Are Changes in Lower Trophic Levels Limiting Prey-Fish Biomass and Production in Lake Michigan?

The Great Lakes Fishery Commission was established by the Convention on Great Lakes Fisheries between Canada and the United States, which was ratified on October 11, 1955. It was organized in April 1956 and assumed its duties as set forth in the Convention on July 1, 1956. The Commission has two major responsibilities: first, develop coordinated programs of research in the Great Lakes, and, on the basis of the findings, recommend measures that will permit the maximum sustained productivity of stocks of fish of common concern; second, formulate and implement a program to eradicate or minimize sea lamprey populations in the Great Lakes.

The Commission is also required to publish or authorize the publication of scientific or other information obtained in the performance of its duties. In fulfillment of this requirement the Commission publishes two types of documents, those that are reviewed and edited for citation indexing and printing and those intended for hosting on the Commission's website without indexing or printing. Those intended for citation indexing include three series: Technical Reports—suitable for either interdisciplinary review and synthesis papers of general interest to Great Lakes fisheries researchers, managers, and administrators, or more narrowly focused material with special relevance to a single but important aspect of the Commission's program (requires outside peer review); Special Publications—suitable for reports produced by working committees of the Commission; and Miscellaneous Publications—suitable for specialized topics or lengthy reports not necessarily endorsed by a working committee of the Commission. One series, Fishery Management Documents, is not suited for citation indexing. It is intended to provide a web-based outlet for fishery-management agencies to document plans or reviews of plans while forgoing review and editing by Commission staff. Those series intended for citation indexing follow the style of the *Canadian Journal of Fisheries and Aquatic Sciences*. The style for Fishery Management Documents is at the discretion of the authors. Sponsorship of publications does not necessarily imply that the findings or conclusions contained therein are endorsed by the Commission.

Cover photograph by Harvey Bootsma and Ben Turschak: A school of Alewife above a bed of *Cladophora* in Lake Michigan.

Are Changes in Lower Trophic Levels Limiting Prey-Fish Biomass and Production in Lake Michigan?

David B. Bunnell[1*], **Hunter J. Carrick**[2], **Charles P. Madenjian**[1], **Edward S. Rutherford**[3], **Henry A. Vanderploeg**[3], **Richard P. Barbiero**[4], **Elizabeth Hinchey-Malloy**[5], **Steven A. Pothoven**[6], **Catherine M. Riseng**[7], **Randall M. Claramunt**[8], **Harvey A. Bootsma**[9], **Ashley K. Elgin**[6], **Mark D. Rowe**[7], **Sara M. Thomas**[10], **Benjamin A. Turschak**[11], **Sergiusz Czesny**[12], **Kevin L. Pangle**[2], **David M. Warner**[1]

May 2018

[1]**D.B. Bunnell, C.P. Madenjian, and D.M. Warner**. U.S. Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor, MI 48105, USA.

[2]**H.J. Carrick and K.L Pangle**. Central Michigan University, Department of Biology, Biosciences 2100, Mount Pleasant, MI 48859, USA.

[3]**E.S. Rutherford and H.A. Vanderploeg**. National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, 4840 South State Road, Ann Arbor, MI 48108, USA.

[4]**R.P. Barbiero**. CSRA LLC, 1359 West Elmdale Ave., Suite 2, Chicago, IL 60660, USA.

[5]**E. Hinchey-Malloy**. Environmental Protection Agency, Great Lakes National Program Office, 77 West Jackson Boulevard, Chicago, IL 60604 USA.

[6]**S.A. Pothoven and A.K. Elgin**. National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, Lake Michigan Field Station, 1431 Beach Street, Muskegon, MI 49441, USA.

[7]**C.M. Riseng and M.D. Rowe**. University of Michigan, School for Environment and Sustainability, Dana Building, 440 Church Street, Ann Arbor, MI 48109, USA.

[8]**R.M. Claramunt**. Michigan Department of Natural Resources, Oden State Fish Hatchery, 8258 South Ayr Road, Alanson, MI 49706, USA.

[9]**H.A. Bootsma**. University of Wisconsin-Milwaukee, School of Freshwater Sciences, Great Lakes Research Facility, 600 East Greenfield Avenue, Milwaukee, WI 53204, USA.

[10]**S.M. Thomas**. Michigan Department of Natural Resources, Waterford Fisheries Station, 7806 Gale Road, Waterford, MI 48327, USA.
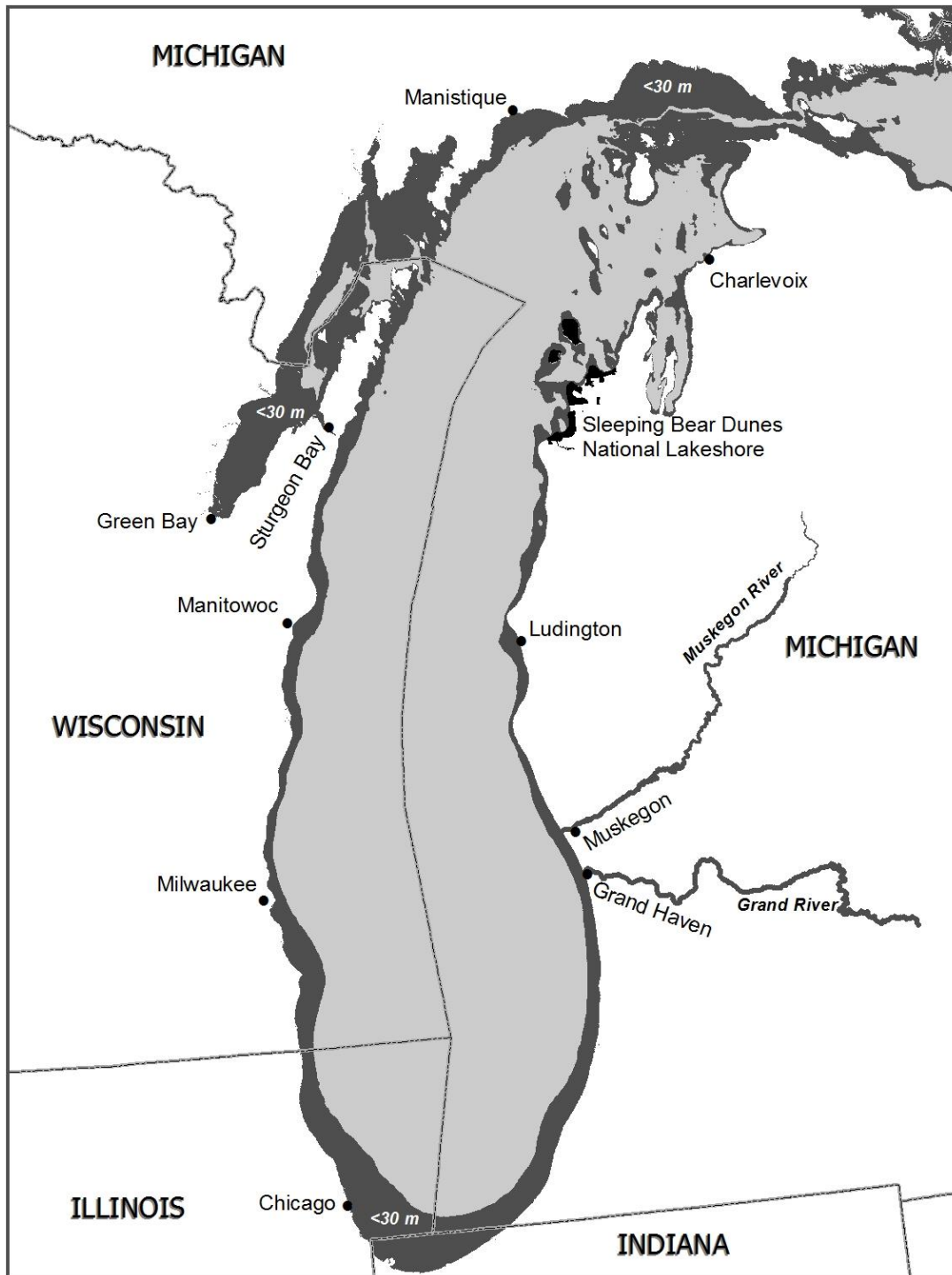
[11]**B.A. Turschak**. Michigan Department of Natural Resources, Charlevoix Fisheries Research Station, 96 Grant Street, Charlevoix, MI 49720, USA.

[12]**S. Czesny**. Illinois Natural History Survey, Lake Michigan Biological Station, 400 17th Street, Zion, IL 60099, USA.

[*]Corresponding author (email: dbunnell@usgs.gov).

Frontispiece. Lake Michigan showing place names discussed in text.

MICHIGAN

Manistique

<30 m

Charlevoix

<30 m

Sturgeon Bay

Green Bay

Sleeping Bear Dunes
National Lakeshore

Manitowoc

Ludington

Muskegon River

MICHIGAN

WISCONSIN

Muskegon

Milwaukee

Grand Haven

Grand River

ILLINOIS

Chicago

<30 m

INDIANA

-Illustration by Lacey Mason, University of Michigan.

TABLE OF CONTENTS

ABSTRACT

To improve understanding of how recent changes in lower trophic levels in Lake Michigan could be affecting prey-fish biomass and production, the Lake Michigan Committee (LMC) convened a Lower Trophic Level Task Group and provided several charges that are responded to in this report. First, we compiled a comprehensive summary of lower trophic-level data in Lake Michigan, separating out nearshore versus offshore trends over time. Declining trends were prevalent in offshore time series for phosphorus, chlorophyll *a*, biomass of total crustacean zooplankton, biomass of herbivorous cladocerans, and density of *Diporeia* spp. In the nearshore, declining trends were evident only for biomass of cyclopoid copepods and density of *Diporeia* spp. Second, we hypothesized specific mechanisms by which changes in lower trophic levels could affect prey-fish biomass and production and described the degree of empirical support for each mechanism. The best-supported hypothesis was that declining invertebrate prey (especially *Diporeia* spp.) was responsible for declining growth of prey fish, especially over the last decade when competition for prey resources should otherwise have been lessened due to declining prey-fish densities. As a result, declining growth potentially limits the prey-fish biomass that could have been attained had growth been maintained at the levels that were achieved in the 1980s and earlier. Third, we prioritized several lower trophic-level indicators that fishery managers could use to better inform decision making. The top-ranked indicator was annual reporting of Alewife (*Alosa pseudoharengus*) condition. Fourth, we prioritized the key monitoring and research gaps that limit our current understanding of how lower trophic levels influence fish production. The highest-priority monitoring gap was coordinated sampling of the nearshore, which, if accomplished, would complement annual reporting on offshore sampling. The top-ranked knowledge gap was identifying bottlenecks that regulate fish recruitment, given that recent changes in zooplankton distribution and abundance could be suppressing survival of larval fish and, ultimately, the biomass and production of prey fish. We provided three specific recommendations for the LMC to consider as they seek to better incorporate lower trophic-level changes into their management decision process: (1) implement a coordinated and standardized nearshore monitoring program, (2) encourage funding agencies to use our prioritized lists in their decision processes, and (3) foster the already improved dialogue between those researching lower trophic levels and those researching fisheries.

INTRODUCTION

Several of the Laurentian Great Lakes have undergone declines in offshore nutrients and primary production over the past several decades owing to reduced total phosphorus (TP) inputs resulting from implementation of the binational Great Lakes Water Quality Agreement (signed in 1972; amended in 1983, 1987, and 2012) and the shunting of phosphorus to benthic habitats resulting from the proliferation of non-indigenous dreissenids (*Dreissena bugensis*, *D. polymorpha*) (Evans et al. 2011; Bunnell et al. 2014). Fishery managers are well informed of the declining trends in prey-fish biomass that began in the 1990s; two lakewide surveys (e.g., bottom trawl and acoustics with midwater trawl) indicate biomass of prey fish in 2010-2017 was at least 88% lower than the average biomass in the 1990s (DBB, CPM, DMW, unpublished data).

Theory predicts that prey-fish biomass is regulated by both predatory demand as well as resource limitation (Carpenter et al. 1985; Downing and Plante 1993). Predator demand in Lake Michigan is well described by models that were developed in close consultation with fishery managers (e.g., Tsehaye et al. 2014), but managers are less certain about the effects of declining nutrients and primary production on prey-fish biomass and production. The Lake Michigan Committee (LMC), comprising senior state and tribal fishery managers and operating under the aegis of the Great Lakes Fishery Commission, created a Lower Trophic Level Task Group in 2016 to provide the LMC with a better understanding of the extent that declines in lower trophic-level production are limiting the capacity of the lake to support prey fish. The LMC seeks to coordinate inter-jurisdictional fisheries management by pursuing fish community objectives (FCOs) developed in 1995 (Eshenroder et al. 1995). One of the objectives for planktivores (referring to prey fish, such as Alewife (*Alosa pseudoharengus*), Bloater (*Coregonus hoyi*), and Rainbow Smelt (*Osmerus mordax*) states that their biomass should be maintained at a level that matches both primary production and predator demands.

In this report, we define the lower food web as biotic components (bacteria, phytoplankton, protists, zooplankton, and benthic invertebrates) that are consumed either directly or indirectly by fish and abiotic factors (nutrients such as phosphorus and water clarity) that can influence trophic interactions. Dreissenids have been hypothesized and demonstrated to exert large-scale changes to some components of the lower food web, including to phytoplankton and *Diporeia* spp. (Nalepa et al. 2009; Vanderploeg et al. 2002, 2010), but their effects on fish are less well understood (see Madenjian et al. 2015). Fishery scientists and managers typically consider how mesozooplankton (200-2,000 µm), such as *Limnocalanus macrurus*, cyclopoid copepods, diaptomid copepods, *Daphnia galeata mendotae*, or *Bythotrephes longimanus*, individually influence fish because they are primary prey for juvenile and adult planktivorous prey fish. However, mesozooplankton are not supported simply by "phytoplankton" but from a complex array of heterotrophic plankton and phototrophic plankton that vary in size from 0.2-2.0 µm (picoplankton), 2-20 µm (nanoplankton), and 20-200 µm (microplankton) (Fig. 1). We also note that larval fish feed on microzooplankton such as rotifers, dreissenid veligers (hereafter, veligers), and copepod nauplii. The key concept is that dreissenids are relatively unique because they can filter not only microplankton (like diatoms) but also the smaller nano- and picoplankton. Hence, dreissenids are competing with daphnids and calanoids for prey resources. Prior to the dreissenid invasions, these micro-, nano-, and picoplankton would have been linked more directly to planktivorous fish through their consumption of daphnids and copepods. Because age-1+ fish, such as Alewife, Bloater, and Rainbow Smelt, do not consume settled dreissenids, energy transfer to fish is likely not as efficient now as in earlier decades. A more-detailed explanation of linkages and their significance to the trophic pathways leading to fish is given in Appendix B.

The LMC charged the task group in a letter of December 11, 2015, to: (1) summarize current status and trends in primary production, zooplankton biomass, and benthic invertebrate biomass; (2) describe empirical or modeled linkages between primary and secondary production and prey-fish biomass; (3) identify data and knowledge gaps; (4) recommend research priorities; (5) identify new indicators of the status of lower trophic levels; and (6) recommend additional resources needed to provide continuing updates of prey-fish biomass and the prospects for meeting the LMC's objectives for prey fish. Because the conclusions from the most-recent state of Lake Michigan report (Robillard et al. 2012) indicated a commitment of the LMC to reexamine their FCOs given the changing conditions in the lake, this report should provide a foundation for future efforts aimed at revising the objective for planktivores.

