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Changes in the Lake Michigan food web following dreissenid mussel invasions: A synthesis



Charles P. Madenjian^{a,*}, David B. Bunnell^a, David M. Warner^a, Steven A. Pothoven^b, Gary L. Fahnenstiel^{c,d}, Thomas F. Nalepa^c, Henry A. Vanderploeg^e, Iyob Tsehaye^f, Randall M. Claramunt^g, Richard D. Clark Jr.^f

^a U. S. Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor, MI 48105, USA

^b National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, Lake Michigan Field Station, 1431 Beach Street, Muskegon, MI 49441, USA

^c University of Michigan, Water Center, 214 South State Street, Suite 200, Ann Arbor, MI 48104, USA

^d Michigan Technological University, Great Lakes Research Center, 1400 Townsend Drive, Houghton, MI 49931, USA

^e National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, 4840 South State Road, Ann Arbor, MI 48108, USA

^f Michigan State University, Department of Fisheries and Wildlife, Quantitative Fisheries Center, 293 Farm Lane, East Lansing, MI 48824, USA

^g Michigan Department of Natural Resources, Charlevoix Fisheries Research Station, 96 Grant Street, Charlevoix, MI 49720, USA

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ABSTRACT

Using various available time series for Lake Michigan, we examined changes in the Lake Michigan food web following the dreissenid mussel invasions and identified those changes most likely attributable to these invasions, thereby providing a synthesis. Expansion of the quagga mussel (*Dreissena rostriformis bugensis*) population into deeper waters, which began around 2004, appeared to have a substantial predatory effect on both phytoplankton abundance and primary production, with annual primary production in offshore (>50 m deep) waters being reduced by about 35% by 2007. Primary production likely decreased in nearshore waters as well, primarily due to predatory effects exerted by the quagga mussel expansion. The drastic decline in *Diporeia* abundance in Lake Michigan during the 1990s and 2000s has been attributed to dreissenid mussel effects, but the exact mechanism by which the mussels were negatively affecting *Diporeia* abundance remains unknown. In turn, decreased *Diporeia* abundance was associated with reduced condition, growth, and/or energy density in alewife (*Alosa pseudoharengus*), lake whitefish (*Coregonus clupeaformis*), deepwater sculpin (*Myoxocephalus thompsonii*), and bloater (*Coregonus hoyi*). However, lake-wide biomass of salmonines, top predators in the food web, remained high during the 2000s, and consumption of alewives by salmonines actually increased between the 1980–1995 and 1996–2011 time periods. Moreover, abundance of the lake whitefish population, which supports Lake Michigan's most valuable commercial fishery, remained at historically high levels during the 2000s. Apparently, counterbalancing mechanisms operating within the complex Lake Michigan food web have enabled salmonines and lake whitefish to retain relatively high abundances despite reduced primary production.

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Introduction

Since the late 1980s, two species of dreissenid mussels have successfully invaded Lake Michigan. The zebra mussel (*Dreissena polymorpha*) was the first to invade, starting during the late 1980s (Marsden, 1992). By 1993, the zebra mussel population in Lake Michigan was well established (Nalepa et al., 1998). The quagga mussel (*Dreissena rostriformis bugensis*) was first observed in Lake Michigan in 1997 (Nalepa et al., 2001), and the quagga mussel population had established itself throughout the lake by 2004 (Nalepa et al., 2009). In fact, the quagga mussel displaced the zebra mussel as the dominant dreissenid by 2005, when the quagga mussel comprised 98% of the total dreissenid population. In addition, the profundal form of the quagga mussel

colonized the offshore (>50 m deep) waters of Lake Michigan during 2004–2007 (Bunnell et al., 2009; Nalepa et al., 2009). Quagga mussels had attained extremely high densities in Lake Michigan by 2010, when lake-wide biomass density of quagga mussels was estimated to be 20 g/m² (dry-weight shell-free basis). In contrast, the peak lake-wide biomass density of *Diporeia*, a native amphipod, observed in Lake Michigan during the 1980s was 6 g/m² (Nalepa et al., 2009). Moreover, even allowing for the substantially higher energy density of *Diporeia* compared with dreissenid mussels, the amount of energy represented by the biomass of dreissenid mussels in Lake Michigan in 2007 exceeded the energy represented by peak *Diporeia* biomass in Lake Michigan by twofold. Thus, the quagga mussel invasion of Lake Michigan eventually led to a substantial increase in the flow of energy to the benthic macroinvertebrate community, despite the dramatic decrease in *Diporeia* abundance during the 1990s and 2000s (Nalepa et al., 2009). To accurately interpret changes in the Lake Michigan

* Corresponding author. Tel.: +1 734 214 7259.

E-mail address: cmadenjian@usgs.gov (C.P. Madenjian).

food web following the dreissenid mussel invasions, this increase in the flow of energy to the benthic macroinvertebrate community must be considered. The decrease in *Diporeia* abundance has been attributed to the dreissenid mussel invasions, although the exact mechanisms by which the dreissenid mussels are negatively affecting *Diporeia* abundance remain unidentified. Clearance rates of dreissenids are high even in cold water, and they filter feed on a broad range of phytoplankton, protozoa, and other seston (Vanderploeg et al., 2002, 2010; Lavrentyev et al., 2014). This filtering by dreissenid mussels has contributed to a substantial increase (110% in spring; 68% over annual cycle) in water clarity in Lake Michigan (Vanderploeg et al., 2010, 2012). In turn, this increased water clarity may serve to increase the foraging efficiency of certain visual predators, such as invasive cladocerans *Bythotrephes longimanus* and *Cercopagis pengoi*, as hypothesized by Vanderploeg et al. (2002, 2012). In addition, this increased water clarity appeared to contribute to an increased abundance of the benthic green algae *Cladophora* in the nearshore zone of Lake Michigan (Bootsma et al., 2015; Brooks et al., 2015). Further, energy sources for fishes and invertebrates appeared to switch from pelagic to nearshore benthic during the course of this dreissenid mussel expansion period in Lake Michigan, based on documenting changes in stable isotope signatures for carbon in these animals over time (Turschak et al., 2014).

