities of deepwater Enchytraeidae and Turbellaria, changes in all other taxa were small and insignificant. *Dreissena*, although established in the Duluth-Superior harbor and encountered on shipwrecks and rocky substrates around the Apostle Islands National Lakeshore, was not collected at our long-term monitoring stations. No changes in the dominant species complex were detected in Lake Superior since the beginning of the monitoring program in 1997.

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APPENDIX A – LIST OF THE SAMPLING AND ANALYTICAL STANDARD OPERATING PROCEDURES SUPPORTING THE GLBMP COMPONENTS

Table 1 below provides a list of the most current version of the sampling and analytical standard operating procedures (SOPs) supporting the GLBMP variables highlighted in this report.

Table 1. Sampling and Analytical Standard Operating Procedures Supporting the GLBMP

GLNPO Method	Title of the Standard Operating Procedure	Version Number, Date
LG400	Standard Operating Procedure for Phytoplankton Sample Collection and Preservation Field Procedures	Revision 09, March 2002
LG401	Standard Operating Procedure for Phytoplankton Analysis	Revision 05, February 2010
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, February 2017
LG406	Standard Operating Procedure for Benthic Invertebrate Field Sampling Procedure	Revision 12, March 2018
LG407	Standard Operating Procedure for Benthic Invertebrate Laboratory Analysis	Revision 09, April 2015
LG408	Standard Operating Procedure for Mysisid Analysis	Revision 02, February 2017
LG409	Standard Operating Procedure for <i>Mysis</i> Sample Collection and Preservation	Revision 02, April 2019