Fig. 1. Schematic trophic interactions of mesozooplankton (200-2,000 µm) and dreissenids with different size categories of phototrophic (right-hand side, in green) and heterotrophic (left-hand side, in brown) components of microbial and classic food webs modified from Fenchel (1988) for marine food webs: picoplankton (<2 µm), nanoplankton (2-20 µm), and microplankton (20-200 µm). Arrows show simplified relations while interactions from dissolved-organic-matter recycling are not shown. Mesozooplankton illustrations (from left to right) include *Limnocalanus macrurus* (*Li*); a representative cyclopoid copepod, *Diacyclops thomasi* (*Cy*, mostly carnivorous); a representative calanoid copepod (represented by diaptomids (*Di*), omnivorous); and an herbivorous daphnid (*Da*, filter feeder). *D. thomasi* and diaptomids are primary prey of *Limnocalanus* (*Li*), and daphnids are a major prey of *Bythotrephes longimanus* (*By*). Arrows on the far right side leading up to daphnids, diaptomids, and dreissenid mussels indicate their ability to access not only phototrophic components but also heterotrophic components (not shown) within a size range. Daphnids are efficient at capturing (filtering) many components of pico- and nanoplankton; diaptomids are efficient at capturing many components of the nano- and microplankton, particularly motile (often heterotrophic) prey; and *D. thomasi* is an obligate predator of motile prey, particularly microzooplankton. Dreissenids are able to access many components of the pico-, nano-, and microplankton but, at the same time, can be selective in their feeding in all size rages. Microplankton illustrations (from left to right) are a ciliate, a rotifer, and an assortment of large diatom colonies and cells. Nanoplankton illustrations (left to right) are heterotrophic flagellates, a detrital particle with bacteria, an assortment of phototrophic flagellates, and a small diatom. The picoplankton illustrations (left to right) are various bacteria and archaea (brown) and the smallest phytoplankton (green).
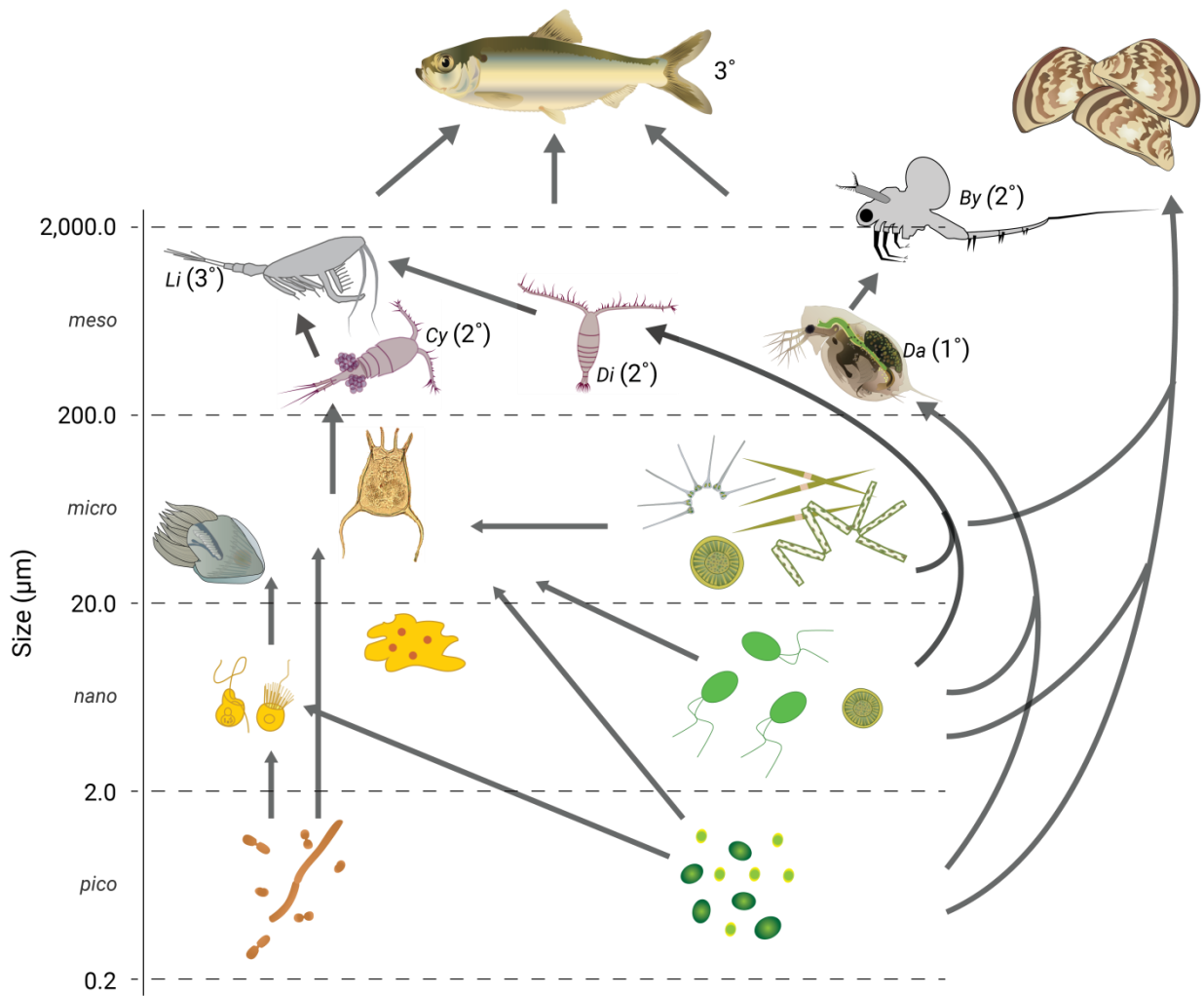
- Illustrations by Kim Kraeer, Tracey Saxby, Jane Thomas, and Lucy Van Essen-Fishman; Integration and Application Network; University of Maryland Center for Environmental Science (http://ian.umces.edu/symbols/).

4

TRENDS IN LOWER TROPHIC LEVELS

This compilation of lower trophic-level data is not the first to document significant changes that have occurred in Lake Michigan (see Bunnell et al. 2014; Madenjian et al. 2015). A unique aspect of this synthesis is that it examines trends in nearshore (<30 m) and offshore (≥30 m) habitats whereas these environments are typically combined in lakewide accounts such as this. Our delineation of the nearshore follows the convention of Edsall and Charlton (1997) where the 30-m depth contour approximates where the thermocline intersects the lake bed in late summer-early fall. Time series were compiled across all available relevant data from monitoring agencies and from universities that conduct research on Lake Michigan. For each time series, we conducted a Spearman rank correlation to determine if a trend was evident ($\alpha = 0.05$).

Nutrients

Annual TP inputs (loadings) from tributaries were compiled by Dave Dolan and colleagues between 1978 and 2008 (Dolan and Chapra 2012). Loadings in 1978-1979 averaged 6,953 metric tonnes but then, over the next 29 years, dropped to levels always lower than 5,000 metric tonnes (Appendix A, Fig. A1). Between 1980 and 2008, annual loadings averaged 3,653 metric tonnes but were variable and without trend ($r = -0.27$, $P = 0.16$).

Offshore TP concentrations in spring, monitored by the Environmental Protection Agency (EPA) Great Lakes National Program Office at 16 stations since 1983, have decreased by more than 50% between 1996 (5.84 µg/L) and 2015 (2.81 µg/L; Fig. 2). Chapra and Dolan (2012) and R.P. Barbiero (unpublished data) have developed models to estimate offshore TP concentrations that should have been realized based on TP loadings, retention time, and settling coefficients (i.e., ignoring within-lake TP cycling processes). The results predicted that TP concentrations would undergo steep declines between 1978 and the 1990s but would be relatively unchanged between 1998 and 2011 (Appendix A, Fig. A1). These models suggest that within-lake TP cycling, perhaps caused by sequestration of TP by dreissenids, can explain the continued decline in offshore TP concentrations since the 1990s.

Fig. 2. Time series of offshore (open circles, left axis) and nearshore (black symbols, right axis) spring total phosphorus (TP) concentrations.
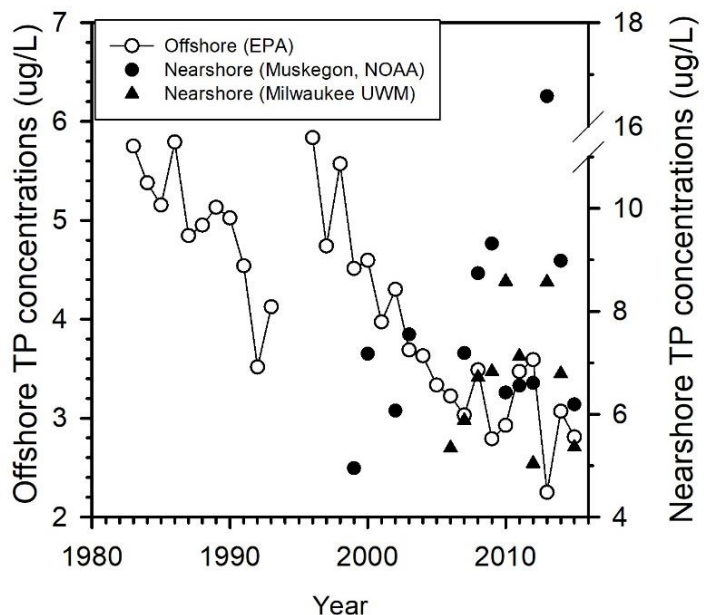
At nearshore (i.e., <30-m bottom depth) sites, however, spring TP concentrations were generally higher than in the offshore and have not declined since 1999 near Muskegon, Michigan, (SAP, unpublished data; Fig. 2) or 2006 near Milwaukee, Wisconsin (HAB, unpublished data; Fig. 2). Nearshore TP concentrations revealed considerable temporal variation. These nearshore time series are relatively recent and localized and should be considered provisional. Spring nearshore TP collected in 1996, 2014, and 2015 off of Grand Haven, which can be affected by high loadings from the Grand River, had values of 85, 16, and 12 µg/L, respectively (SAP, unpublished data).

Water Clarity

Mean Secchi-disk depth measured during spring and summer offshore EPA surveys underwent a remarkable step-wise increase in 2004: Secchi depths averaged 8.6 m in 1983-2003 and 13.9 m in 2004-2015, a 5.3-m increase (Fig. 3). No time series of clarity were available for the nearshore, but Auer et al. (2010) reported a decline in nearshore light extinction coefficients from 1975-1990 to 2002-2006. Our assumption is that water clarity has increased more in the offshore over the past decade or so than in the nearshore. Nearshore water clarity is highly episodic driven by loading and resuspension of sediments (see Vanderploeg et al. 2015).

Fig. 3. Time series of offshore Secchi-disk depth collected by the EPA (compiled by RPB) averaged for April and August each year in Lake Michigan. Dashed lines indicate averages for 1983-2003 and 2004-2014.
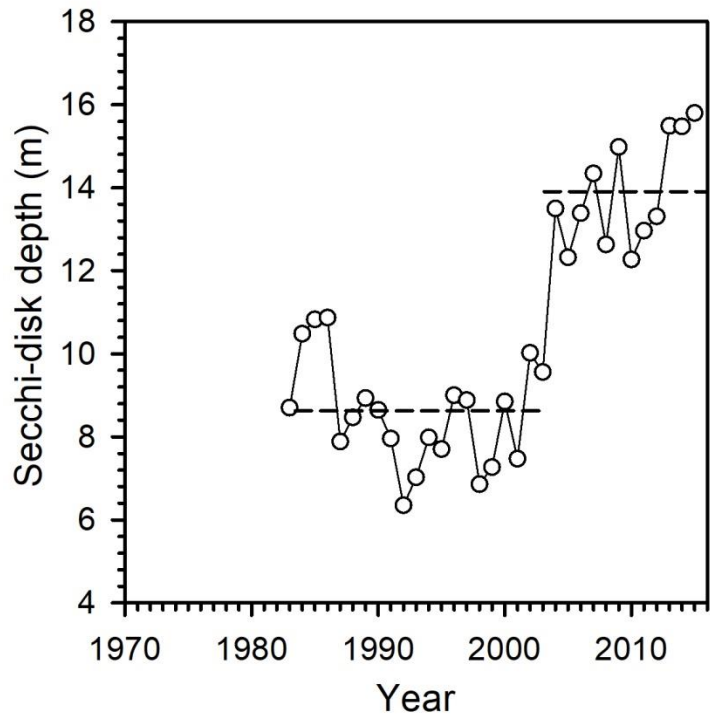
Phytoplankton

Phytoplankton abundance, as reflected by chlorophyll *a* concentrations (a proxy of biomass), declined in both the nearshore and offshore zones in Lake Michigan from the early 1970s to 1994-1995 when an intensive spatiotemporal sampling effort occurred (Carrick et al. 2001). An analysis of time-series data covering more-recent years revealed divergent patterns between nearshore and offshore sites. A steep decline in satellite-derived estimates of offshore epilimnetic chlorophyll *a* (April to May) was observed from the late 1990s (~1.4 μg/L) to the 2010s (~0.70 μg/L; Fig. 4, open circles) (B.M. Lesht, University of Illinois at Chicago and RPB, unpublished data). Time series of *in situ* nearshore chlorophyll *a* have been compiled for waters near Muskegon (1999-2015, SAP, unpublished data; Fig. 4, closed circles) and Milwaukee (2006-2015, HAB, unpublished data; Fig. 4, closed triangles). Neither nearshore time series revealed any trend in spring chlorophyll *a* concentrations during the period when dreissenids were present.

Fig. 4. Time series for indices of spring primary production in Lake Michigan. Open circles indicating the time series for offshore (Barry M. Lesht, University of Illinois-Chicago, 2017) remotely sensed chlorophyll *a* are plotted on the left axis. Black symbols indicating the time series for nearshore *in situ* chlorophyll *a* for Muskegon (circles, NOAA, compiled by SAP) and Milwaukee (triangles, University of Wisconsin-Milwaukee, compiled by HAB), are plotted on the right axis.
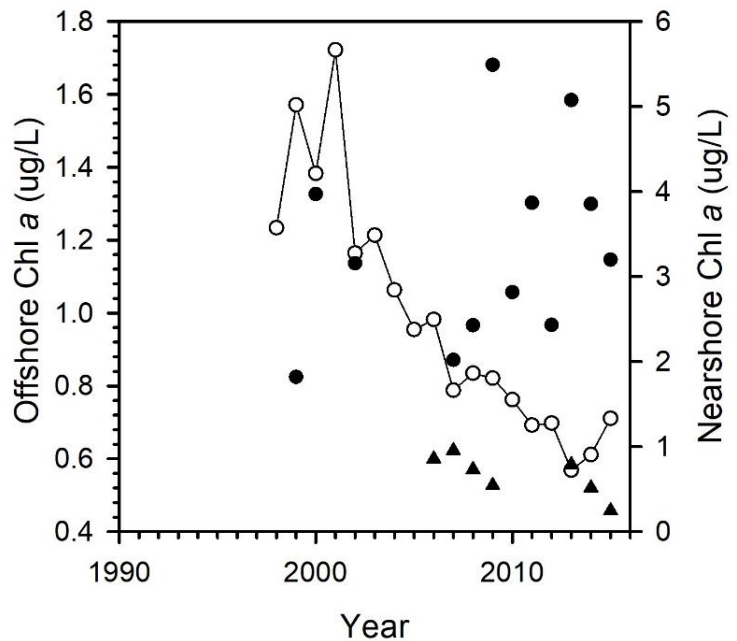
Phytoplankton taxonomic composition at an offshore site near Muskegon, Michigan, has undergone dramatic changes since 1980. Prior to 1995, the assemblage was typically composed of a mixed assemblage of phototrophic pico- (cyanobacteria), nano- (chrysophytes, cryptophytes), and micro- (diatoms) plankton (Carrick et al. 2001; Fahnenstiel et al. 2010b). The assemblage exhibited considerable shifts in composition around 2007 when the spring diatom bloom nearly disappeared (Fahnenstiel et al. 2010a, 2010b). An analysis of the Muskegon offshore phytoplankton assemblage in 2013 indicated a shift towards pico- and nanoplankton dominance as compared with the assemblage present in 1987 (Carrick et al. 2015). Specifically, the percent composition of picoplankton within total chlorophyll increased twofold from 1987 to 2013, resulting in more than 50% of the chlorophyll in 2013 being less than 2 μm in size.

Primary production in offshore waters near Muskegon has also undergone significant decadal changes since 1983 (Fahnenstiel et al. 2010b). While production levels have been stable during mid- and late-stratification periods, production during the spring period has declined 78% from 1983-1987 to 2007-2008. Furthermore, in low-productivity systems like Lake Michigan, the highest chlorophyll *a* or primary production values during stratification are commonly within the deep chlorophyll layer (DCL) below the epilimnion (i.e., in the metalimnion or even hypolimnion). At two sites (45 m, 110 m) offshore of Muskegon that are sampled monthly, the DCL has been decreasing in size since the late 1990s (Pothoven and Fahnenstiel 2013; Pothoven et al. 2016), and the likely mechanisms are declining availability of phosphorus and filtration by dreissenids (especially at the 45-m site).

Benthic Macroalgae

Cladophora spp. and other benthic macroalgae appear to have benefited from higher nearshore TP (relative to the offshore) and increasing water clarity, both of which could be influenced by excretion of phosphorus and nitrogen by dreissenids (Carrick and Lowe 1988, 2007; Bootsma et al. 2015). Brooks et al. (2015) validated a remote sensing method to generate a time series of submerged aquatic vegetation (SAV) presumably dominated by *Cladophora* spp. near Sleeping Bear Dunes National Lakeshore, Michigan, and Milwaukee, Wisconsin. SAV increased at least fourfold at both sites between 1994 and 2009, a time period corresponding to increased abundance of zebra and quagga mussels in the nearshore zone. During the 1980s, the nearshore benthic algal assemblage was dominated by a diverse, native diatom assemblage (see Kingston et al. 1983).

Microzooplankton

The available time series for microzooplankton (e.g., protists, rotifers, veligers, copepod nauplii) are limited. Carrick et al. (2015) compared the abundance of smaller microzooplankton (flagellated and ciliated protists) between 1987 and 2013 at an offshore site near Muskegon, and they reported significant declines in the densities of ciliated protists, while the flagellated protist population remained stable. Time-series data for other microzooplankton from the EPA (includes epilimnetic estimates for nauplii, rotifers, and veligers) are being recompiled and were incomplete for this synthesis. This is unfortunate, given that larval fish consume copepod nauplii during their first weeks of life, and more-recent analyses indicate that veligers are also being consumed (Withers et al. 2015). The contribution of protists to the diet of larval fish in Lake Michigan is currently unknown, although these organisms are known to support fish production in marine systems. Nearshore microzooplankton data were available only from the Illinois waters of the lake, and neither rotifers nor nauplii exhibited any linear trend between 1998 and 2015 (Illinois Natural History Survey (INHS), unpublished data; Appendix A, Fig. A2). Results from observations with net tows and a Plankton Survey System during the 2015 Cooperative Science and Monitoring Initiative field year near Muskegon showed that veligers were the dominant zooplankter in nearshore to mid-depth waters during June and a codominant zooplankter during July (HAV, unpublished data).

Mesozooplankton

Two complementary time series for mesozooplankton exist for the offshore: a lakewide survey (16 sites) that the EPA conducts each April and August (data available from 1998-2013) and a 110-m site offshore of Muskegon that the National Oceanic and Atmospheric Administration (NOAA) surveys between March and November (usually biweekly during the stratified period; data available from 1986-2015 with missing years in 1987 and 2004-2006) depending on weather conditions. Both surveys use a 153-µm mesh net—NOAA samples the entire water column and EPA samples down to a 100-m depth or to 2 m above the bottom at sites shallower than 100 m. For each survey, we averaged biomass for broad taxa (i.e., herbivorous cladocerans, calanoid copepods, cyclopoid copepods, predatory cladocerans) across sampling months in each year. We also

summed across the groups for an average annual crustacean biomass estimate. Because the biomass estimates are not comparable owing to differences in how animals are measured and which length-weight regressions are applied, we relativized each time series based on the year of maximum biomass. In the nearshore, two surveys were available: the Muskegon site (15-m bottom depth) conducted by NOAA (data available 1999-2015, missing 2004-2006) at a monthly interval similar to the offshore survey and a biweekly survey between June and October conducted by the INHS at two to three sites in Illinois waters at bottom depths ranging from 3 to 10 m (data available 1999-2013).