Dynamics of the Lake Michigan food web during 1970–2000 were characterized by Madenjian et al. (2002), who identified the preliminary effects of the dreissenid mussel invasions on the food web. These researchers concluded that the dreissenid mussel invasions had not yet caused a significant decline in primary production in the offshore waters of Lake Michigan. The decline in *Diporeia* abundance during the 1990s was attributed to the dreissenid mussel invasions. Madenjian et al. (2002) also concluded that the abundances of important fish populations in Lake Michigan apparently had not yet decreased in response to the dreissenid mussel invasions. However, decreases in growth and condition of lake whitefish (*Coregonus clupeaformis*) and alewives (*Alosa pseudoharengus*) during the late 1990s were attributed, at least in part, to decreased *Diporeia* abundance (Madenjian et al., 2002; Pothoven et al., 2001), and subsequent research has corroborated these contentions (DeBruyne et al., 2008; Madenjian et al., 2003, 2006; Pothoven and Madenjian, 2008). The importance of *Diporeia* in the diet of both lake whitefish and alewives in Lake Michigan substantially decreased with the decline of *Diporeia* abundance in the 1990s, apparently leading to decreased growth and condition of both fishes. Alewife energy density also decreased between the 1979–1981 and 2002–2004 periods likely due to decreased importance of *Diporeia* in alewife diet (Madenjian et al., 2006).

The expansion of quagga mussels into deeper waters coupled with the extremely high quagga mussel densities during the late 2000s has sparked further research into the effects of the quagga mussel invasion on the Lake Michigan lower food web (Fahnenstiel et al., 2010a). Emerging evidence has indicated that the filtering activities of quagga mussels caused a disappearance of the spring diatom bloom in the offshore waters of Lake Michigan during the late 2000s, resulting in a significant reduction in annual primary production (Fahnenstiel et al., 2010b; Mida et al., 2010; Pothoven and Fahnenstiel, 2013; Vanderploeg et al., 2010). During the 2000s, zooplankton community structure in Lake Michigan has become more similar to that of Lake Superior, as cladocerans and cyclopoid copepods have decreased in abundance while the calanoid copepod *Limnocalanus macrurus* has increased in abundance (Barbiero et al., 2012; Bunnell et al., 2014; Vanderploeg et al., 2012). Vanderploeg et al. (2012) hypothesized that the changes in cyclopoid copepod abundance may be partially influenced by the quagga mussel expansion.

Our intent here is to formulate an updated synthesis on the changes in the Lake Michigan food web following the dreissenid mussel invasions, with an emphasis on food web changes accompanying the quagga mussel expansion. We use an approach similar to the one used by Madenjian et al. (2002) in that we examine time series for various

components of the food web and review the pertinent literature. Then, we characterize the changes in the food web following the dreissenid mussel invasions, and we identify those changes most likely attributable to the dreissenid mussel invasions. Likewise, we identify the food web changes that were probably not due to the dreissenid mussel invasions. For purposes of this synthesis, the period of dreissenid mussel establishment corresponds with the years following 1993, and the start of the quagga mussel expansion is identified as 2004. In developing our synthesis, we consider the findings and ideas of Bunnell et al. (2014), Rogers et al. (2014), and Turschak et al. (2014), who have provided new perspectives on the recent changes in the Lake Michigan food web, in identifying those changes likely due to the dreissenid mussel invasions and those changes not likely attributable to the dreissenid mussel invasions. Finally, we offer some suggestions for future research directed at trying to disentangle the effects of the dreissenid mussel invasions from the effects of other factors influencing the Lake Michigan food web.

Phytoplankton and primary production

Phosphorus has been identified as the major nutrient limiting primary production in Lake Michigan (Schelske and Stoermer, 1971; Schelske et al., 1974). In response to a control program, phosphorus loadings to Lake Michigan substantially decreased during the 1980s (Bunnell et al., 2014; Madenjian et al., 2002). Phosphorus loadings to Lake Michigan have varied without trend since 1990 (Bunnell et al., 2014).

Annual primary production in the offshore waters of Lake Michigan has been estimated to have decreased by 35% between the 1983–1987 and 2007–2008 periods, and this decrease was attributed to the filtering activities of quagga mussels during spring mixing (Fahnenstiel et al., 2010b; Vanderploeg et al., 2010). During the spring isothermal period, the entire water column may be influenced by quagga mussel filtering. A spring diatom bloom was a prominent feature of the annual phytoplankton dynamics in offshore waters of Lake Michigan during 1983–1998, but this bloom had disappeared by 2007. Based on filtering rate calculations by Vanderploeg et al. (2010), quagga mussels alone could account for the reduction in phytoplankton biomass during the spring between the 1983–1987 and 2007–2008 periods. Thus, the quagga mussel population appeared to be exerting some degree of consumer control on phytoplankton during the spring by 2007 in Lake Michigan's offshore waters (Fahnenstiel et al., 2010b; Mida et al., 2010; Vanderploeg et al., 2010). Spring chlorophyll *a* concentration, an indicator of phytoplankton biomass in the spring, showed a modest decrease between the 1983–1987 and 1995–1998 periods in the offshore waters of Lake Michigan, but then decreased substantially by 2007–2008 (Fig. 1). Spring total phosphorus concentration (TP), an indicator of primary production, in the offshore waters of Lake Michigan exhibited a temporal pattern similar to that of spring chlorophyll *a* concentration (Fig. 1).

Although the above-mentioned temporal trends in primary production and spring phytoplankton biomass were based on sampling the 110-m bottom depth site off Muskegon, MI by the National Oceanic and Atmospheric Administration (NOAA) Great Lake Environmental Research Laboratory (GLERL), these trends appear to be reflective of the entire lake. These trends at Muskegon were in accord with the trends documented by the lake-wide survey conducted by the U. S. Environmental Protection Agency (USEPA) Great Lakes National Program Office (GLNPO) at 16 offshore sites in April and August of each year, 1998–2011. The GLNPO survey also documented substantial decreases in both spring TP and spring chlorophyll *a* concentration in the offshore waters during the quagga mussel expansion (Barbiero et al., 2012). Similarly, satellite-derived estimates of spring chlorophyll *a* concentrations, on a lake-wide basis, indicated a considerable reduction in spring phytoplankton biomass in offshore waters of Lake Michigan during the quagga mussel expansion (Lesht et al., 2013).

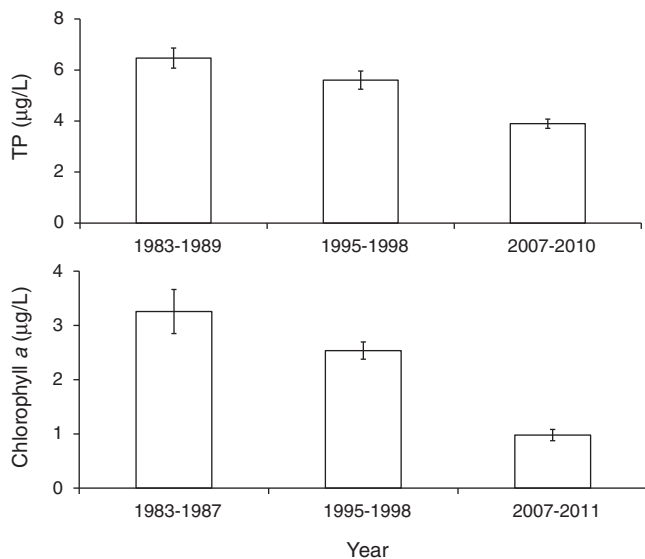


Fig. 1. Average spring total phosphorus (TP) concentration (upper panel) and average spring chlorophyll *a* concentration (lower panel) (from March until water temperature reached 4 °C) at an offshore (110-m bottom depth) station off Muskegon, MI in Lake Michigan during three time periods between 1983 and 2011. Refer to Fahnenstiel et al. (2010b) and Mida et al. (2010) for sampling details.