Total mesozooplankton biomass in the offshore declined over both of the southern-basin time series: EPA (Fig. 5b, 1998-2013) and NOAA (Fig. 5c, 1986-2015). For the northern basin, however, the EPA time series revealed no significant trend (Fig. 5a). In the nearshore, total crustacean biomass also exhibited a declining trend from 1999 to 2015 in the NOAA time series (Fig. 6a) on the southeastern side of the lake. However, on the southwestern side of the lake, the INHS time series showed no significant decline from 1999-2013 (Fig. 6b). These trends in total zooplankton biomass can obscure more taxa-specific trends, which we describe below.

Fig. 5. Time series of total crustacean relativized biomass at three different sites in the offshore waters of Lake Michigan. No trend was detected in the northern sites (panel a, $P = 0.41$, collected by the EPA and compiled by RPB). Significant linear trends were detected in southern sites (panel b, $P = 0.003$, EPA; panel c, $P < 0.001$, collected by NOAA, compiled by SAP).
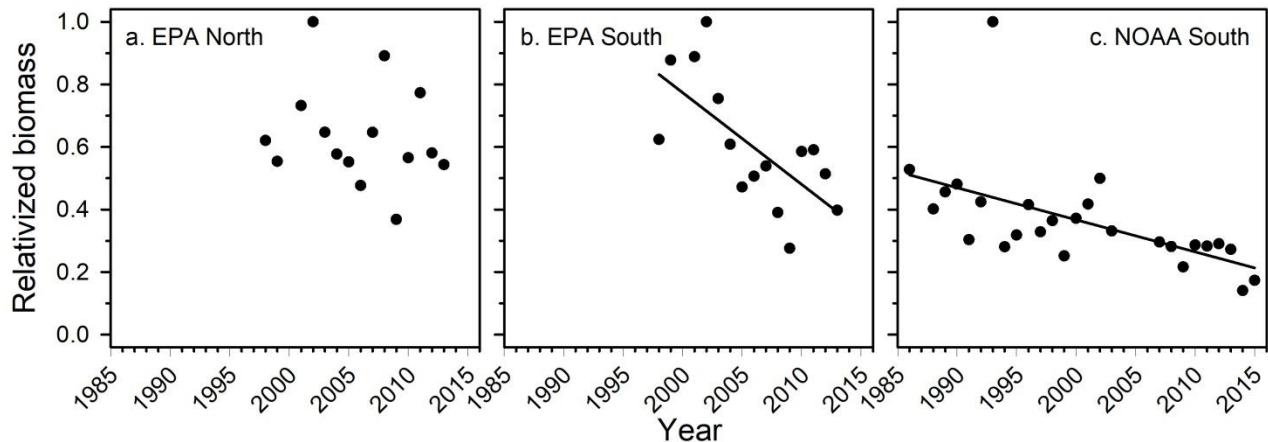
Herbivorous cladocerans (primarily *Daphnia galeata mendotae* and *Bosmina* spp.) in the offshore declined in all three time series. The EPA time series revealed declines from 1998 to 2013 (northern basin, $P = 0.01$; southern basin, $P = 0.01$) while the NOAA time series for the southern basin revealed declines from 1986 to 2015 ($P = 0.03$). In the nearshore, however, herbivorous cladocerans have not declined significantly since 1999 in either the NOAA ($P = 0.45$) or INHS time series ($P = 0.07$).

Fig. 6. Time series of total crustacean relativized biomass at two sites in the nearshore waters of southern Lake Michigan. Significant linear trends were detected in panel a ($P = 0.02$, collected by NOAA, compiled by SAP). No trend was detected in panel b ($P = 0.38$, collected by Illinois Natural History Survey (INHS), compiled by SMT).
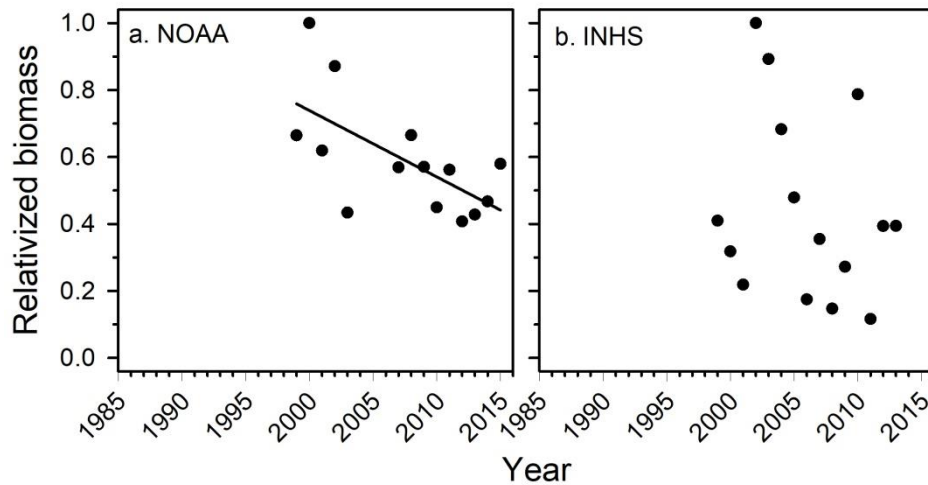
High abundance of cyclopoid copepods has occurred in Lake Michigan during periods of high abundances of Alewife, which preferentially selects larger calanoid copepods over smaller cyclopoids (Wells 1970; Vanderploeg et al. 2012). Cyclopoid copepods are largely carnivorous (LeBlanc et al. 1997) and more abundant in more-productive systems that support higher concentrations of microzooplankton and of visual predators (Hessen et al. 1995). Despite the reductions in offshore TP, only the NOAA time series detected a significant decline in cyclopoids ($P = 0.05$) between 1986 and 2015. In the EPA time series, cyclopoids were estimated to be at relatively low abundance in seven out of nine years since 2005 but exhibited high biomass levels in 2011 and 2013, which likely accounted for a non-significant negative trend. In the nearshore, both time series (NOAA, $P = 0.045$; INHS, $P = 0.02$) revealed a significant decline in cyclopoids between 1999 and 2014.

Calanoid copepods have been and still are dominant contributors to zooplankton biomass in Lake Michigan and have increased relative to other crustacean groups since 2004 (Vanderploeg et al. 2012; Pothoven and Fahnenstiel 2015). In particular, one key calanoid species, *L. macrurus*, has increased in Lake Michigan recently (Barbiero et al. 2009; Vanderploeg et al. 2012; Pothoven and Fahnenstiel 2015). For all calanoids, however, neither of the offshore EPA time series exhibited increasing biomass (EPA north, $P = 0.33$; EPA south, $P = 0.14$) between 1998 and 2013. In fact, calanoid copepods actually declined in biomass in the offshore NOAA time series from 1986-2015 ($P = 0.0002$) even though they still dominate the biomass of the mesozooplankton community. In the nearshore, neither time series (NOAA, $P = 0.21$; INHS, $P = 0.93$) trended significantly between 1999 and either 2013 (INHS) or 2015 (NOAA).

Trends in densities of predatory cladocerans, which include the non-indigenous spiny water flea (*B. longimanus*) and fishhook water flea (*Cercopagis pengoi*) as well as the native *Leptodora kindtii*, were not significant in any of the offshore (EPA north, $P = 0.48$, 1998-2013; EPA south, $P = 0.75$, 1998-2013; NOAA, $P = 0.31$, 1986-2015) or nearshore (NOAA, $P = 0.70$, 1999-2015; INHS, $P = 0.31$, 1999-2013) surveys. Alewife predation likely regulates *B. longimanus* densities, especially in nearshore waters (Pothoven et al. 2007; Keeler et al. 2015; Vanderploeg et al. 2015).

Mysis diluviana

Mysids are large (4-20 mm) omnivorous invertebrates that are important diet items for many prey fish (Hondorp et al. 2005; Pothoven et al. 2010). Although abundance trends of *Mysis diluviana* vary by survey, mysid densities in the past 10 years are lower than estimated between 1995 and 2000 but not markedly different from 1985-1989. The U.S. Geological Survey (USGS) and Michigan DNR conduct an annual lakewide survey (N ~ 20 sites) each August since 2005 and found declining densities through 2015 ($P = 0.01$, Fig. 7). NOAA has conducted monthly sampling of a 110-m site offshore of Muskegon between March and November dating back to 1985 but with gaps between 1990 and 1994 and in 2001 and 2006. Average densities of $111/m^2$ (SE = 27) from 1985-1989, $191/m^2$ (SE = 43) from 1995-2000, and $72/m^2$ (SE = 10) from 2007-2015 (Fig. 7) were reported.

Fig. 7. Time series of *Mysis diluviana* densities in Lake Michigan estimated by NOAA (black bars, compiled by SAP) and the USGS and Michigan DNR) (gray bars, compiled by DMW).
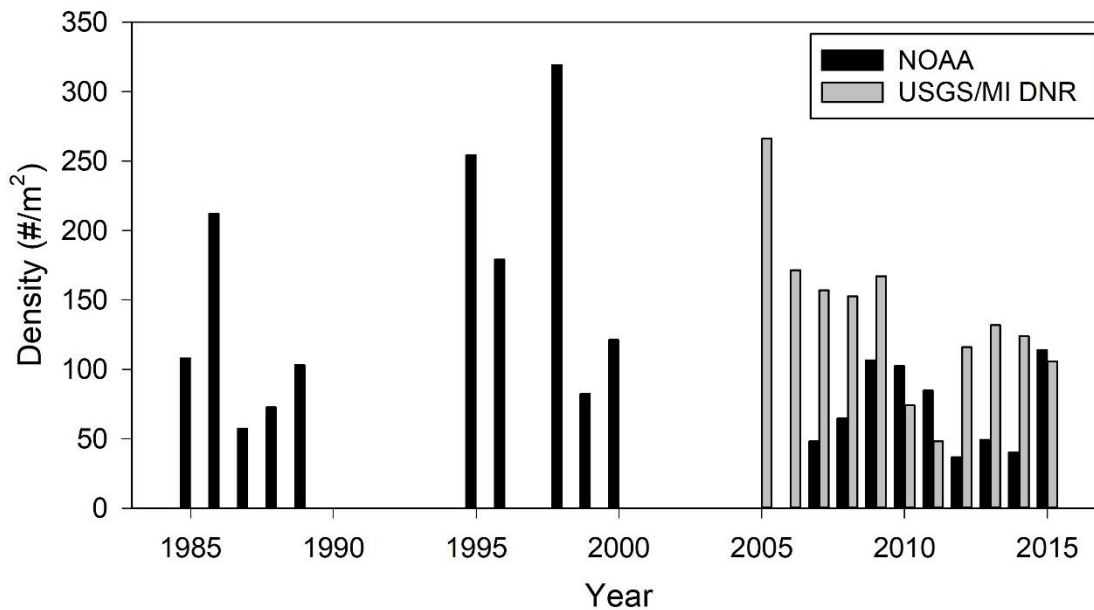
Benthic Invertebrates

Benthic invertebrate biomass has been dominated by dreissenids since the late 1990s after previously being dominated by *Diporeia* spp. Dreissenid density on soft (i.e., sand, mud) substrates has been estimated annually since 1998 in the southern basin by NOAA (Fig. 8). Quagga biomass reached higher levels than zebra mussels ever attained, in part, because zebra mussels were limited to bottom depths less than 50 m (Fig. 8b). Quagga biomass in the southern basin appears to have leveled out since 2010 (black "weighted" line in Fig. 8a), although trajectories have varied between depth zones. Appendix B provides more-detailed descriptions and hypotheses regarding how dreissenids disrupted the pelagic food web.

Fig. 8. Time series of quagga (panel a) and zebra (panel b) mussels for different depth regions of southern Lake Michigan as estimated by NOAA (compiled by AKE).
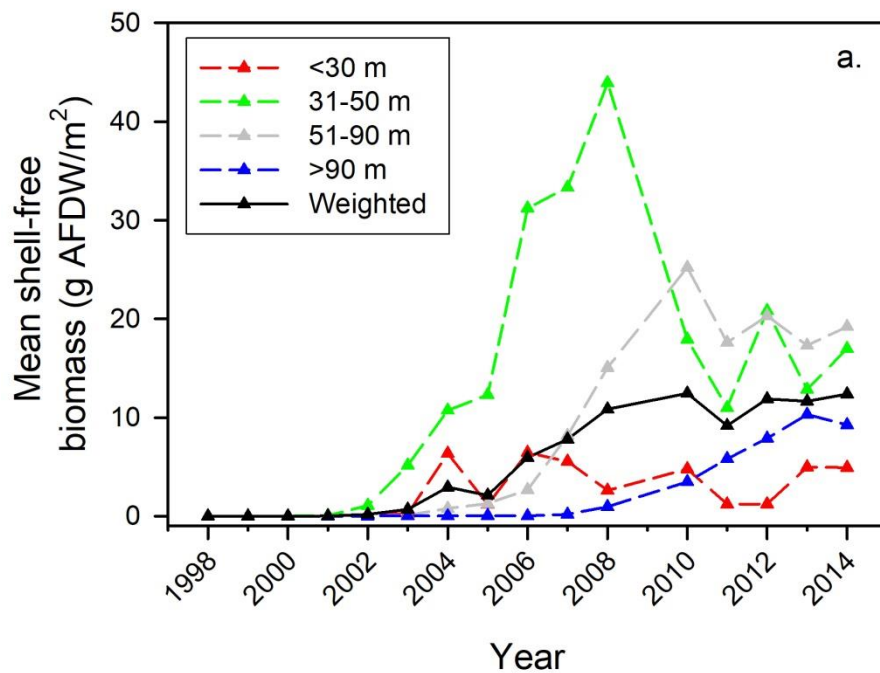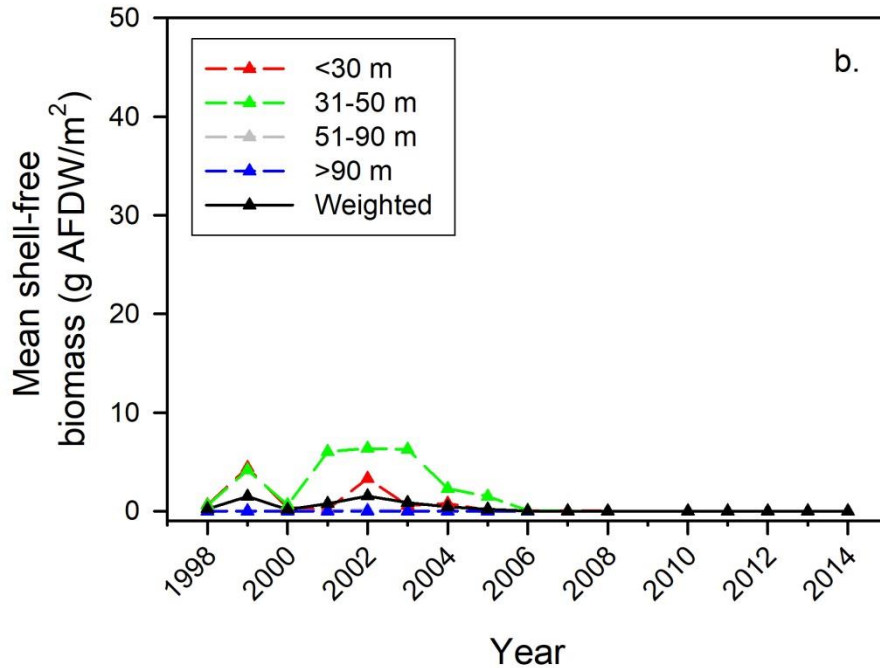
Diporeia spp. densities on soft substrates declined precipitously from 1994-1995 to 2000 coincident with the invasion of dreissenids, although the underlying mechanism is unknown (Nalepa et al. 2009). An EPA dataset, produced lakewide at 16 sites since 1997, indicates a steep decline in density between 1997 and 1998 even at deeper sites where dreissenids were absent (Fig. 9b). In a NOAA survey of 40 sites in southern waters sampled irregularly since 2000, *Diporeia* spp. are now only consistently found at one of six sites deeper than 90 m (Fig. 9a). Both surveys, especially that of the EPA, indicate that, since 2004, densities have remained relatively stable at depths greater than 90 m. Although other benthic invertebrates are consumed by fish (e.g., chironomids, oligochaetes), time series of their densities were not available for this paper.

Proportional density of benthic invertebrates differed between soft and hard substrates in surveys conducted in nearshore Illinois waters by the INHS. On soft substrates at two-three sites monitored monthly between June and October since 1999, chironomids dominated in all years (Appendix A, Fig. A3a), although nematodes and oligochaetes comprised increasing proportions in the past five or so years. The decline in *Diporeia* spp. abundance is also apparent in these data. On hard substrates for five of the past eight years, the proportional density of dreissenids was higher than the proportional density of chironomids, opposite to that on soft substrates (Appendix A, Fig. A3b).