The magnitude of the deep chlorophyll layer (DCL) in offshore waters of southeastern Lake Michigan substantially decreased between the 1995–2000 and 2007–2011 periods (Pothoven and Fahnenstiel, 2013). This decrease occurred despite the increase in water clarity. Moreover, this decrease has been attributed to the quagga mussel expansion: (1) causing the elimination of the spring diatom bloom, and (2) altering the flow of nutrients from the nearshore to the offshore. Pothoven and Fahnenstiel (2013) also concluded that although chlorophyll *a* concentration in the summertime surface mixed layer in the offshore waters of southeastern Lake Michigan did not significantly change between the 1995–2000 and 2007–2011 periods, chlorophyll *a* concentration in the near bottom zone (bottom 20 m of water column) decreased by 63% and 54% in the early summer and late summer, respectively, between these two periods. Reasons given for this decrease in near bottom chlorophyll *a* were identical to the reasons given for the reduced DCL.

The most significant change in the phytoplankton community structure of Lake Michigan's offshore waters between 1983 and 2007–2008 was the dramatic decrease in diatom (Bacillariophyceae) biomass in spring between the 1995–1998 and 2007–2008 periods (Fahnenstiel et al., 2010b). Similarly, biomass of Chrysophyceae and small flagellates underwent a drastic decrease in spring between 1995–1998 and 2007–2008. While diatom biomass substantially decreased in the mid-stratification period (typically July through September) between 1995–1998 and 2007–2008, biomass of cyanobacteria and chlorophytes actually increased between these two periods of time. Biomass of Chrysophyceae and small flagellates in the late-stratification period (October through December) was more than 5 times higher during 1995–1998 and 1983–1987 than that during 2007–2008 (Fahnenstiel et al., 2010b). In examining changes in the <53 µm and >53 µm size fractions of chlorophyll *a* concentration between these two time periods, Vanderploeg et al. (2010) noted the greater decrease in the >53 µm size fraction, which is typically dominated by colonial diatoms (Bundy et al., 2005).

Based on results from remote sensing imagery and primary production modeling, Yousef et al. (2014) estimated that spring primary production in southern Lake Michigan declined to a greater degree in waters between 30 and 90 m deep than in waters >90 m deep during 1998–2010. Further, these researchers attributed these decreases in

primary production to predatory effects exerted by quagga mussels. Coincidentally, quagga mussels attained their highest biomass densities in the 31 to 50 m bottom depth range, and their second highest biomass densities in the 51 to 90 m bottom depth range during 2005–2010 in southern Lake Michigan (Nalepa et al., 2009). Although Yousef et al. (2014) concluded that the reduced primary production in southern Lake Michigan was driven by grazing effects of the quagga mussel expansion on phytoplankton lake-wide biomass, they acknowledged that the reduction in phosphorus loadings to Lake Michigan during the 1980s and sequestration of nutrients by the expanded quagga mussel population may have made minor contributions to the reduced primary production since quagga establishment. The findings from Yousef et al. (2014) indicated that the effects exerted by the quagga mussel population on phytoplankton biomass occurred in both the offshore and nearshore (≤50 m deep) waters of Lake Michigan, with primary production reduced in both regions of the lake during 1998–2010.

Although not assessed by Yousef et al. (2014), benthic primary production in nearshore waters of Lake Michigan has increased since 1990 (Bootsma et al., 2015; Brooks et al., 2015). This increase in benthic primary production has been driven by an increase in the abundance of the green algae *Cladophora* in association with increased water clarity brought about, at least in part, by the dreissenid mussel invasions. This increased benthic primary production in the nearshore zone would partly compensate for the above-mentioned reduction in pelagic primary production in the nearshore zone of Lake Michigan (Bootsma et al., 2015; Brooks et al., 2015). In addition, sloughed-off *Cladophora* and associated periphyton from the nearshore zone has been suspected of being transported offshore, thereby providing a subsidy to the offshore zone (Bootsma et al., 2015; Turschak et al., 2014). If this subsidy is indeed being realized, then the increase in *Cladophora* abundance, as well as the increase in abundance of periphyton associated with *Cladophora*, may be having far-reaching effects on the Lake Michigan food web. Note that spatial distribution of *Cladophora* within the nearshore zone of Lake Michigan was extremely patchy, with *Cladophora* being abundant in some areas and absent in others.

Benthic macroinvertebrates

Diporeia abundance in Lake Michigan dramatically decreased during 1994–2005, whereas quagga mussels rapidly increased in abundance during 2000–2010 (Fig. 2). Decreased *Diporeia* abundance has been attributed to the dreissenid mussel invasions, but the mechanisms by which the dreissenid mussels may have caused a reduction in *Diporeia* abundance have yet to be identified (Fahnenstiel et al., 2010a; Nalepa et al., 1998, 2000, 2009). In the southern basin, biomass density of quagga mussels was greatest in the 31–50 m bottom depth range, and reached a peak density of >40 g/m² by 2008, and then slightly decreased during 2008–2010 (Fig. 3). Quagga mussel biomass density was second highest in the 51–90 m bottom depth region, and steadily increased during 2000–2010. Quagga mussel biomass density in the 16–30 m bottom depth region attained a peak density of about 7 g/m² in 2006, and then decreased during 2007–2010 (Fig. 3). Lowest biomass densities of quagga mussels were observed in the >90 m bottom depth region, but densities in this region appear to still be increasing. Zebra mussel biomass density was greatest in the 31–50 m bottom depth region, where a peak density of about 7 g/m² was observed in 2003, but zebra mussel biomass densities quickly declined during 2003–2006 (Fig. 3). This decline has been attributed to the rapid increase of quagga mussel abundance (Nalepa et al., 2009). Nalepa et al. (2010) observed a decrease in the condition index of quagga mussels in the waters <50 m deep of southern Lake Michigan between 2004 and 2008, whereas lipid content and glycogen content of the quagga mussels did not decline during this time period. Given the huge increase in quagga mussel abundance over this time period, at least part of this

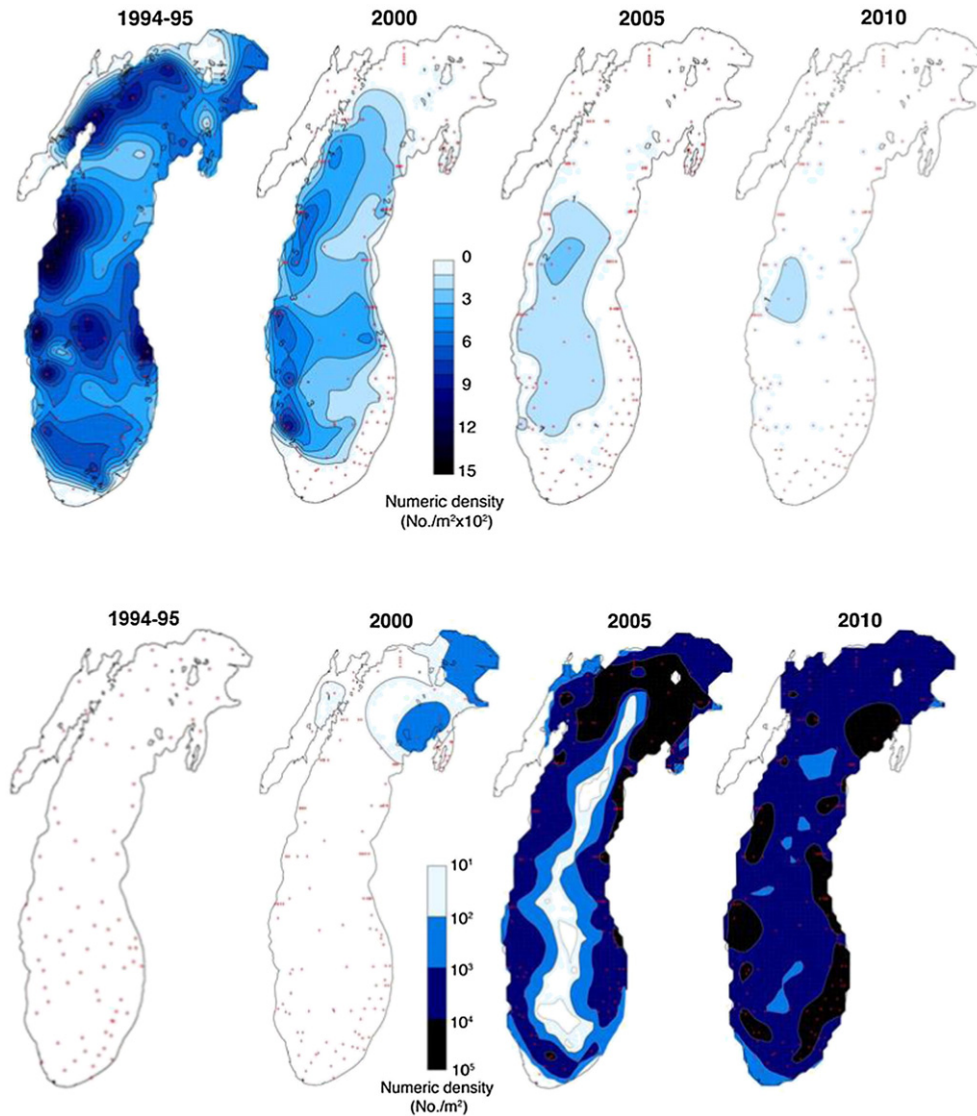


Fig. 2. Changes in *Diporeia* numeric density in Lake Michigan during 1994–2010 (upper panel) and in quagga mussel numeric density in Lake Michigan during 1994–2010 (lower panel). Note difference in numeric scales between the panels. This figure was modified from one presented by Nalepa et al. (2014b).

decrease in condition index may be attributable to compensatory density-dependent effects.

Zooplankton

Total zooplankton biomass in offshore waters of Lake Michigan showed wide variation across years but trended neither downward nor upward during 1994–2011 (Fig. 4), suggesting that the dreissenid mussel invasions did not affect total zooplankton biomass. However, zooplankton community structure underwent major changes during this time period (Vanderploeg et al., 2012). Calanoid copepod biomass density appeared relatively stable during 1994–2011, whereas cyclopoid copepod biomass density showed an overall decreasing trend during the 2000s (Fig. 4). Although biomass density of herbivorous cladocerans declined during the 2000s, biomass density of certain omnivorous and predatory zooplankters, including *Leptodiantomus ashlandi*, *Leptodiantomus sicilis*, *Epischura lacustris*, *L. macrurus*, and *B. longimanus*, increased during the 2000s (Vanderploeg et al., 2012). These changes in zooplankton community structure have been primarily attributed to depressed abundance of age-1 and older alewives

during the late 2000s and an associated increase in *B. longimanus* abundance, but quagga mussel effects were also likely involved. *B. longimanus* abundance increased during the late 2000s, due at least in part to depressed levels of age-1 and older alewives which serve as predators on *B. longimanus*. With increased light penetration arising from filtering activities of quagga mussels, foraging efficiency of *B. longimanus* likely increased (Vanderploeg et al., 2012). In turn, increased abundance and foraging efficiency of *B. longimanus* likely led to decreased abundance of certain herbivorous cladocerans, including *Daphnia mendotae*, and cyclopoid copepods, notably *Diacyclops thomasi*. Not only is *B. longimanus* capable of preying upon these zooplankters, but increased abundance of *B. longimanus* could also have had important indirect negative effects on the abundances of these zooplankters, by causing them to undertake greater diel migrations into cold water, where feeding rate and growth potential could potentially be lower (Pangle and Peacor, 2006). The increase in *L. macrurus* abundance during the late 2000s may also have been partly attributable to the depressed abundance of age-1 and older alewives (Vanderploeg et al., 2012). In addition, Vanderploeg et al. (2012) hypothesized that the *D. thomasi* crash was partly due to a decline in protozoan