Fig. 9. Time series of *Diporeia* spp. estimated by NOAA (panel a, compiled by AKE) and the EPA (panel b, compiled by RPB) for different depth regions in Lake Michigan.
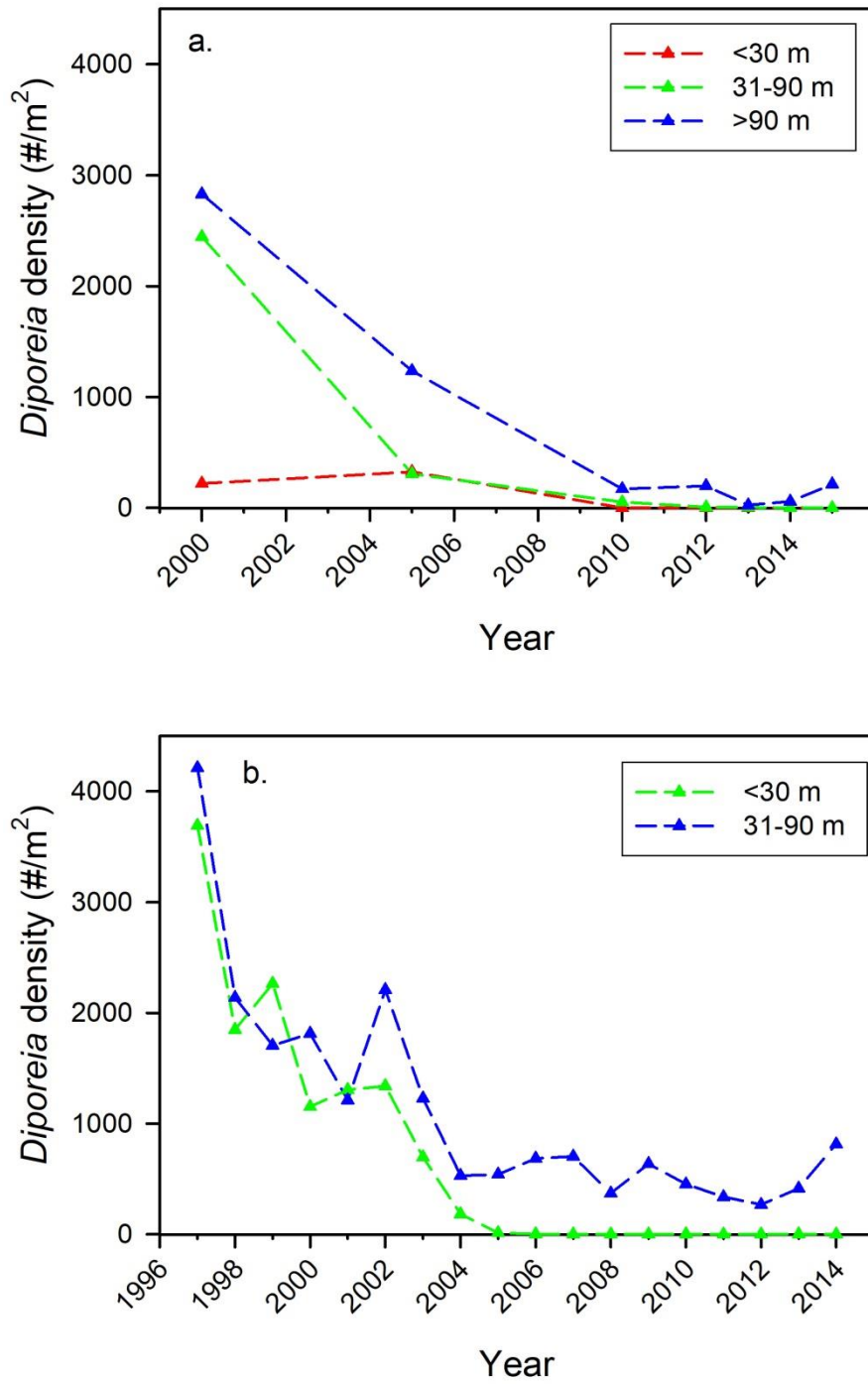
Summary of Trends

Lower trophic-level data trended more in offshore waters, where federal monitoring provides broad spatial coverage, than in nearshore waters (Table 1; Appendix A, Fig. A4). Key trends include increased water clarity, decreased TP, decreased chlorophyll *a* and phytoplankton abundance, declines in herbivorous cladocerans, declines in *Diporeia* spp., and increases in quagga mussels. Monitoring efforts in the nearshore, although spatially restricted, depict increases in benthic macroalgae, declines in cyclopoid copepods, and declines in *Diporeia* spp. Compared to the offshore, in the nearshore there was less evidence for declines in phosphorus, chlorophyll *a*, and zooplankton, although the shorter span of the nearshore time series makes it more difficult to discern trends. Quantification of the effects of lower trophic levels on fish populations will, therefore, likely depend on the extent to which fish species use nearshore versus offshore habitats at different life-history stages and on the match or mismatch of preferred prey items in different seasons.

Table 1. Summary of lower trophic-level trends in Lake Michigan as determined by analyses of time series.

Variable	Offshore (≥30 m)	Nearshore (<30 m)
TP loading	No trend (1980-2008)	
TP concentrations	Declining (1983-2015)	No trend (1999-2014)
Water clarity	Increasing (1998-2015)	No data
Chlorophyll *a*	Declining (1998-2015)	No trend (1999-2015)
Microzooplankton	No time series available	No trend (1998-2015)
Total mesozooplankton	Mixed: Declining in two time series (1986-2015); no trend in one time series (1998-2013)	Mixed: Declining in one time series (1999-2015); no trend in one time series (1999-2013)
Herbivorous cladocerans	Declining in all three time series (1986-2015)	No trend in two time series (1999-2015)
Cyclopoid copepods	Mixed: Declining in one time series (1986-2015); no trend in two time series (1998-2013)	Declining in two time series (1999-2015)
Calanoid copepods	Mixed: Declining in one time series (1986-2015); no trend in other two time series (1998-2013)	No trend in two time series (1999-2015)
Predatory cladocerans	No trend (1994-2015)	No trend (1999-2015)
Mysis diluviana	Declining (2005-2015), but 2005-2015 densities not different from 1985-1989	Not relevant
Dreissenids	Increasing to asymptote (1998-2014)	No trend, very noisy (1998-2014)
Diporeia spp.	Declining (2000-2014)	Declining (2000-2014)

MECHANISMS BY WHICH CHANGES IN LOWER TROPHIC LEVELS COULD AFFECT FISH

Above, we provided empirical evidence for changes in lower trophic levels in Lake Michigan noting that most of the changes are in offshore waters. At the same time, the less-monitored nearshore could also be undergoing large changes, too. Fish typically are at least one trophic level above zooplankton or benthic invertebrates. Accordingly, we investigate four mechanisms (see Fig. 10) by which prey fish could be affected by changes in lower trophic levels or in important abiotic factors (e.g., water clarity): (1) prey-fish abundance is reduced by increased piscivory associated with increasing water clarity; (2) fewer invertebrate prey cause declining growth rates of juvenile and adult fish; (3) fewer invertebrate prey cause declining condition of adult fish, which, in turn, reduces the quantity and quality of fish eggs and larvae; and (4) declining zooplankton prey and/or altered vertical distribution of zooplankton prey reduce survival of larval fish. We discuss the likelihood of each mechanism. Although these hypothesized mechanisms are written as if independent, we recognize that some may interact and that the Lake Michigan food web is much more complex than the simple illustration in Fig. 10. As an example, mass-balance ecosystem models parameterized for Lake Michigan have revealed that no single factor (e.g., declines in phosphorus and phytoplankton, proliferation of dreissenids, changing zooplankton abundance or composition, or salmonine predation) appears to underlie declines in prey fish (see Kao et al. 2017; ESR, unpublished data). Rather, multiple factors, perhaps working synergistically, are driving the declines.
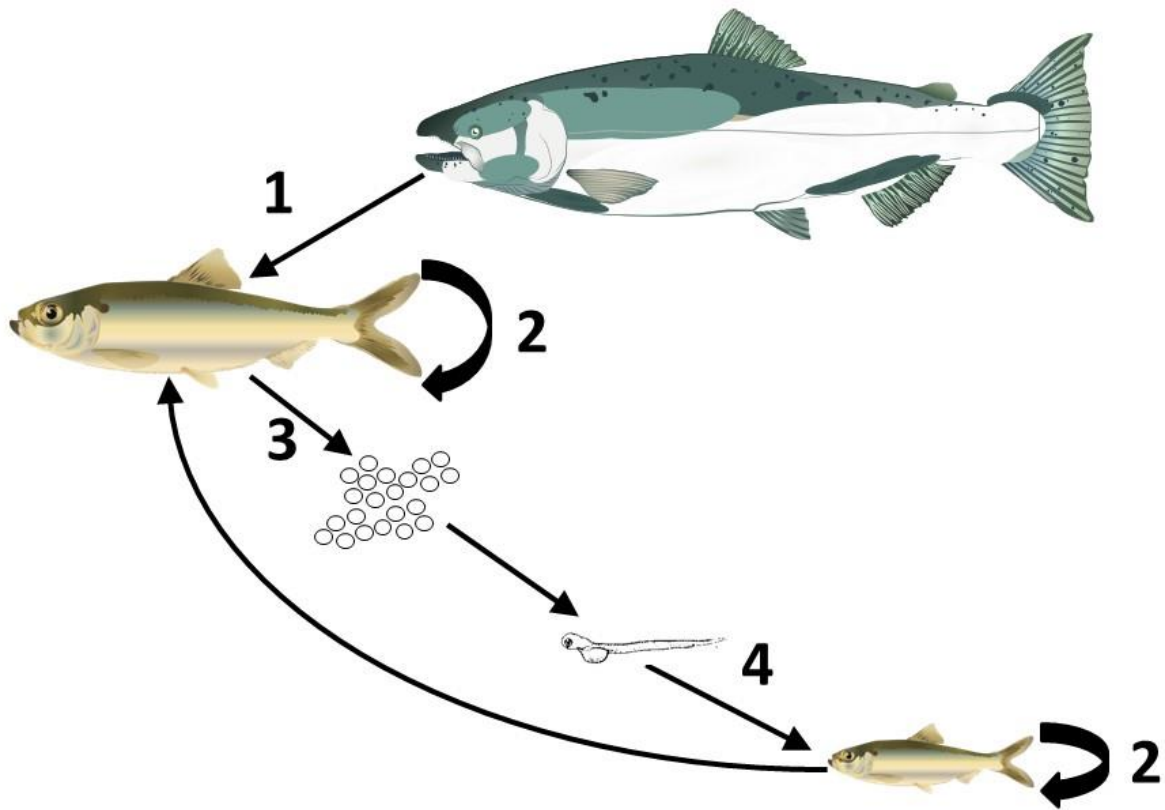
Hypothesis 1

We hypothesize that prey-fish abundance is reduced by increased piscivory owing to increased water clarity associated with oligotrophication and the eruption of quagga mussels, including mussel filtration of seston (Vanderploeg et al. 2010; Rowe et al. 2015; see Fig. 10, pathway 1). As Vanderploeg et al. (2015) noted, water clarity has increased in Lake Michigan so that visually preying planktivores (e.g., *B. longimanus*; fish, including larvae) can likely see plankton at far greater depths during the daytime than before. Likewise, piscivores, such as Chinook Salmon (*Oncorhynchus tshawytscha*), can likely detect prey fish more easily in clearer water.

Given that offshore water clarity increased by more than 60% around 2004 and has henceforth remained clear (Fig. 3), what evidence exists that the salmonine community has increased or maintained its foraging efficiency on pelagic prey fish? In particular, has search efficiency (γ) actually declined? In the current statistical catch-at-age models for salmonines, γ is modeled as a Type II functional response where consumption increases with prey density but eventually reaches satiation, is assumed to be time-invariant, and is estimated to be higher for Lake Trout (*Salvelinus namaycush*) than for Chinook Salmon (Tsehaye et al. 2014). Given that Alewife density has declined by at least 40% from 2002-2004 to 2012-2016 (USGS 2017), density possibly has declined to such low levels that γ has declined, too. We hypothesize, however, that increased water clarity has allowed γ to increase or to be maintained at higher than predicted levels, although no direct evidence for such a situation exists. Future models could explore if allowing γ to increase during the period of increased water clarity would improve model fits. Other factors already known to affect consumption rates of prey fish include: (1) the numbers of piscivores (e.g., arising from increased Chinook Salmon natural recruitment aided by immigration of wild Chinook Salmon from Lake Huron (Clark et al. 2016)), (2) diet composition, and (3) energy density of prey fish (see Madenjian et al. 2015).

In the nearshore zone, water clarity has not increased to the same degree as in the offshore. However, Walleye (*Sander vitreus*) is a nearshore predator that likely can maintain relatively high predation rates in even turbid waters (Ryder 1977; Lester et al. 2004). In summary, the hypothesis that prey-fish abundance has been reduced by increased piscivory owing to increased water clarity associated with oligotrophication has not been specifically evaluated but is plausible and worthy of future research.

Fig. 10. Potential mechanisms by which changes in lower trophic levels can influence the production of prey fish in Lake Michigan: (1) increased predation by salmonines on prey fish owing to increasing water clarity, (2) reduced growth rates by juveniles and adults owing to declining invertebrate prey, (3) fewer and lower-quality eggs owing to reduced adult energetic condition, and (4) slower growth and reduced survival of larvae owing to either reduced densities of zooplankton prey or altered zooplankton spatial distribution.


-Illustrations by Kim Kraeer, Lucy Van Essen-Fishman, Emily Nastase; Integration and Application Network (IAN); University of Maryland Center for Environmental Science (http://ian.umces.edu/imagelibrary/); Auer (1982).

Hypothesis 2

We hypothesize declining growth rates (i.e., wet weight-at-age) of juvenile and adult prey fish owing to fewer invertebrate prey resources contributed to declines in prey-fish biomass (Fig. 10, pathway 2). We recognize that fish abundance is the most-important driver of fish biomass but note that declines in growth rates can be secondary contributors to biomass declines. Hypothesis 2 requires that recent lower trophic-level changes resulted in fewer invertebrate prey for juvenile and adult prey fish. As Table 1 indicates, the only invertebrate prey that has undergone a lakewide decline is *Diporeia* spp. Some mesozooplankton trends have been negative (i.e., herbivorous cladocerans in the offshore), but declining trends for most taxa were not apparent. Secondary indications of a declining invertebrate prey base are shifts in prey-fish diet (Pothoven and Madenjian 2008; Bunnell et al. 2015) or in stable isotopes (Turschak et al. 2014) of key prey fish. Dreissenids, for sure, have become more abundant; only round goby (*Neogobius melanostomus*), a benthic prey fish that invaded Lake Michigan in 1993, has demonstrated an ability to exploit juvenile and adult dreissenids. In total, the evidence does not support lakewide declines for aggregated invertebrate prey (given the proliferation of dreissenids). Alternatively, for non-dreissenid invertebrate prey, our synthesis indicates that biomass is either unchanged or lower than what was documented in the late 1990s. Of the three prey groups mentioned above (*Diporeia* spp., zooplankton, dreissenids), the steep decline in *Diporeia* spp. density during the 1990s and 2000s is most consistent with changes in prey-fish growth.

Given that densities of prey fish declined over the past two decades (USGS 2017), one might reasonably predict that growth rates would be relatively stable despite reduced prey densities, e.g., of *Diporeia* spp. However, mean weight of age-3 Alewife estimated from USGS trawl surveys exhibited a decline between 1990 and 2001 (Fig. 11a) but has been relatively stable from 2002 through 2015. Madenjian et al. (2003) reported declining growth through 2001 and attributed it to declining *Diporeia* spp. densities. On average, the weight of an age-3 Alewife declined 33% between the 1980s (41 g) and the 2000s (28 g). Also, mean weight of age-3 Bloater has exhibited a gradual long-term decline (Fig. 11b). We interpret the decline in mean weight of Bloater between 1980 and 1990 to have resulted from high intraspecific competition; Bloater mean biomass during this period was five times higher than in the 2000s. Bloater growth appeared relatively stable from 1990 through 2004 but has declined gradually over the past decade in the absence of any substantive increase in Bloater biomass. In total, the average weight of an age-3 Bloater declined 44% between the 1980s (79 g) and the 2000s (45 g). Hence, Alewife and Bloater, which are associated primarily with the offshore, are attaining a smaller weight-at-age in the 2000s than previously, coinciding with a period of changing lower trophic levels and declining fish densities. In conclusion, there is good evidence that prey-fish growth has declined since the 1980s owing to declining invertebrate prey resources, especially of *Diporeia* spp. One caveat, however, is that reduced growth rates could also lead to reductions in natural mortality rates owing to stronger immune defenses or bone development associated with slower growth in weight (see Mangel and Stamps 2001). These changes could compensate, at least in part, for the potential increase in predation mortality described in Hypothesis 1 and for the theoretical reduction in population biomass associated with slower growth rates.

Fig. 11. Time series of growth rates (mean weight at age 3) for Alewife (panel a) and Bloater (panel b) in Lake Michigan.
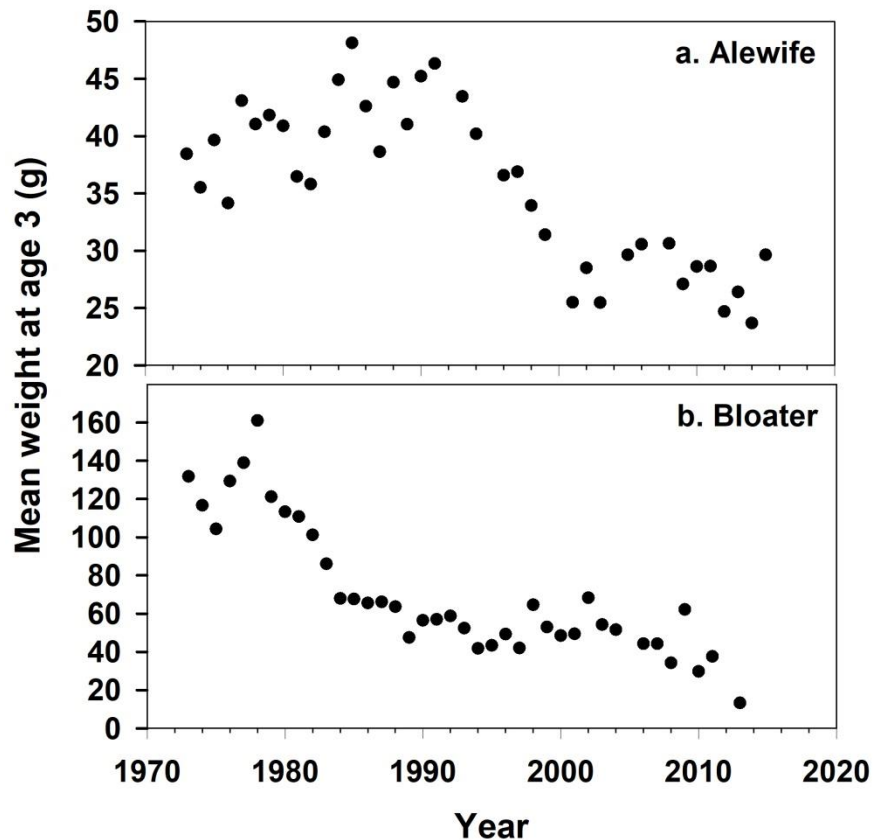
Overall, the hypothesis that declining growth rates owing to fewer invertebrate prey have contributed to declines in prey-fish biomass has equivocal support. That said, the potential for compensatory increases in survival (sensu Mangel and Stamps 2001) of prey fish causes uncertainty regarding the effects of reduced growth rates (or condition; see Hypothesis 3) on prey-fish biomass.

Hypothesis 3

We hypothesize that limited invertebrate prey (i.e., zooplankton, *Diporeia* spp., mysids) is causing reductions in adult prey-fish condition, such that the quantity (e.g., fecundity) and quality (e.g., larval size at hatch, size of yolk-sac) of offspring are compromised (also known as "maternal effects"; see Fig. 1, pathway 3). The best criterion in support of this hypothesis would be documentation of a reduction in energetic condition of prey fish. Several studies have estimated the energy density of different species over about the past 20 years when abundance for most prey-fish species was declining. As summarized in Madenjian et al. (2015), Alewife (Madenjian et al. 2003, 2006; Hondorp et al. 2005), Bloater (Pothoven et al. 2012), Deepwater Sculpin (*Myoxocephalus thompsonii)* (Hondorp et al. 2005; Pothoven et al. 2011), and Lake Whitefish (*Coregonus clupeaformis*) (Pothoven et al. 2001; Pothoven and Madenjian 2008) all have been documented to either have experienced reductions in mean energy density or no compensatory increase in energy density despite having fewer intraspecific competitors.

Given that changes in lower trophic levels are the most likely explanation for the reduced energetic condition, better support for the hypothesis would derive from research that links maternal energetic condition to quantity or quality of offspring. For marine fish species, this linkage has been well documented in a variety of studies (e.g., Kjesbu et al. 1991; Berkeley et al. 2004). For Great Lakes prey fish, however, this linkage has not been demonstrated consistently. In one supporting study of Bloater where Bloater fecundity was compared for similar-sized fish from the 2000s and late 1960s, average fecundity was 24% lower in the 2000s than in the 1960s, which corresponded with a 40% lower energetic condition in the 2000s compared to the 1960s (Bunnell et al. 2009). Conversely, Muir et al. (2014) found minimal evidence that female Lake Whitefish in better physiological condition produce eggs of higher quality (e.g., larger size, higher lipid content, higher concentrations of desirable fatty acids) than those in poorer condition. The impact of maternal condition on percid eggs and larvae also has produced equivocal results with other factors, such as stock effects (Wang et al. 2012) or climate (Farmer et al. 2015; Feiner et al. 2016), being more-important predictors of offspring characteristics than maternal characteristics. Given that the importance of maternal effects likely varies by species, research will be required to determine if reduced energetic condition of Alewife, for example, is resulting in fewer or poorer-quality eggs and offspring and thereby limiting its reproductive potential.

Negative trends in larval fish densities would be consistent with the hypothesis that declining condition or growth was indeed limiting production of offspring (via maternal effects). These densities are influenced by many factors, including the number of adult spawners; abiotic conditions (e.g., temperature, precipitation); biotic factors (predation, prey availability); and, potentially, adult energetic condition. No larval time series exist for Lake Michigan fish; however, from two lakewide surveys, the USGS estimates densities of age-0 Alewife in late summer, for example, that feed into a stock assessment model that predicts age-0 densities. In the model, Tsehaye et al. (2014) estimated age-0 Alewife densities based on not only these two surveys but also on modeled consumption of Alewife, and they found that age-0 Alewife densities in the fall exhibited no trend between 1990 through 2010, a period when adult condition declined (see Madenjian et al. 2015). Even when accounting for the effect of spawning-stock size, there was no downward trend in Alewife recruitment as measured by numbers of fall age-0 fish in the 2000s (Bunnell et al. 2017). Similarly, age-0 Bloater densities estimated from the same two surveys increased over the same period when fecundity and adult condition had declined (USGS 2017). The hypothesis that reduced adult energetic condition reduced the density of offspring is not supported by the available data.

Hypothesis 4

We hypothesize that survival of larvae from key prey fish decreased relative to previous decades (i.e., prior to 2004) owing to fewer zooplankton prey resources or to an altered vertical distribution of zooplankton prey (see Fig. 10, pathway 4). For some species (e.g., Alewife, Bloater), whose age-0 numbers have not trended downward based on models or surveys since the early 2000s, this hypothesis is not supported. For rhetorical reasons, we still describe tangential evidence for this hypothesis in the low probability that survey or model estimates are inaccurate.

This hypothesis would be supported if lower trophic-level changes resulted in fewer small zooplankton prey for first-feeding larvae or in reduced spatial overlap between fish larvae and their prey (Hjort 1914; Cushing 1990). In evaluating this hypothesis, consider that some larvae hatch in nearshore waters (e.g., Alewife, Rainbow Smelt, Yellow Perch (*Perca flavescens*), and others hatch in offshore waters (e.g., Bloater, Deepwater Sculpin). Such research may be complicated by advection of larvae from nearshore to offshore waters within the first two weeks of life (Dettmers et al. 2005; Weber et al. 2015).

Have zooplankton prey densities declined throughout the lake? Our compilation of lower trophic-level trends showed equivocal support for a reduced availability of microzooplankton prey that could support first-feeding larvae. Trends for larger microzooplankton prey (rotifers, copepod nauplii) were available only for nearshore waters in Illinois, and those time series showed no decline between 1998 and 2015. However, abundance of smaller microzooplankton (ciliated protists) trended downward strongly between 1987 and 2013 in offshore waters (Carrick et al. 2015). Abundance of other smaller, easily captured, mesozooplankton prey (e.g., herbivorous cladocerans, cyclopoid copepods) did not trend downward across data sets (Table 1). For example, herbivorous cladocerans were declining in all three offshore time series (potentially negative effect on Bloater larvae) but showed no trends in two nearshore time series (potentially neutral effect on Alewife, Rainbow Smelt, and Yellow Perch larvae). Although no time series were available for veligers, which are of unknown nutritional quality, they are appearing in the diets of larval fish, such as Alewife (Withers et al. 2015). We presume veligers would be abundant given the high density of adult dreissenids throughout the lake. Our time series are too sparse and rarely occur during early stratification (June-July), making them unsuitable for evaluating if densities of preferred zooplankton (abundance of prey weighted by selectivity; Vanderploeg and Scavia 1979) are adequate for larval fish when they switch to exogenous feeding.

Has the vertical distribution of zooplankton prey over the last 10 years changed with increasing water clarity? Because larval fish are visual predators, daytime overlap with their prey is critical to their survival. During thermal stratification, many zooplankters undergo some degree of diel vertical migration, occupying deeper metalimnetic or hypolimnetic waters during the day and migrating to shallower waters at night (see Vanderploeg et al. 2015). For example, in Lake Michigan, *Daphnia galeata mendotae* undergoes large vertical migrations (up to 30 m) from the metalimnetic-hypolimnetic boundary during the day into the epilimnion at night; cyclopoid and calanoid copepods exhibit somewhat shorter migrations. These vertical migrations allow zooplankters to escape the visually preying non-indigenous *B. longimanus* that inhabits mostly the epilimnion and metalimnion (Pangle et al. 2007; Bourdeau et al. 2015; Ptáčníková et al. 2015; Vanderploeg et al. 2015). With increasing water clarity, however, *B. longimanus* may feed successfully in deeper waters and thereby cause zooplankton to migrate even deeper (Vanderploeg et al. 2015). Recent changes in the DCL also may induce a deeper daytime vertical distribution of herbivorous zooplankters; the DCL depth and width appear to be undergoing changes associated with increasing water clarity and reduced nutrient concentrations (Pothoven and Fahnenstiel 2013). Deeper daytime distributions of zooplankton may result in decreased overlap between larval prey fish and their invertebrate prey as proposed by Eshenroder and Lantry (2012) for juvenile Alewife. Improved descriptions of the daytime vertical distribution of fish larvae and their prey will be required to determine if lower trophic-level changes, such as the proliferation of *B. longimanus* or increasing water clarity, have reduced the foraging efficiency of larval prey fish. These studies are particularly relevant during the setup of stratification in late spring and early summer, an important time for fish larvae, which has received little attention.

Has the seasonal timing of zooplankton densities changed in recent decades? The temporal overlap between first-feeding larvae and zooplankton prey has been recognized as a critical period going back to Hjort (1914). In some other systems, climate warming can cause phenological shifts for phytoplankton and zooplankton (Adrian et al. 2009). Similarly, Vanderploeg et al. (2012) reported earlier plankton development in warm springs, particularly in 1998, which was extremely warm. On the contrary, Pothoven and Vanderploeg (2017) reported that, at NOAA's 45-m and 110-m sites near Muskegon, spring zooplankton biomass peaked later in 2007-2015 as compared to 1995-2002, which could be associated with a decline in spring primary production.

Slower growing larval Alewife and Bloater likely have a lower probability of survival, assuming size confers a survival advantage (see Miller et al. 1988). Unpublished data collected during the 2015 CSMI year on Lake Michigan at four sites in July revealed that larval Alewife growth rates were more than 40% lower than in 2001-2006 (Hook et al. 2007; Weber et al. 2015). Likewise, Bloater growth rates in 2015 (ESR and D. Eppehimer, Great Lakes Science Center, personal communication, 2017) were more than 40% lower than in 1982-1983 (Rice et al. 1987). The high frequency of empty larval stomachs noted in recent studies (e.g., Withers et al. 2015) provides further support for the proposition that growth rates of larval prey fish have slowed in a more-oligotrophic Lake Michigan. Although larval-fish survival rates in the Great Lakes are estimated too rarely to make comparisons across the decades where lower trophic-level conditions have varied starkly, studies estimating larval-fish growth rates are more numerous and afford more opportunities for comparison. Slower growing larvae may have a lower probability of survival assuming size confers a survival advantage (see Miller et al. 1988).

In summary, evidence is emerging that Bloater and Alewife larvae are growing more slowly over the last decade coincident with the changing zooplankton community, but there is no supporting evidence for decreased survival of these larvae to the juvenile stage in the fall. Thus, we reject the hypothesis that reduced survival of age-0 prey fish accounts for fewer older prey fish but caution that the resilience of existing adult populations may have been compromised by the observed declines in larval growth.

EXPERT OPINION FOR LOWER TROPHIC-LEVEL INDICATORS AND MONITORING AND KNOWLEDGE GAPS

Among its charges, the LMC sought an identification of predictive lower trophic-level indicators, monitoring gaps, and knowledge gaps. Lists of indicators were developed during a workshop in the summer of 2016, and these were refined further and prioritized by conference calls and emails.

Lower Trophic-Level Indicators for Fishery Managers

We discuss the top-four-ranked indicators below; the entire list and ranking can be found in Appendix A, Table A1.

1) Condition of adult Alewife:
This relatively simple measure of Alewife condition (e.g., predicted wet weight for a selected length) integrates the effects of changes in lower trophic levels. The Great Lakes Science Center has a long-term time series for this metric so no new sampling is required.

2) Satellite-derived chlorophyll *a* estimates:
Chlorophyll *a* is routinely sampled *in situ* at several nearshore and offshore sites around the lake, but satellite estimates of epilimnetic chlorophyll *a* provide broader spatiotemporal coverage. Several recent papers use this approach (e.g., Warner and Lesht 2015; Fahnenstiel et al. 2016), and the EPA is willing to continue to compile and report this information as part of its annual reporting (EH-M). One caveat is that a considerable fraction of primary and secondary production likely occurs in the DCL or metalimnion (Pothoven and Fahnenstiel 2013; Vanderploeg et al. 2015), which is not included in satellite surveys.

3) Density of *M. diluviana*:
Nearly all of the key prey fish rely on *M. diluviana* as a high-energy food item during at least part of the year. Declines in this key offshore prey would likely be detrimental to production of prey fish. Because several agencies (NOAA, EPA, USGS) monitor mysids annually, an interagency index could be developed readily.

4) Spring TP:
Phosphorus is the limiting nutrient for primary production, and, similar to the chlorophyll *a* estimate (Indicator 2 above), spring TP is a key indicator of potential productivity at the base of the food web. The EPA quantifies spring TP in the offshore waters annually. Other routine monitoring includes NOAA's monthly sampling along a nearshore to offshore transect offshore of Muskegon and nearshore sampling by the Bootsma Lab (University of Wisconsin-Milwaukee) on the southwestern shore.

Monitoring Gaps

We discuss the top-four-ranked monitoring gaps below; the entire list and ranking can be found in Appendix A, Table A2.

1) **Coordinated nearshore sampling of lower trophic levels, including fish larvae:** Several agencies and at least two universities conduct localized nearshore sampling of lower trophic levels and fish (see Appendix A, Fig. A4), but this limited nearshore work is not standardized or reported in a coordinated manner. Every five years beginning in 2010, the EPA funds the National Coastal Condition Assessment in all five Great Lakes, which encompasses more than 50 nearshore sites in Lake Michigan sampled for nutrients, benthic invertebrates, and fish contaminants. Additional work would be required to standardize or relativize the data in the nearshore such that a more-comprehensive status of the nearshore could be described. Ideally, additional nearshore sampling sites could be established given the dynamic nature of the inshore and its importance as spawning and nursery habitat for key fish. Targeted sampling near river mouths may also be required given that both field observations (Yurista et al. 2012; Pothoven and Fahnenstiel 2015) and modeling (Rowe et al. 2017) suggest primary productivity is centered around tributary sources of nutrients or areas of upwelling or both.

2) **Direct measurements of primary production:** *In situ* estimation of carbon fixation by primary producers is not estimated as routinely as it was in past decades, and several members of the task group emphasized the importance of maintaining this measurement even as more indirect measures of primary production are being developed. Maintaining this capability will insure proper calibration of indirect estimates.

3) **Phosphorus loading by tributary:** The last year of estimated TP loading into Lake Michigan by tributary was 2008. The historical time series illustrated no trend from about 1980 through 2008 yet there are at least two reasons to justify updating the time series. First, considerable funding from the Great Lakes Restoration Initiative has been invested since 2010 to further reduce TP loading. Have TP loadings begun a declining trend over the past decade? We do not know. Second, our workshop deliberations revealed limited understanding of how nutrient loadings influence offshore TP concentrations, suggesting a potential decoupling owing to a greater importance of within-lake TP cycling. To support future modeling, within-lake phosphorus concentrations, updated TP loadings, and the fate of TP once it enters the lake are important unknowns. In addition, TP loadings by tributary will allow scientists to better understand the spatiotemporal dynamics of nearshore productivity.

4) **Simultaneous sampling of the physical environment, lower trophic levels, and fish:** The task group recognized how simultaneous sampling of abiotic factors (nutrients, temperature, light), lower trophic levels (chlorophyll *a*, benthic macroinvertebrates, zooplankton, *M. diluviana*), and fish is critical for an improved understanding of factors that influence the distribution and abundance of prey fish. This contemporaneous sampling of multiple trophic levels already is undertaken by many agencies regionally and over broader spatial scales during CSMI years, but the task group believes there are still considerable opportunities for this approach to be expanded.

Knowledge Gaps

We assume that such knowledge gaps may be used as research priorities by funding agencies. We discuss the top-four-ranked knowledge gaps below; the entire list and ranking can be found in Appendix A, Table A3.

1) What lower trophic-level changes bottleneck the recruitment of age-0 fish to the age-1 and older populations?

   Some members of the task group believe that known changes in lower trophic levels may be having their greatest impact on fish abundance by affecting their recruitment past larval stages. Although existing time series of age-0 fish do not indicate a bottleneck, further testing of this hypothesis in a system as large as Lake Michigan will require a coordinated effort across agencies and universities.

2) What is the relative importance of reduced nutrients and quagga mussel filtration and their potential interaction in driving declining pelagic primary production?

   Published studies recently identified these two factors as the key drivers of declining pelagic primary production (e.g., Warner and Lesht 2015; Rowe et al. 2017), but the task group recommends additional research to determine which factor is more important. Knowing which factor most underlies the ongoing oligotrophication of Lake Michigan would allow for more-targeted remediation, i.e., should lakewide control of dreissenids be pursued or should phosphorus targets be reconsidered. Recent biophysical models that simulate different nutrient inputs, nutrient concentrations, and mussel filtering rates indicate that both factors have contributed to the observed spatiotemporal changes in phytoplankton production and abundance (e.g., Pilcher et al. 2017; Rowe et al. 2017).

3) Have changes in the zooplankton community affected prey-fish biomass to the extent that fishery managers should reconsider their objectives?

   Our report summarized changes in mesozooplankton: declining offshore herbivorous cladoceran density, increasing relative importance of calanoid copepods, and declining total biomass in southern Lake Michigan. But whether or not these changes affect prey-fish biomass and, by extension, imply a need for altered management policy is unresolved. This research gap relates to Knowledge Gap 1 above where changes in the zooplankton community have been hypothesized to limit survival of larval fish. A critical gap would be estimation of zooplankton species composition and abundance lakewide more often than for April and August and especially during early stratification.