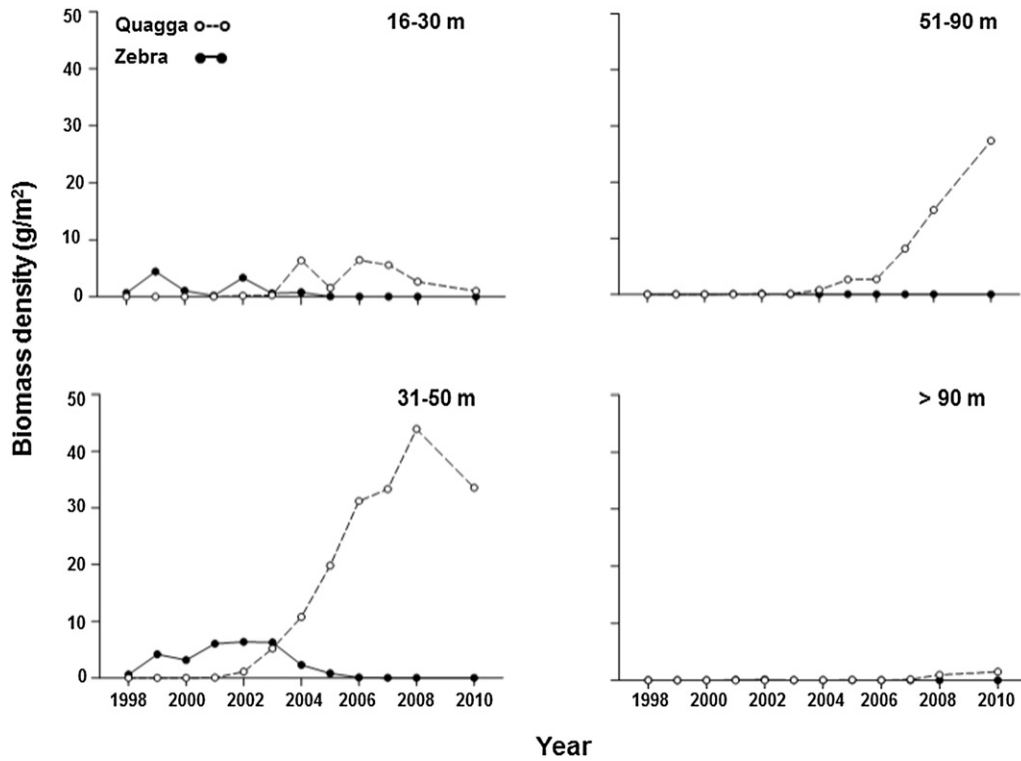


Fig. 3. Biomass densities (in grams of shell-free, ash-free dry weight per m²) of zebra mussels and quagga mussels in four bottom depth zones of the southern basin of Lake Michigan during 1998–2010. This figure was modified from one presented by Nalepa et al. (2013).

microzooplankton associated with quagga mussels cropping the protozoan microzooplankton and their phytoplankton prey; *D. thomasi* is heavily dependent on microzooplankton for food. Finally, Vanderploeg et al. (2012) concluded that the strong alewife year-class of 1998 was likely a driver of low zooplankton abundance in 1999.

The GLNPO time series for total zooplankton biomass in offshore waters of Lake Michigan showed a decreasing trend during 1998–

2011 (Barbiero et al., 2012; R. Barbiero, CSC and Loyola University Chicago, 1359 W. Elmdale Ave., Chicago, IL 60660, personal communication, 7/16/2014), while the GLERL time series lacked a long-term trend. This discrepancy between the GLNPO and GLERL time series was apparently not driven by the difference in spatial coverage between the two surveys. The GLNPO time series was based on a lake-wide survey of offshore waters of Lake Michigan, whereas the

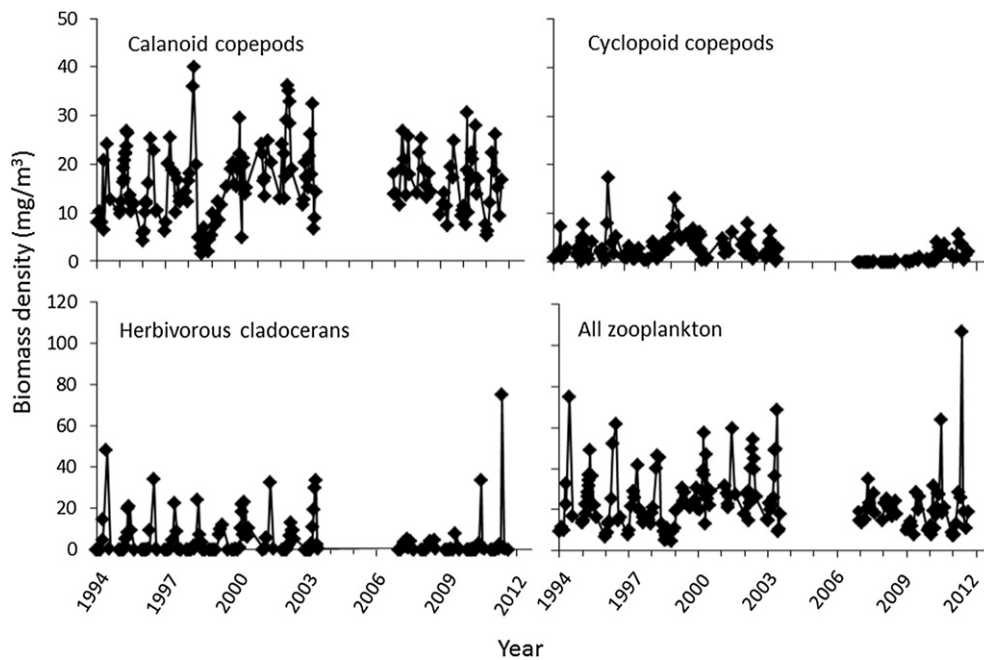


Fig. 4. Biomass densities (in grams of dry weight per m³) of calanoid copepods, cyclopoid copepods, herbivorous cladocerans, and all crustacean zooplankton at an offshore (110-m bottom depth) station off Muskegon, MI in Lake Michigan during 1994–2011. Nauplii were not included in the biomass density calculations for calanoid copepods and cyclopoid copepods, but were included in the calculation of total zooplankton biomass density. Refer to Vanderploeg et al. (2012) for sampling details.

GLERL survey was based on sampling the 110-m bottom depth site off Muskegon, MI. Rather, the decreasing trend in the GLNPO time series was likely a consequence of the time series being based on once-a-year sampling in August. In contrast, the GLERL time series was based on sampling at least once a month from March/April through November/December. Selection of only the August observations in the GLERL data set, and then calculation of an average August value for each year, yielded a time series exhibiting a downward trend during 1998–2011 (Fig. 5). In essence, the August time series from the GLERL data set mimicked the GLNPO time series. These results indicated that even though total zooplankton biomass in August declined during 1998–2011, annual total zooplankton biomass in the offshore waters did not decline.

Although a long-term time series for total zooplankton biomass in the nearshore waters of Lake Michigan is unavailable, Pothoven and Fahnenstiel (2015) contended that total zooplankton biomass in nearshore waters decreased in response to the quagga mussel expansion in Lake Michigan. Their contention was based on tracking zooplankton biomasses at the 15-m, 45-m, and 110-m sites off Muskegon, MI across seasons during 2007–2012, and then comparing their estimates of total zooplankton biomass with those at similar depths from previous studies conducted during the late 1970s in southeastern Lake Michigan. If their contention is correct, it would suggest that the reduction in primary production in nearshore waters, which was a consequence of the quagga mussel expansion, led to a decline in total zooplankton biomass in nearshore waters via bottom-up effects. Again, this reduced primary production has been attributed primarily to grazing effects of the quagga mussels on phytoplankton biomass (Yousef et al., 2014).