4) What are the key drivers of phosphorus recycling?

   Declines in offshore TP are well documented, but, as with Knowledge Gap 2, a full understanding of why TP levels are so low is elusive. Work by two members of the task group (MDR and RPB) indicates that the decline in TP cannot be explained entirely by a decline in TP loading (see Monitoring Gap 3 above). Their work does not predict the observed steep decline in TP from 1998 to 2011 (Appendix A, Fig. A1), which suggests that within-lake TP cycling, perhaps influenced by sequestration of TP by dreissenids, is playing a critically important role in offshore TP dynamics. The role of dreissenids on P recycling should be investigated, including their impact on: (1) soluble and particulate C, N, and P excretion; (2) retention of such nutrients in body tissues and shells; and (3) impacts of burial of C, N, and P in sediments (e.g., Bootsma et al. 2015; Rowe et al. 2017; Vanderploeg et al. 2017).

RECOMMENDATIONS

We provide three recommendations for the LMC as it seeks to accommodate its management objectives to the reality of the poorly understood impacts of changes in lower trophic levels on prey-fish biomass.

1) Implement a coordinated and standardized nearshore monitoring program to complement ongoing efforts by federal agencies in the offshore. Although offshore monitoring is not as well coordinated as it could be given that the EPA, the USGS, and NOAA sample multiple trophic levels in different locations, the LMC, nevertheless, is accustomed to annual reporting on offshore surveys by these agencies and has a sense of how offshore monitoring affects decision making. The nearshore, however, is much more dynamic and supports spawning and nursery habitats for valuable fish, such as Alewife, Yellow Perch, Rainbow Smelt, Lake Whitefish, and Cisco (*C. artedi*). Presently, a handful of state and federal agencies and universities sample trophic levels and fish in different regions of the nearshore. As a starting point, organize a workshop where agencies and universities that are currently monitoring nearshore lower trophic levels (NOAA, INHS, UW-Milwaukee, Central Michigan University, Little Traverse Bay Band of Odawa Indians) meet and establish an agreed-upon standardized protocol. This protocol should then be shared with other state agencies and universities that sample to better answer if the large-scale lower trophic-level changes that have been documented in the offshore are prominent in the nearshore. Much can be gained, too, from examining interagency lower trophic-level monitoring in Lakes Erie and Ontario.

2) Funding agencies are encouraged to use our prioritized list of monitoring and knowledge gaps in their decision-making processes. Filling these gaps would facilitate development of more-realistic scenario-based models that could be used by managers to inform their stakeholders. For example, there are several different scenario-based models either completed (Kao et al. 2017) or in development (H. Zhang, University of Michigan; ESR). For example, Kao et al. (2017) explored different scenarios of TP loading, dreissenid filtration, and fish stocking and concluded that native lake trout and rainbow trout are better suited to the current Lake Michigan ecosystem than Chinook Salmon.

3) Continue to improve dialogue between those with expertise in lower trophic levels and those in fisheries. Specific opportunities include inviting scientists from the EPA or NOAA to report regularly on lower trophic levels at the annual meetings of the lake committees and continuing coordination between those involved in the Lake Michigan Lakewide Management Plan and the technical committee of the LMC.

ACKNOWLEDGEMENTS

REFERENCES

Adrian, R., O'Reilly, C.M., Zagarese, H., Baines, S.B., Hessen, D.O., Keller, W., Livingstone, D.M., Sommaruga, R., Straile, D., Van Donk, E., Weyhenmeyer, G.A., and Winder, M. 2009. Lakes as sentinels of climate change. Limnol. Oceanogr. **54**(6): 2283-2297.

Auer, N.A. [ED.]. 1982. Identification of larval fishes of the Great lakes basin with emphasis on the Lake Michigan drainage [online]. Available from http://www.glfc.org/pubs/SpecialPubs/Sp82_3.zip [accessed 16 May 2018].

Auer, M.T., Tomlinson, L.M., Higgins, S.N., Malkin, S.Y., Howell, E.T., and Bootsma, H.A. 2010. Great Lakes *Cladophora* in the 21st century: same algae—different ecosystem. J. Great Lakes Res. **35**: 248-255.

Barbiero, R.P., Balcer, M., Rockwell, D.C., and Tuchman, M.L. 2009. Recent shifts in the crustacean zooplankton community of Lake Huron. Can. J. Fish. Aquat. Sci. **66**(5): 816-828.

Berkeley, S.A., Chapman, C., and Sogard, S.M. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecology **85**(5): 1258-1264.

Bootsma, H.A., Rowe, M.D., Brooks, C.N., and Vanderploeg, H.A. 2015. Commentary: the need for model development related to *Cladophora* and nutrient management in Lake Michigan. J. Great Lakes Res. **41**: 7-15.

Bourdeau, P.E., Pangle, K.L., and Peacor, S.D. 2015. Factors affecting the vertical distribution of the zooplankton assemblage in Lake Michigan: the role of the invasive predator *Bythotrephes longimanus*. J. Great Lakes Res. **41**: 115-124.

Brooks, C., Grimm, A., Shuchman, R., Sayers, M., and Jessee, N. 2015. A satellite-based multi-temporal assessment of the extent of nuisance *Cladophora* and related submerged aquatic vegetation for the Laurentian Great Lakes. Remote Sens. Environ. **157**: 58-71.

Bunnell, D.B., David, S.R., and Madenjian, C.P. 2009. Decline in bloater fecundity in Southern Lake Michigan after decline of *Diporeia*. J. Great Lakes Res. **35**(1): 45-49.

Bunnell, D.B., Barbiero, R.P., Ludsin, S.A., Madenjian, C.P., Warren, G.J., Dolan, D.M., Brenden, T.O., Briland, R., Gorman, O.T., He, J.X., Johengen, T.H., Lantry, B.F., Lesht, B.M., Nalepa, T.F., Riley, S.C., Riseng, C.M., Treska, T.J., Tsehaye, I., Walsh, M.G., Warner, D.M., and Weidel, B.C. 2014. Changing ecosystem dynamics in the Laurentian Great Lakes: bottom-up and top-down regulation. Bioscience **64**(1): 26-39.

Bunnell, D.B., Davis, B.M., Chriscinske, M.A., Keeler, K.M., and Mychek-Londer, J.G. 2015. Diet shifts by planktivorous and benthivorous fishes in northern Lake Michigan in response to ecosystem changes. J. Great Lakes Res. **41**: 161-171.

Bunnell, D.B., Hook, T.O., Troy, C.D., Liu, W.T., Madenjian, C.P., and Adams, J.V. 2017. Testing for synchrony in recruitment among four Lake Michigan fish species. Can. J. Fish. Aquat. Sci. **74**(3): 306-315.

Carpenter, S.R., Kitchell, J.F., and Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. BioScience **35**: 634-639.

Carrick, H.J., and Lowe, R.L. 1988. Response of Lake Michigan benthic algae to *in situ* enrichment with Si, N, and P. Can. J. Fish. Aquat. Sci. **45**: 271-279.

Carrick, H.J., and Lowe, R.L. 2007. Are benthic algae in Lake Michigan limited by silica? J. Phycol. **43**: 228-234.

Carrick, H.J., Barbiero, R., and Tuchman, M.L. 2001. Variation in Lake Michigan plankton: temporal, spatial, and historical trends. J. Great Lakes Res. **27**: 467-485.

Carrick, H.J., Butts, E., Daniels, D., Fehringer, M., Frazier, C., Fahnenstiel, G.L., Pothoven, S., and Vanderploeg, H.A. 2015. Variation in the abundance of pico, nano, and microplankton in Lake Michigan: Historic and basin-wide comparisons. J. Great Lakes Res. **41**: 66-74.

Chapra, S.C., and Dolan, D.M. 2012. Great Lakes total phosphorus revisited: 2. Mass balance modeling. J. Great Lakes Res. **38**(4): 741-754.

Clark, R.D., Jr., Bence, J.R., Claramunt, R.M., Johnson, J.E., Gonder, D., Legler, N.D., Robillard, S.R., and Dickinson, B.D. 2016. A spatially explicit assessment of changes in Chinook Salmon fisheries in Lakes Michigan and Huron from 1986 to 2011. North Amer. J. Fish. Manage. **36**: 1068-1083.

Cushing, D.H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv. Mar. Biol. **26**: 249-293.

Dettmers, J.D., Janssen, J., Pientka, B., Fulford, R.S., and Jude, D.J. 2005. Evidence across multiple scales for offshore transport of yellow perch (*Perca flavescens*) larvae in Lake Michigan. Can. J. Fish. Aquat. Sci. **62**(12): 2683-2693.

Dolan, D.M., and Chapra, S.C. 2012. Great Lakes total phosphorus revisited: 1. Loading analysis and update (1994-2008). J. Great Lakes Res. **38**(4): 730-740.

Downing, J.A., and Plante, C. 1993. Production of fish populations in lakes. Can. J. Fish. Aquat. Sci. **50**: 110-120.

Edsall, T.A., and Charlton, M.N. 1997. Nearshore waters of the Great Lakes. Background paper for the 1996 State of the Lakes Ecosystem Conference [online]. Available from https://archive.epa.gov/solec/web/pdf/nearshore_waters_of_the_great_lakes.pdf [accessed 14 May 2018].

Eshenroder, R.L., and Lantry, B. 2012. Recent changes in successional state of the deep-water fish communities of Lakes Michigan, Huron, and Ontario and management implications. *In* Great Lakes fisheries policy and management: a binational perspective, 2nd edition. *Edited by* W.W. Taylor, A.J. Lynch, and N.J. Leonard. Mich. State Univ. Press, East Lansing, MI. pp. 137-165.

Eshenroder, R.L., Holey, M.E., Gorenflo, T.K., and Clark, Jr., R.D. 1995. Fish-community objectives for Lake Michigan [online]. Available from http://www.glfc.org/pubs/SpecialPubs/Sp95_3.pdf [accessed 14 May 2018].

Evans, M.A., Fahnenstiel, G., and Scavia, D. 2011. Incidental oligotrophication of North American Great Lakes. Environ. Sci. Technol. **45**(8): 3297-3303.

Fahnenstiel, G., Nalepa, T, Pothoven, S., Carrick, H., and Scavia, D. 2010a. Lake Michigan's lower food web: long-term observations and *Dreissena* impact. J. Great Lake Res. **36**: 1-4.

Fahnenstiel, G., Pothoven, S., Vanderploeg, H., Klarer, D., Nalepa, T., and Scavia, D. 2010b. Recent changes in primary production and phytoplankton in the offshore region of southeastern Lake Michigan. J. Great Lake Res. **36**: 20-29.

Fahnenstiel, G., Sayers, M.J., Shuchman, R.A., Yousef, F., and Pothoven, S.A. 2016. Lake-wide phytoplankton production and abundance in the upper Great Lakes. J. Great Lakes Res. **42**(3): 619-629.

Farmer, T.M., Marschall, E.A., Dabrowski, K., and Ludsin, S.A. 2015. Short winters threaten temperate fish populations [online]. Available from https://www.nature.com/articles/ncomms8724 [accessed 14 May 2018].

Feiner, Z.S., Coulter, D.P., Guffey, S.C., and Hook, T.O. 2016. Does overwinter temperature affect maternal body composition and egg traits in yellow perch *Perca flavescens*? J. Fish Biol. **88**(4): 1524-1543.

Fenchel, T. 1988. Marine plankton food chains. Ann. Rev. Ecol. Systemat. **19:** 19-38.

Hessen, D.O., Faafeng, B.A., and Andersen, T. 1995. Replacement of herbivore zooplankton species along gradients of ecosystem productivity and fish predation pressure. Can. J. Fish. Aquat. Sci. **52**(4): 733-742.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe. Rapports et Procès-verbaux des Réunions, Conseil Permanent International pour l'Exploration de la Mer. **20**: 1-228.

Hondorp, D.W., Pothoven, S.A., and Brandt, S.B. 2005. Influence of *Diporeia* density on diet composition, relative abundance, and energy density of planktivorous fishes in southeast Lake Michigan. Trans. Am. Fish. Soc. **134**(3): 588-601.

Hook, T.O., Rutherford, E.S., Mason, D.M., and Carter, G.S. 2007. Hatch dates, growth, survival, and overwinter mortality of age-0 alewives in Lake Michigan: implications for habitat-specific recruitment success. Trans. Am. Fish. Soc. **136**(5): 1298-1312.

Kao, Y.C., Rogers, M.W., and Bunnell, D.B. 2017. Evaluating stocking efficacy in an ecosystem undergoing oligotrophication [online]. Available from https://doi.org/10.1007/s10021-017-0173-5 [accessed 14 May 2018].

Keeler, K.M., Bunnell, D.B., Diana, J.S., Adams, J.V., Mychek-Londer, J.G., Warner, D.M., Yule, D.L., and Vinson, M.R. 2015. Evaluating the importance of abiotic and biotic drivers on *Bythotrephes* biomass in Lakes Superior and Michigan. J. Great Lakes Res. **41**: 150-160.

Kingston, J.C., Lowe, R.L., Stoermer, E.F., and Ladewski, T.B. 1983. Spatial and temporal distribution of benthic diatoms in northern Lake Michigan. Ecology **64**: 1566-1580.

Kjesbu, O.S., Klungsoyr, J., Kryvi, H., Witthames, P.R., and Walker, M.G. 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. Can. J. Fish. Aquat. Sci. **48**(12): 2333-2343.

LeBlanc, J.S., Taylor, W.D., and Johannsson, O.E. 1997. The feeding ecology of the cyclopoid copepod *Diacyclops thomasi* in Lake Ontario. J. Great Lakes Res. **23**(3): 369-381.

Lester, N.P., Dextrase, A.J., Kushneriuk, R.S., Rawson, M.R., and Ryan, P.A. 2004. Light and temperature: key factors affecting walleye abundance and production. Trans. Am. Fish. Soc. **133**(3): 588-605.

Madenjian, C.P., Holuszko, J.D., and Desorcie, T.J. 2003. Growth and condition of alewives in Lake Michigan, 1984-2001. Trans. Am. Fish. Soc. **132**(6): 1104-1116.

Madenjian, C.P., Pothoven, S.A., Dettmers, J.M., and Holuszko, J.D. 2006. Changes in seasonal energy dynamics of alewife (*Alosa pseudoharengus*) in Lake Michigan after invasion of dreissenid mussels. Can. J. Fish. Aquat. Sci. **63**(4): 891-902.

Madenjian, C.P., Bunnell, D.B., Warner, D.M., Pothoven, S.A., Fahnenstiel, G.L., Nalepa, T.F., Vanderploeg, H.A., Tsehaye, I., Claramunt, R.M., and Clark, R.D. 2015. Changes in the Lake Michigan food web following dreissenid mussel invasions: a synthesis. J. Great Lakes Res. **41**: 217-231.

Mangel, M., and Stamps, J. 2001. Trade-offs between growth and mortality and the maintenance of individual variation in growth. Evol. Ecol. Res. **3**: 583-593.

Miller, T.J., Crowder, L.B., Rice, J.A., and Marschall, E.A. 1988. Larval size and recruitment mechanisms in fishes—toward a conceptual framework. Can. J. Fish. Aquat. Sci. **45**(9): 1657-1670.

Muir, A.M., Arts, M.T., Koops, M.A., Johnson, T.B., Krueger, C.C., and Sutton, T.M. 2014. Reproductive life-history strategies in lake whitefish (*Coregonus clupeaformis*) from the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. **71**(8): 1256-1269.

Nalepa T.F, Fanslow, D.L, and Lang, G.A. 2009. Transformation of the offshore benthic community in Lake Michigan: a recent shift from the native amphipod *Diporeia* spp. to the invasive mussel *Dreissena bugensis*. Freshwat. Biol. **54**: 466-479.

Pangle, K.L., Peacor, S.D., and Johannsson, O.E. 2007. Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. Ecology **88**(2): 402-412.

Pilcher, D.J., McKinley, G.A., Kralj, J., Bootsma, H.A., and Reavie, E.D. 2017. Modeled sensitivity of Lake Michigan productivity and zooplankton to changing nutrient concentrations and quagga mussels. J. Geophys. Res. Biogeosci. **122**(8): 2017-2032.

Pothoven, S.A., and Fahnenstiel, G.L. 2013. Recent change in summer chlorophyll *a* dynamics of southeastern Lake Michigan. J. Great Lakes Res. **39**(2): 287-294.

Pothoven, S.A., and Fahnenstiel, G.L. 2015. Spatial and temporal trends in zooplankton assemblages along a nearshore to offshore transect in southeastern Lake Michigan from 2007 to 2012. J. Great Lakes Res. **41**: 95-103.

Pothoven, S.A., and Madenjian, C.P. 2008. Changes in consumption by alewives and lake whitefish after dreissenid mussel invasions in Lakes Michigan and Huron. N. Am. J. Fish. Manage. **28**(1): 308-320.

Pothoven, S.A., and Vanderploeg, H.A. 2017. Changes in *Mysis diluviana* abundance and life history patterns following a shift toward oligotrophy in Lake Michigan. Fund. Applied Limnol. **190**(3): 199-212.

Pothoven, S.A., Nalepa, T.F., Schneeberger, P.J., and Brandt, S.B. 2001. Changes in diet and body condition of lake whitefish in southern Lake Michigan associated with changes in benthos. N. Am. J. Fish. Manage. **21**(4): 876-883.

Pothoven, S.A., Vanderploeg, H.A., Cavaletto, J.F., Krueger, D.M., Mason, D.M., and Brandt, S.B. 2007. Alewife planktivory controls the abundance of two invasive predatory cladocerans in Lake Michigan. Freshwat. Biol. **52**(3): 561-573.

Pothoven, S.A., Fahnenstiel, G.L., and Vanderploeg, H.A. 2010. Temporal changes in *Mysis relicta* abundance, production, and life-history characteristics in southeastern Lake Michigan. J. Great Lakes Res. **36**: 60-64.

Pothoven, S.A., Hondorp, D.W., and Nalepa, T.F. 2011. Declines in deepwater sculpin *Myoxocephalus thompsonii* energy density associated with the disappearance of *Diporeia* spp. in Lakes Huron and Michigan. Ecol. Freshwat. Fish **20**(1): 14-22.

Pothoven, S.A., Bunnell, D.B., Madenjian, C.P., Gorman, O.T., and Roseman, E.F. 2012. Energy density of bloaters in the upper Great Lakes. Trans. Am. Fish. Soc. **141**(3): 772-780.

Pothoven, S.A., Fahnenstiel, G.L., Vanderploeg, H.A., and Nalepa, T.F. 2016. Changes in water quality variables at a mid-depth site after proliferation of dreissenid mussels in southeastern Lake Michigan. Fundam. Appl. Limnol. **188**(3): 233-244.

Ptáčníková, R. Vanderploeg, H.A., and Cavaletto, J.F. 2015. Big versus small: does *Bythotrephes longimanus* predation regulate spatial distribution of another invasive predatory cladoceran, *Cercopagis pengoi*? J. Great Lakes Res. **41**(Suppl. 3): 143-149.

Rice, J.A., Crowder, L.B., and Holey, M.E. 1987. Exploration of mechanisms regulating larval survival in Lake Michigan bloater—a recruitment analysis based on characteristics of individual larvae. Trans. Am. Fish. Soc. **116**(5): 703-718.

Robillard, S.R., Breidert, B., Eggold, B.T., Gorenflo, T.K., and Wesley, J. 2012. Conclusions. *In* The state of Lake Michigan in 2011. *Edited by* D.B. Bunnell [online]. Available from http://www.glfc.org/pubs/SpecialPubs/Sp12_1.pdf [accessed 14 May 2018].

Rowe, M.D., Anderson, E.J., Wang, J., and Vanderploeg, H.A. 2015. Modeling the effect of invasive quagga mussels on the spring phytoplankton bloom in Lake Michigan. J. Great Lakes Res. **41**: 49-65.

Rowe, M.D., Anderson, E.J., Vanderploeg, H.A., Pothoven, S.A., Elgin, A.K., Wang, J., and Yousef, F. 2017. Influence of invasive quagga mussels, phosphorus loads, and climate on spatial and temporal patterns of productivity in Lake Michigan: a biophysical modeling study [online]. Available from https://www.glerl.noaa.gov/pubs/fulltext/2017/20170018.pdf [accessed 14 May 2018].

Ryder, R.A. 1977. Effects of ambient light variations on behavior of yearling, subadult, and adult walleyes (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. **34**: 1481-1491.

Tsehaye, I., Jones, M.L., Bence, J.R., Brenden, T.O., Madenjian, C.P., and Warner, D.M. 2014. A multispecies statistical age-structured model to assess predator-prey balance: application to an intensively managed Lake Michigan pelagic fish community. Can. J. Fish. Aquat. Sci. **71**(4): 627-644.

Turschak, B.A., Bunnell, D., Czesny, S., Hook, T.O., Janssen, J., Warner, D., and Bootsma, H.A. 2014. Nearshore energy subsidies support Lake Michigan fishes and invertebrates following major changes in food web structure. Ecology **95**(5): 1243-1252.

USGS (U.S. Geological Survey). 2017. Compiled reports to the Great Lakes Fishery Commission of the annual bottom trawl and acoustics surveys for 2016 [online]. Available from http://www.glfc.org/pubs/lake_committees/common_docs/Compiled%20Reports%20from%20USGS%202017.pdf [accessed 16 May 2018].

Vanderploeg, H.A., and Scavia, D. 1979. Calculation and use of selectivity coefficients of feeding: zooplankton grazing. Ecol. Model. **7**: 135-149.

Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., Mills, E.L., Holeck, K.T., Liebig, J.R., Grigorovich, I.A., and Ojaveer, H. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. **59**: 1209-1228.

Vanderploeg, H.A., Liebig, J.R., Nalepa, T.F., Fahnenstiel, G.L., and Pothoven, S.A. 2010. *Dreissena* and the disappearance of the spring phytoplankton bloom in Lake Michigan. J. Great Lakes Res. **36**: 50-59.

Vanderploeg, H.A., Pothoven, S.A., Fahnenstiel, G.L., Cavaletto, J.F., Liebig, J.R., Stow, C.A., Nalepa, T.F., Madenjian, C.P., and Bunnell, D.B. 2012. Seasonal zooplankton dynamics in Lake Michigan: disentangling impacts of resource limitation, ecosystem engineering, and predation during a critical ecosystem transition. J. Great Lakes Res. **38**(2): 336-352.

Vanderploeg, H.A., Pothoven, S.A., Krueger, D., Mason, D.M., Liebig, J.R., Cavaletto, J.F., Ruberg, S.A., Lang, G.A., and Ptáčníková, R. 2015. Spatial and predatory interactions of visually preying nonindigenous zooplankton and fish in Lake Michigan during midsummer. J. Great Lakes Res. **41**: 125-142.

Vanderploeg, H.A., Sarnelle, O., Liebig, J.R., Morehead, N.R., Robinson, S.D., Johengen, T.H., and Horst, G.P. 2017. Seston quality drives feeding, stoichiometry and excretion of zebra mussels. Freshw. Biol. **62:** 664-680.

Wang, H.Y., Einhouse, D.W., Fielder, D.G., Rudstam, L.G., Vandergoot, C.S., VanDeValk, A.J., Zorn, T.G., and Hook, T.O. 2012. Maternal and stock effects on egg-size variation among walleye *Sander vitreus* stocks from the Great Lakes region. J. Great Lakes Res. **38**(3): 477-489.

Warner, D.M., and Lesht, B.M. 2015. Relative importance of phosphorus, invasive mussels and climate for patterns in chlorophyll *a* and primary production in Lakes Michigan and Huron. Freshwat. Biol. **60**(5): 1029-1043.

Weber, M.J., Ruebush, B.C., Creque, S.M., Redman, R.A., Czesny, S.J., Wahl, D.H., and Dettmers, J.M. 2015. Early life history of alewife *Alosa pseudoharengus* in southwestern Lake Michigan. J. Great Lakes Res. **41**(2): 436-447.

Wells, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnol. Oceanogr. **15**(4): 556-565.

Withers, J.L., Sesterhenn, T.M., Foley, C.J., Troy, C.D., and Hook, T.O. 2015. Diets and growth potential of early stage larval yellow perch and alewife in a nearshore region of southeastern Lake Michigan. J. Great Lakes Res. **41**: 197-209.

Yurista, P.M., Kelly, J.R., Miller, S.E., and Van Alstine, J.D. 2012. Water quality and plankton in the United States nearshore waters of Lake Huron. Environ. Manage. **50**(4): 664-678.

APPENDICES

Appendix A: Supplementary Figures and Tables

Fig. A1. Time series of total phosphorus (TP) inputs (open circles, left axis) and predicted offshore TP concentrations (RPB, unpublished data; black triangles, right axis) in Lake Michigan.
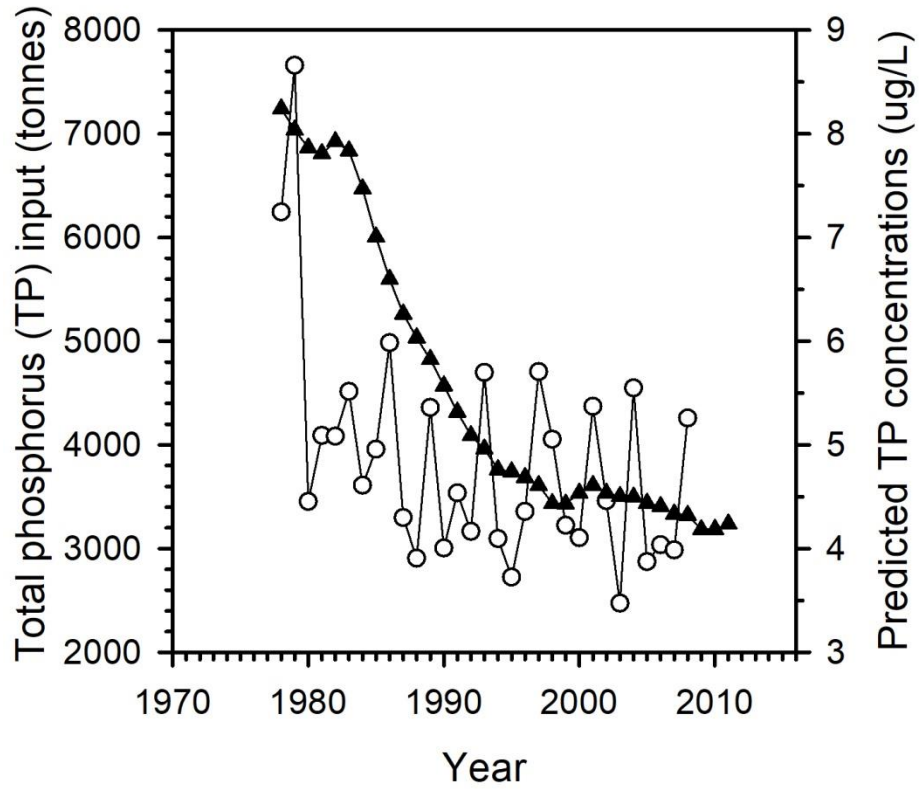
Fig. A2. Time series of microzooplankton (rotifers and copepod nauplii) in the southwestern nearshore waters of Lake Michigan (SMT, SC, unpublished data).
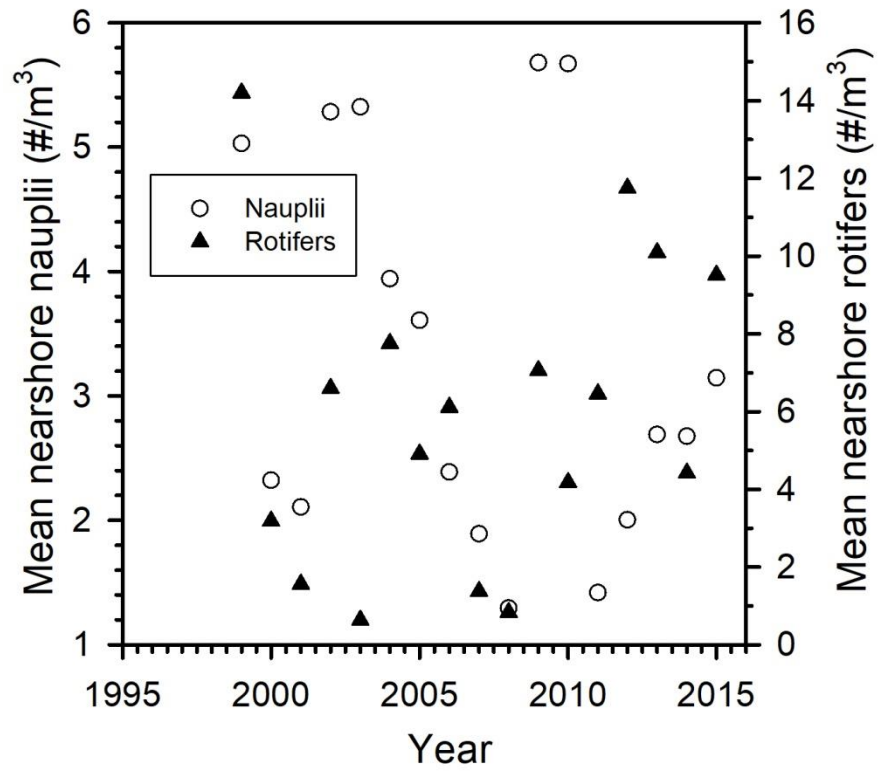
Fig. A3. Time series of community composition of benthic invertebrate samples in nearshore waters on soft (panel a) and hard (panel b) substrate in Lake Michigan (SMT, SC, unpublished data).
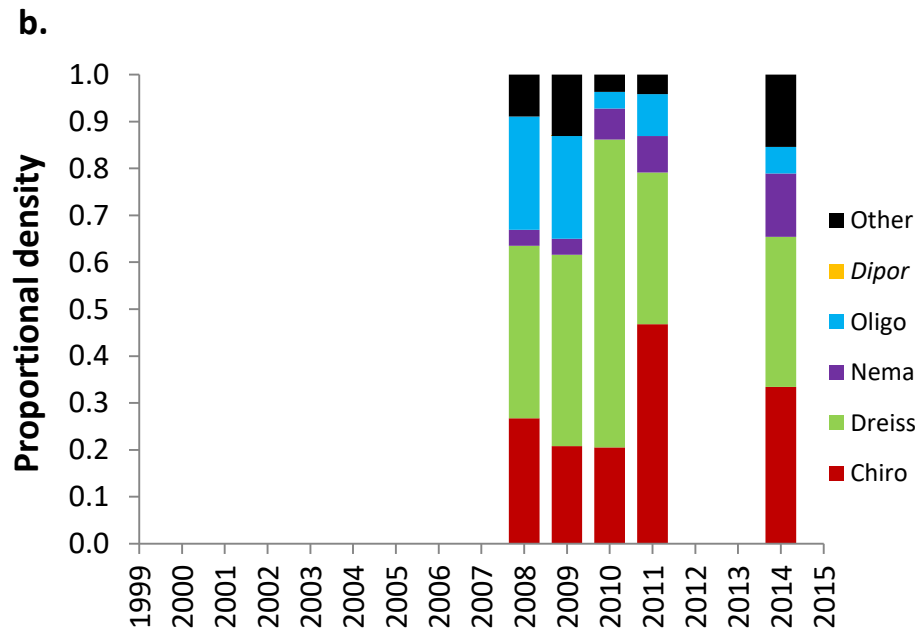
a.

b.
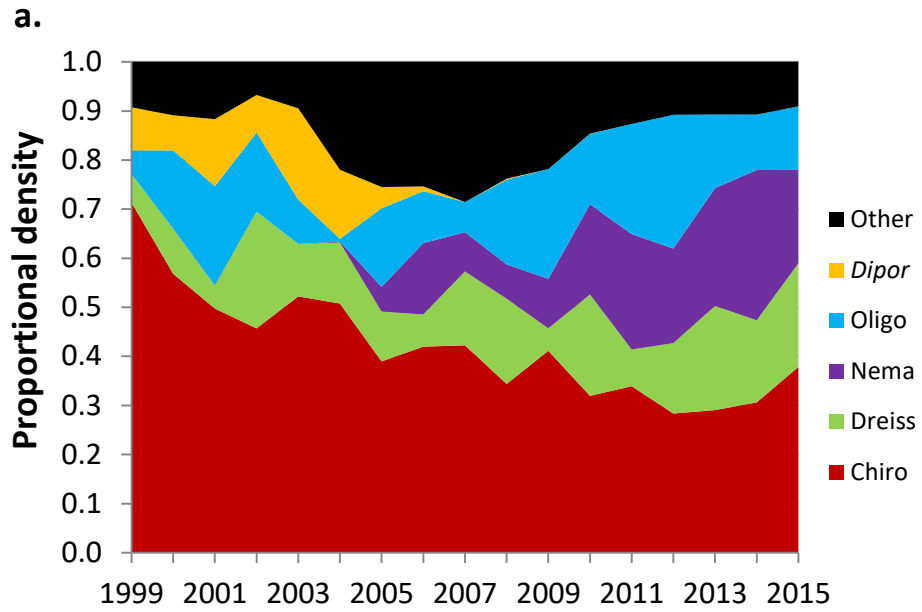
Fig. A4. Map of sampling locations routinely monitored in Lake Michigan. Most of the nearshore monitoring data included in this paper derive from the Illinois Natural History Survey (IL NHS) and NOAA. Most of the offshore monitoring data are from NOAA, the USEPA GLNPO, and the USGS. Note that the USEPA National Coastal Condition Assessment (NCCA) sites are only sampled every five years, and data from 2010 have not been incorporated into this report. The Great Lakes Ecological Indicators (GLEI) sampling locations are a completed study funded by the USEPA to assess the ecological condition of the US coastal region.
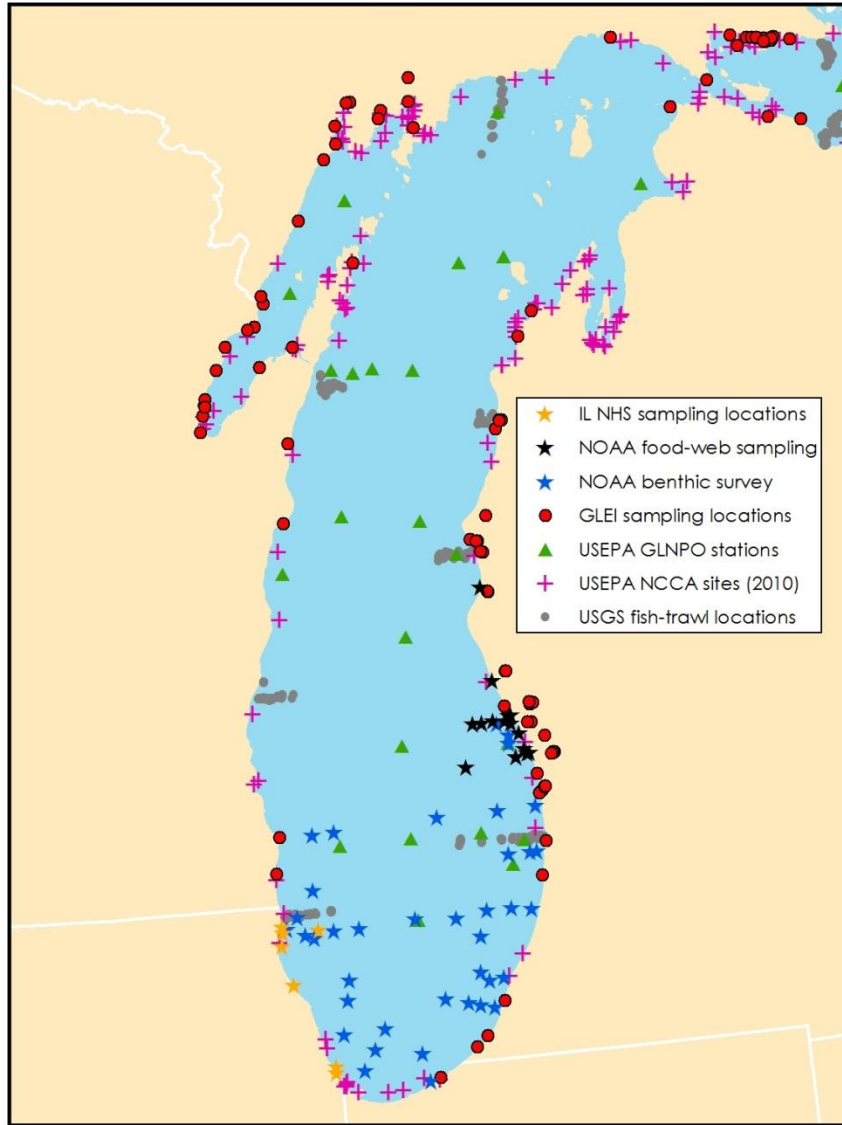
-Great Lakes Aquatic Habitat Framework (see http://glahf.org/).