Mysis diluviana

Based on the available data, long-term trends in opossum shrimp *M. diluviana* abundance in Lake Michigan during 1985–2010 were not readily apparent (Fig. 6), indicating that the dreissenid mussel invasions had not affected *M. diluviana* abundance. Data on *M. diluviana* abundance in Lake Michigan at the lake-wide scale are quite limited. Lehman et al. (1990) sampled in August 1985–1989 across a wide geographic scale at 5–10 sites per year with bottom depths up to 210 m. In 2000, Pothoven et al. (2004) sampled seasonally (spring, summer, and fall) at 16 sites over a wide geographic range at bottom depths ≤ 100 m. Unpublished data (D.M. Warner) from August 2005–2010 were based on sampling 12–30 sites each year with bottom depths ranging from 18 m to over 200 m. In all three studies, vertical tows were made using nets with a 1-m diameter, but Lehman et al. (1990) used mesh sizes ranging from 130–300 μm , whereas 1000- μm mesh was used in the other two studies. Chipps and Bennett (1996) found, based on comparing performances between 333- μm and 1000- μm mesh sizes, that *M. diluviana* catch did not significantly vary between the two mesh sizes. Similarly, using the data from Lehman et al. (1990), we found that *M. diluviana* density did not significantly

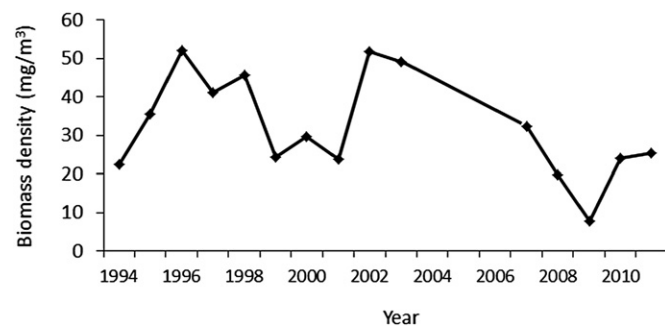


Fig. 5. Biomass densities (in grams of dry weight per m^3) of all crustacean zooplankton at an offshore (110-m bottom depth) station off Muskegon, MI in Lake Michigan during August, 1994–2011. Refer to Vanderploeg et al. (2012) for sampling details.

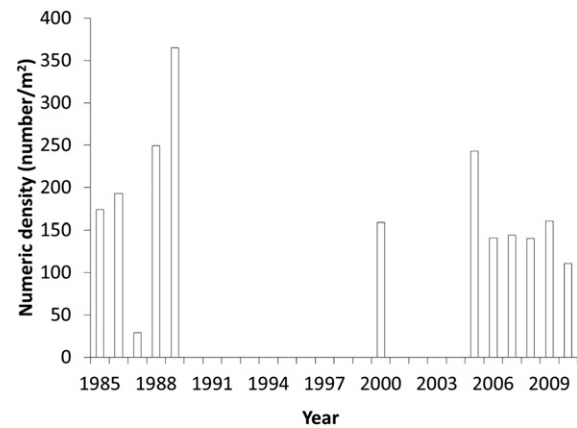


Fig. 6. Summer numeric densities of *Mysis diluviana* in Lake Michigan during 1985–2010. Data taken from Lehman et al. (1990), Pothoven et al. (2004), and D. M. Warner (unpublished data). Refer to text for additional sampling details.

vary between the 130- μm and 300- μm mesh sizes (t test: $t = 0.19$; $P = 0.42$; $N = 5$ per mesh size). Thus, the Lehman et al. (1990) data should be at least roughly comparable with the data from the two more recent studies. In another study in waters 45-m to 110-m deep off Muskegon, MI, Pothoven et al. (2010) documented a decrease in *M. diluviana* abundance during 1995–2008. One plausible explanation for this abundance decline at Muskegon was that a portion of the *M. diluviana* population moved to deeper waters, perhaps triggered by increased water clarity brought about by the dreissenid mussel invasions. *M. diluviana* has been shown to have a high degree of light sensitivity (Gal et al., 1999). Moreover, *M. diluviana* abundance at the 110-m deep site at Muskegon during 2007–2008 was similar to *M. diluviana* abundance at a 100-m deep site off Grand Haven, MI (just 20 km from the Muskegon site) during 1985–1989, suggesting no change in abundance between the two time periods (Pothoven et al., 2010).

Growth and reproductive characteristics of *M. diluviana* did not appear to have been affected by the quagga mussel expansion in Lake Michigan, as these characteristics did not change between the 1995–2002 and 2007–2008 periods (Pothoven et al., 2010). However, lipid content of *M. diluviana* from Lake Michigan was lower during 2009–2010 than during the 1980s, 1990s, or early 2000s, and this relatively low lipid content was attributed to the disappearance of the spring diatom bloom and the DCL decline, both of which were believed to be consequences of the quagga mussel expansion (Pothoven et al., 2012a,b). The *M. diluviana* population in Lake Michigan has provided, and continues to provide, a high-energy food source for many planktivorous and benthivorous fishes (Bunnell et al., 2015; Davis et al., 2007; Hondorp et al., 2005; Wells, 1980).

Prey fish

Alewife

The alewife population in Lake Michigan has been under top-down control by salmonines since the early 1980s (Madenjian et al., 2002, 2005b; Tsehaye et al., 2014a). Accordingly, biomass density of YAO (yearling and older) alewives has generally remained at relatively low levels since 1982 (Fig. 7). Biomass density of YAO alewives was exceptionally low during 2004–2011, concomitant with increased predation by salmonines (Fig. 8; Tsehaye et al., 2014a,b). This increased predation was attributable to: (1) increased production of wild Chinook salmon smolts from tributaries to Lake Huron during the late 1990s serving as a new source of recruitment to the Lake Michigan Chinook salmon population, because Chinook salmon have been documented to migrate from Lake Huron to Lake Michigan (Adlerstein et al., 2007;