Table A1. Summary of indicators that could be developed to help managers detect imminent changes in lower trophic levels with consequences for sustaining the biomass and production of key prey fish. Possible indicators were generated from discussions during a two-day workshop of the Lower Trophic Level Task Group in the summer of 2016 and were then edited and supplemented through conference calls and emails in February 2017. The indicators were ranked from strongest to weakest by 16 members of the task group with the lowest average score indicative of the strongest indicator. The top four indicators are bolded and are briefly described in this report.

Average Ranking	Indicator
5.7	**Condition of adult Alewife**
5.7	**Satellite-derived chlorophyll *a* estimates**
6.2	**Density of *Mysis diluviana***
6.3	**Spring TP**
7.0	Spring in situ chlorophyll *a*
7.3	Benthic invertebrate (dreissenids, *Diporeia* spp.) densities
7.4	Ratio of total invertebrate:prey-fish biomass
7.6	Species composition of the zooplankton community
8.1	Mean spring/summer water temperature
8.9	Spring and summer Secchi-disk depth
9.8	Proportion of sampled sites that yield key prey-fish species
9.9	Ratio pelagic:benthic invertebrate biomass
10.3	Mean spring/summer water-temperature warming rates
11.3	Biomass size spectrum
12.0	Patchiness of prey-fish biomass (signal:noise ratio)
12.5	Ratio of diatoms:non-diatoms

Table A2. Summary of monitoring gaps associated with an understanding of how changes in lower trophic levels influence prey-fish biomass and production. Possible monitoring gaps were generated from discussion during a two-day workshop of the task group in the summer of 2016 and were then edited and supplemented through conference calls and emails in February 2017. The indicators were ranked from most important to least important by 16 members of the task group with the lowest average score indicative of the most important. The top four monitoring gaps are bolded and are briefly described in this report.

Average Ranking	Monitoring Gap
3.4	**Coordinated nearshore sampling of lower trophic levels (including larval fish)**
5.0	**Direct measurement of primary production**
5.1	**Phosphorus loading by tributary**
5.2	**Simultaneous sampling of physical environment, lower trophic levels, and fish**
5.7	Annual lakewide dreissenid estimate
5.9	Benthic invertebrate sampling on hard substrates
6.3	Use of gliders, autonomous underwater vehicles, and remote sensing to improve spatiotemporal coverage of lower trophic-level monitoring
6.8	*Cladophora* spp. biomass and distribution
7.4	Abundance of dreissenid veligers over time
7.5	Production estimates for individual zooplankton species (e.g., *Daphnia galeata mendotae*)
7.7	Nanoplankton and picoplankton monitoring

Table A3. Summary of knowledge gaps that limit our understanding of how changes in lower trophic levels influence prey-fish biomass and production. Possible knowledge gaps were generated from discussion during a two-day workshop of the task group in the summer of 2016 and were edited and supplemented through conference calls and emails in February 2017. The indicators were ranked from most important to least important by 16 members of the task group with the lowest average score indicative of the most important. The top four knowledge gaps are bolded and are briefly described in this report.

Average Ranking	Knowledge Gap
2.4	**What lower trophic-level changes bottleneck recruitment of age-0 fish to age 1+?**
3.8	**What is the relative importance of reduced nutrients and quagga mussel filtration and their potential interaction in driving declining pelagic primary production?**
4.1	**Have changes in the zooplankton community affected prey-fish biomass to the extent that fishery managers should reconsider their objectives?**
4.1	**What are the key drivers of phosphorus recycling?**
4.9	Does increasing benthic production compensate for decreasing pelagic production?
4.9	Where do dreissenid veligers and other microzooplankton fit in the food web?
5.4	What is Lake Michigan's carrying capacity for quagga mussels? Do profundal forms of quagga mussel reproduce offshore? What limits quagga mussel recruitment to the settled stage?
6.5	Where do benthic macroalgae (e.g., *Cladophora* spp.) decompose? What proportion is transported offshore knowing some proportion ends up on beaches?

Appendix B. How Dreissenids Can Disrupt the Food Web of Lake Michigan

The introduction of *Dreissena polymorpha* and *D. bugensis* (hereafter, dreissenids) appears to have disrupted the fabric of the entire pelagic food web so that this phenomenon may represent one of the single, largest perturbations ever observed to Lake Michigan. The large impact occurred because dreissenids have high clearance rates over a broad range of particles (~1-200 μm) that encompass many elements of the entire plankton assemblage (Fig. 1, main text). Dreissenid feeding is unique because no native invertebrate in Lake Michigan is able to consume plankton from all size categories (pico, nano, and microplankton; Fig. 1), and, furthermore, grazing likely has led to complex changes at higher trophic levels (zooplankton and fish; Fig. 1, main text).

First, dreissenids are capable of removing plankton in such large quantities (Denef et al. 2017) that their introduction can account for the decline observed from 1987 to 2013 for three size-classes of the Lake Michigan food web (Carrick et al. 2015). Specifically, mussel filter-feeding appears to have diminished larger microplankton, including ciliated protists (Fig. 1, main text, left side) and diatoms (Fig. 1, main text, right side). Plankton in the nanoplankton- and picoplankton-size categories have also been depleted, although not as dramatically as seen in the microplankton. These differential changes among plankton size groups probably occurred because pico- and nanoplankton grow fast enough to counterbalance the effects of mussel grazing (see Carrick et al. 2015).

Second, the interactions between dreissenids and specific components of the food web have had important implications that are not straightforward particularly for the larger organisms that make up the diet of key prey fish, such as Alewife. For example, there is considerable evidence that dreissenids may be outcompeting mesozooplankton (e.g., *Daphnia galeata mendotae*, diaptomids, *Diacyclops thomasi*) for food because they can prey on the entire size spectrum of available plankton prey (Jørgensen et al. 1984; Lavrentyev et al. 2014; Tang et al. 2014) unlike their mesozooplankton counterparts that each feed very narrowly on specific plankters (Vanderploeg 1994; see Table B1). This constraint, in turn, has negative consequences for organisms that eat mesozooplankton, such as larger predaceous macrozooplankton (i.e., *Bythotrephes longimanus*) and planktivorous fish (i.e., Alewife). In fact, trophic position and size may not be well correlated (Table B1); therefore care must be exercised in using size as a proxy for trophic position.

Lastly, the fact that mussels now occupy a niche that overlaps both seasonally and spatially with native mesozooplankton species has created strong ecological bottlenecks between the two groups. During the isothermal seasons (fall and spring), dreissenids have access to much of the water column due to vertical mixing (Vanderploeg et al. 2010; Rowe et al. 2015); therefore, dreissenids could reduce resources available to mesozooplankton, which are found throughout the water column. During summer, dreissenid filtering will affect the deep-chlorophyll layer, now partially descended to the upper hypolimnion. Such filtering has potential impacts during the day on hypolimnetic mesozooplankton, such as diaptomids and *D. galeata mendotae*, the latter of which shows very-strong diel-vertical migration. During early stratification, when zooplankton is concentrated in the epilimnion, phytoplankton populations in the same layer possibly will not have recovered from dreissenid filtering. Thus, the perturbation from the introduction of dreissenids will likely have varying consequences on specific components of the mesozooplankton, which in turn affects the feeding success of different life stages of planktivorous fish (see Vanderploeg et al. 2012).

Table B1. Equivalent spherical-diameter (ESD) ranges and feeding modes compared to trophic position above primary producers (estimated from stable isotopes) (Driscoll et al. 2015; Turschak and Bootsma 2015) relative to *Daphnia galeata mendotae*, the primary daphnid herbivore in Lake Michigan. The size ranges are those best used for separating taxa with an optical plankton counter (Liebig and Vanderploeg 2008; HAV, unpublished data).

ESD (mm)	Taxon	Feeding Mode/Preferred Prey	Trophic Position
0.25-0.50	Nauplii, copepodites, and small adult copepods[13]	Omnivores and carnivores	2°
0.50-0.75	Small *D. galeata mendotae* instars	Filter feeder	1°
	Large diaptomids (adults)	Omnivores	2°
0.75-1.50	Large *D. galeata mendotae* instars	Filter feeder	1°
	Limnocalanus macrurus adults	Predator of copepods	3°
1.50-3.00	*Bythotrephes longimanus*	Predator with preference for cladocerans	2°

[13]*Diacyclops thomasi* and *Leptodiaptomus minutus.*

References

Carrick, H.J., Butts, E., Daniels, D., Fehringer, M., Frazier, C., Fahnenstiel, G.L., Pothoven, S. and Vanderploeg, H.A. 2015. Variation in the abundance of pico, nano, and microplankton in Lake Michigan: historic and basin-wide comparisons. J. Great Lakes Res. **41**: 66-74.

Denef, V.J., Carrick, H.J., Cavaletto, J., Chiang, E., Johengen, J.H., and Vanderploeg, H.A. 2017. Lake bacterial assemblage composition is sensitive to biological disturbance caused by and invasive filter feeder [online]. Available from http://msphere.asm.org/content/2/3/e00189-17 [accessed 14 May 2018].

Driscoll, Z.G., Bootsma, H.A., and Christiansen, E. 2015. Zooplankton trophic structure in Lake Michigan as revealed by stable carbon and nitrogen isotopes. J. Great Lakes Res. **41:** 104-114.

Jørgensen, C.B., Kiørboe, T., Møhlenberg, F., and Riisgärd, H.U. 1984. Ciliary and mucus-net filter feeding, with special reference to fluid mechanical characteristics. Mar. Ecol. Prog. Ser. **15**: 283-292.

Lavrentyev, P.J., Vanderploeg, H.A., Franze, G., Chacin, D.H., Liebig, J.R., and Johengen, T.H. 2014. Microzooplankton distribution, dynamics, and trophic interactions relative to phytoplankton and quagga mussels in Saginaw Bay, Lake Huron. J. Great Lakes Res. **40**: 95-105.

Liebig, J.R., and Vanderploeg, H.A. 2008. Selecting optical plankton counter size bins to optimize zooplankton information in Great Lakes studies [online]. Available from https://www.glerl.noaa.gov/pubs/tech_reports/glerl-143/tm-143.pdf [accessed 14 May 2018].

Rowe, M.D., Anderson, E.J., Wang, J., and Vanderploeg, H.A. 2015. Modeling the effect of invasive quagga mussels on the spring phytoplankton bloom in Lake Michigan. J. Great Lakes Res. **41**: 49-65.

Tang H., Vanderploeg, H.A., Johengen, T.H., and Liebig, J.R. 2014. Quagga mussel (*Dreissena rostriformis bugensis*) selective feeding of phytoplankton in Saginaw Bay. J. Great Lakes Res. **40**: 83-94.

Turschak B.A., and Bootsma, H.A. 2015. Lake Michigan trophic structure as revealed by stable C and N isotopes. J. Great Lakes Res. **41**: 185-196.

Vanderploeg, H. 1994. Zooplankton particle selection and feeding mechanisms. *In* The biology of particles in aquatic systems. *Edited by* R.S. Wotton. Lewis Publishers, Ann Arbor, MI. pp. 205-234.

Vanderploeg, H.A., Liebig, J.R., Nalepa, T.F., Fahnenstiel, G.L., and Pothoven, S.A. 2010. *Dreissena* and the disappearance of the spring phytoplankton bloom in Lake Michigan. J. Great Lakes Res. **36**: 50-59.

Vanderploeg, H.A., Pothoven, S.A., Fahnenstiel, G.L., Cavaletto, J.F., Liebig, J.R., Stow, C.A., Nalepa, T.F., Madenjian, C.P., and Bunnell, D.B. 2012. Seasonal zooplankton dynamics in Lake Michigan: disentangling impacts of resource limitation, ecosystem engineering, and predation during a critical ecosystem transition. J. Great Lakes Res. **38**: 336-352.

Miscellaneous Publications

1981-01   A Joint Strategic Plan for Management of Great Lakes Fisheries. Edited by Great Lakes Fishery Commission.

1992-01   Strategic Vision of the Great Lakes Fishery Commission for the Decade of the 1990s. Great Lakes Fishery Commission.

1993-01   What's Next? The Prediction and Management of Exotic Species in the Great Lakes. Edward L. Mills, Joseph Leach, Carol L. Secor, and James T. Carlton.

1993-02   A Survey of Fish-Community and Habitat Goals/Objectives/Targets and Status in Great Lakes Areas of Concern. John H. Hartig.

1993-03   Toward Integrating Remedial-Action and Fishery-Management Planning in Great Lakes Areas of Concern. John H. Hartig.

1994-01   Walleye-Rehabilitation Guidelines for the Great Lakes Area. Peter J. Colby, Cheryl A. Lewis, Randy L. Eshenroder, Robert C. Haas, and Larry J. Hushak.

1995-01   Review of Progress under the Strategic Vision. Great Lakes Fishery Commission.

1996-01   A Lake Trout Restoration Plan for Lake Superior. Edited by Michael J. Hansen.

1998-01   A Lake Trout Rehabilitation Guide for Lake Huron. Edited by Mark P. Ebener.

2003-01   A Rehabilitation Plan for Walleye Populations and Habitats in Lake Superior. Edited by Michael H. Hoff.

2003-02   A Lake Sturgeon Rehabilitation Plan for Lake Superior. Nancy A. Auer [ED.].

2003-03   A Brook Trout Rehabilitation Plan for Lake Superior. Edited by Lee E. Newman, Robert B. DuBois, and Theodore N. Halpern.

2006-01   A Mid-Decade Review of Progress under a "Strategic Vision of the Great Lakes Fishery Commission for the First Decade of the New Millennium". Great Lakes Fishery Commission.

2006-02   Application of a Dichotomous Key to the Classification of Sea Lamprey Marks on Great Lakes Fish. Mark P. Ebener, Everett Louis King, Jr., and Thomas A. Edsall.

2007-01   A Joint Strategic Plan for Management of Great Lakes Fisheries. Edited by Great Lakes Fishery Commission.

2007-02   Application of a Dichotomous Key to the Classification of Sea Lamprey *Petromyzon marinus* Marks on Lake Sturgeon *Acipenser fulvescens*. Holly K. Patrick, Trent M. Sutton, and William D. Swink.

2008-01   A Guide for the Rehabilitation of Lake Trout in Lake Michigan. Charles R. Bronte, Charles C. Krueger, Mark E. Holey, Michael L. Toneys, Randy L. Eshenroder, and Jory L. Jonas.

2008-02   A Strategic Plan for the Rehabilitation of Lake Trout in Lake Erie, 2008-2020. James Markham, Andy Cook, Tom MacDougall, Larry Witzel, Kevin Kayle, Chuck Murray, Michael Fodale, Elizabeth Trometer, Fraser Neave, John Fitzsimons, Jim Francis, and Martin Stapanian.

2008-03   Strategic Vision of the Great Lakes Fishery Commission for the First Decade of the New Millennium. Great Lakes Fishery Commission.

2010-01   Genetic Guidelines for the Stocking of Lake Sturgeon (*Acipenser fulvescens*) in the Great Lakes Basin. Amy B. Welsh, Robert F. Elliott, Kim T. Scribner, Henry R. Quinlan, Edward A. Baker, Bradley T. Eggold, J. Marty Holtgren, Charles C. Krueger, and Bernie May.

2010-02   Identification of Michigan Fishes Using Cleithra. Daniel Traynor, Ashley Moerke, and Roger Greil.

2010-03   Strategic Plan for Lake Champlain Fisheries. J. Ellen Marsden, Brian D. Chipman, Bernie Pientka, William F. Schoch, and Bradley A. Young.

2011-01   Parasites of Fish from the Great Lakes: A Synopsis and Review of the Literature, 1871-2010. Patrick M. Muzzall and Gary Whelan.

2011-02   A Field Guide to the Taxonomy of Ciscoes in Great Slave Lake, Northwest Territories, Canada. Andrew M. Muir, Paul Vecsei, and J.D. Reist.

2011-03   Strategic Vision of the Great Lakes Fishery Commission 2011-2020. Edited by Great Lakes Fishery Commission.

2016-01   Ciscoes (*Coregonus*, subgenus *Leucichthys*) of the Laurentian Great Lakes and Lake Nipigon. Randy L. Eshenroder, Paul Vecsei, Owen T. Gorman, Daniel L. Yule, Thomas C. Pratt, Nicholas E. Mandrak, David B. Bunnell, and Andrew M. Muir.

2017-01   A Mid-Decade Review of Progress under a *Strategic Vision of the Great Lakes Fishery Commission 2011-2020.* Great Lakes Fishery Commission.