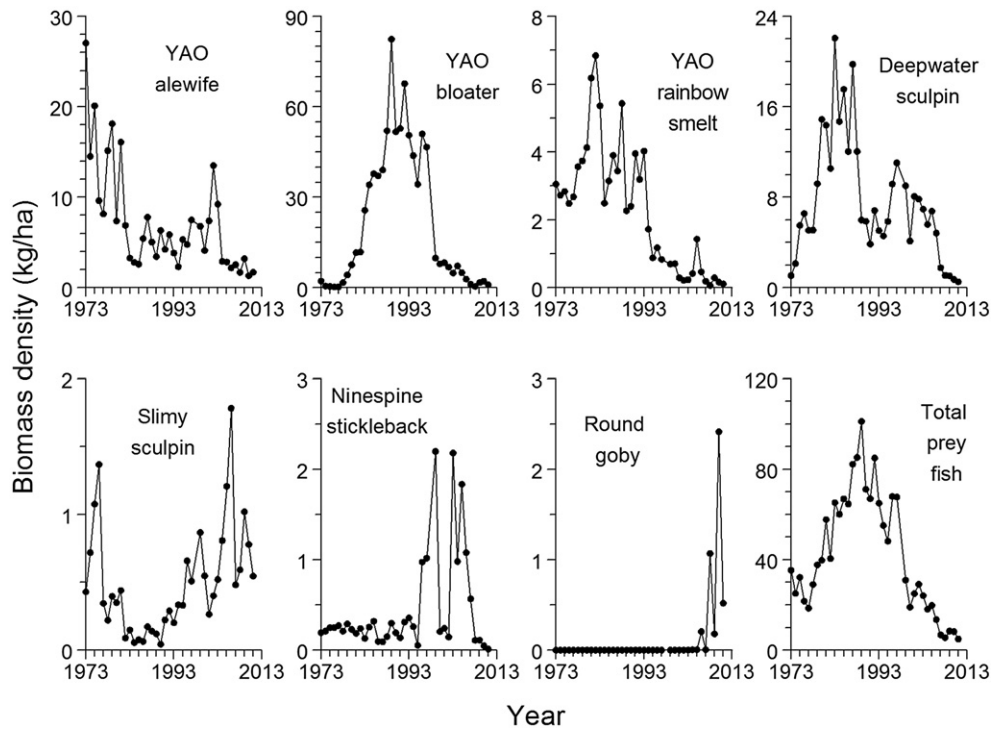


Fig. 7. Biomass densities (wet-weight basis) of prey fish in Lake Michigan during 1973–2011, based on the U.S. Geological Survey (USGS) Great Lakes Science Center (GLSC) annual bottom trawl survey (Madenjian et al., 2014). Note that vulnerabilities to the bottom trawl may vary across prey fish species.

Tsehaye et al., 2014a,b; Williams, 2012), (2) increased importance of alewives in the diet of Lake Michigan Chinook salmon during the late 1990s or 2000s (Jacobs et al., 2013), and (3) an increase in feeding rates of individual Chinook salmon that was likely linked to a decrease in energy density of adult alewives during the late 1990s (Madenjian et al., 2006). This decrease in adult alewife energy density, as well as decreases in alewife growth and condition (Madenjian et al., 2003), were most likely due to decreased importance of *Diporeia* in adult alewife diet brought about by the decrease in *Diporeia* abundance. Because the drop in *Diporeia* abundance is presumed to be an effect of the dreissenid mussel invasions, these declines in alewife energy density, growth, and condition are also considered consequences of the dreissenid mussel invasions. Adult alewife condition dropped in a stepwise fashion in 1995, but has not exhibited any further declines since that time (Fig. 9). Earlier research suggested that cold winters had a negative influence on alewife abundance in Lake Michigan (Eck and Brown, 1985), but results from regression analyses applied to the Great Lakes Science Center (GLSC) bottom trawl time series indicated otherwise. Specifically, results from linear regression modeling of the spawner–recruit relationship indicated that winter severity did not have a significant effect on alewife recruitment in Lake Michigan, and a similar conclusion was reached for Lake Huron as well (Collingsworth et al., 2014; Madenjian et al., 2005b). In addition, results from bioenergetics modeling applied to predator populations showed that predation was an important driver of the alewife collapse during 2002–2004 in Lake Huron (He et al., 2015). Several researchers have attributed decreases in alewife abundance in Lakes Huron and Ontario to relatively cold winter water temperatures (Dunlop and Riley, 2013; O’Gorman and Schneider, 1986; Ridgway et al., 1990). Perhaps relatively cold winters do contribute, in some cases, to enhanced overwinter mortality of alewives. Perhaps sudden drops in water temperature during the spring and early summer can also lead to enhanced mortality of alewives in some cases, as hypothesized by Stanley and Colby (1971). Nevertheless, the population modeling by Tsehaye et al. (2014a) indicated that predation by salmonines has been, and continues to be, the

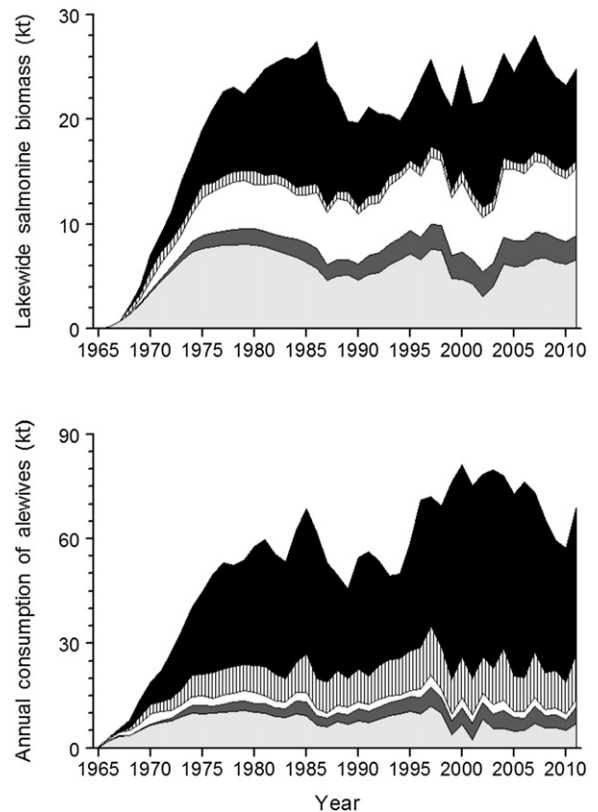


Fig. 8. Lake-wide biomass (wet-weight basis) of salmonines in Lake Michigan (upper panel) and annual lake-wide consumption of alewives (wet-weight basis) by the salmonine populations in Lake Michigan (lower panel), as estimated by the Tsehaye et al. (2014a,b) predator–prey model, during 1965–2011. Salmonines included lake trout (light shading), brown trout (dark shading), rainbow trout (open), coho salmon (vertical bars), and Chinook salmon (solid).

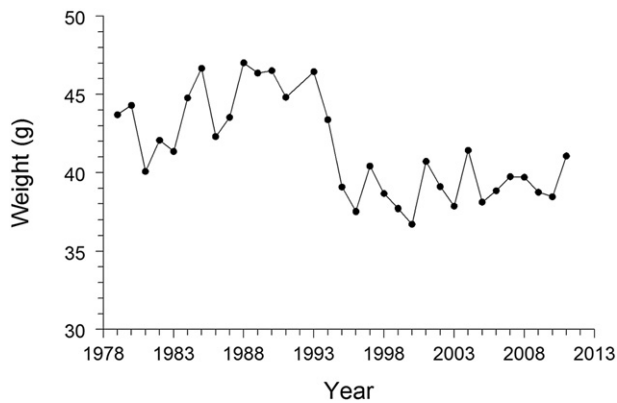


Fig. 9. Wet weight of a 175-mm (total length) alewife from Lake Michigan during 1979–2011, based on length–weight regression analysis applied to data from the GLSC annual bottom trawl survey (Madenjian et al., 2014).

primary driver of alewife abundance in Lake Michigan, and predation mortality has remained the predominant source of mortality experienced by alewives in the lake since the early 1980s.

Apparently, the dreissenid mussel invasions have not impaired the ability of alewives to reproduce in Lake Michigan. According to the predator–prey statistical age-structured model developed by Tsehaye et al. (2014a), predicted alewife year-class strength was higher, on average, during 1994–2010 (9.2 billion fish) than during 1973–1993 (6.7 billion fish) (Fig. 10). Further, according to the modeling results, the largest alewife year-class produced in Lake Michigan since 1970 was the 1998 year-class. Thus, even when alewife condition was relatively low, the alewife population was still capable of producing very large year-classes. In addition, acoustic survey estimates of alewife year-class strength indicated that the frequency of large year-classes did not change between the 1992–1996 and 2002–2010 periods (Warner et al., 2014), further supporting the contention that the quagga mussel expansion has not affected the alewife population's capacity to reproduce. The 1992–1996 period yielded one strong year-class (1995 year-class), and the 2002–2010 period yielded two strong year-classes (2005 and 2010 year-classes). Moreover, results from linear regression modeling of the spawner–recruit relationship, using bottom-trawl estimates, indicated that primary production did not have a significant effect on alewife recruitment in Lake Michigan during 1962–2002 (Madenjian et al., 2005b).

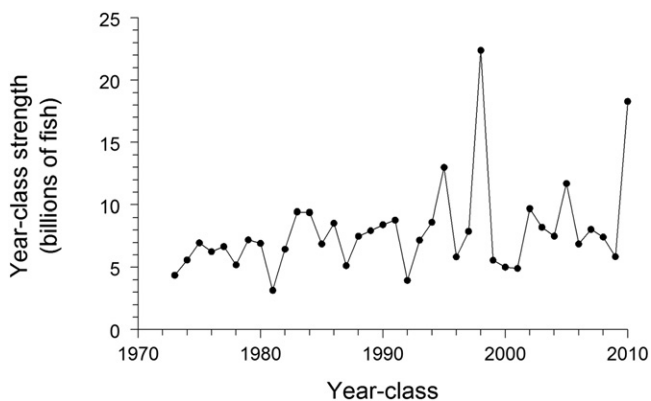


Fig. 10. Year-class strengths of alewives, as determined from the Tsehaye et al. (2014a) predator–prey model estimates of number of age-0 alewives in Lake Michigan during the fall, for years 1973–2010.

Bloater

YAO bloater (*Coregonus hoyi*) biomass density dramatically declined during the late 1990s and 2000s (Fig. 7), and this decline has been attributed to a prolonged period of generally low recruitment during 1992–2011 (Bunnell et al., 2009; Madenjian et al., 2014). This prolonged period of low recruitment was probably not attributable to the dreissenid mussel invasions, because bloater recruitment in Lake Superior exhibited a temporal pattern similar to that in Lake Michigan even though dreissenid mussels have not successfully invaded Lake Superior (Madenjian et al., 2008; Bunnell et al., 2010). Moreover, strong year-classes of bloomers have been produced in Lake Huron during the past five years despite the increasing population biomass of quagga mussels in the lake (Riley et al., 2014). Surveillance via bottom trawling and via acoustics coupled with midwater trawling indicated that the bloater population in Lake Michigan showed some signs of recovery during the late 2000s, but the recovery has stalled (Madenjian et al., 2014; Warner et al., 2014). This stall in the recovery could possibly be explained by: (1) predation on juvenile bloomers preventing the recovery (see Warner et al. (2008) for a specific example of a potential mechanism), or (2) movement of bloomers to deeper waters. Warner et al. (2008) suggested that predation on juvenile bloomers by juvenile Chinook salmon could potentially represent an impediment to bloater recovery in Lake Michigan. Reports from Lake Michigan commercial fishers have suggested that a substantial portion of the bloater population has moved to waters deeper than those sampled by the GLSC bottom trawl survey (i.e., 9–110 m bottom depths). If bloomers have indeed moved to deeper waters in Lake Michigan, perhaps this movement was driven by the apparent migration to deeper waters by *M. diluviana*, which has become the predominant prey of bloomers during the 2000s (Bunnell et al., 2015). Bloater biomass in Lake Michigan could possibly have increased since 2010, but the GLSC bottom trawl survey has been unable to detect this potential increase due to changes in bloater depth distribution and behavior.

Dreissenid mussels may be affecting the bloater population in at least two ways. First, bloater energy density appeared to have been affected by the decreased abundance of *Diporeia*, as bloater energy density in 2008–2009 was similar to that during 1998–2001 even though YAO bloater biomass density was substantially higher in 1998–2001 than in 2008–2009 (Pothoven et al., 2012a,b). A substantial increase in energy density was expected between 1998 and 2009 due to density-dependent effects, but no increase was actually observed. In contrast, lipid content, which is closely linked to energy density (Madenjian et al., 2006), of Lake Michigan bloomers decreased by about 50% during the 1980s, when bloater population size underwent a dramatic increase (Madenjian et al., 2002). *Diporeia* was an important diet constituent for Lake Michigan bloomers during 1970–1995 (Davis et al., 2007; Rudstam et al., 1994), but its importance in bloater diet decreased during the 2000s (Bunnell et al., 2015; Hondorp et al., 2005). Second, dreissenid mussels could be reducing catchability of bloomers in the GLSC daytime bottom trawl survey, perhaps by increased water clarity or by inducing bloomers to move to deeper waters and/or to spend more time off the lake bottom.

Rainbow smelt

YAO rainbow smelt (*Osmerus mordax*) biomass density in Lake Michigan remained relatively high through the 1980s, but then underwent a drastic decrease during 1993–2001, and has remained at relatively low levels thereafter (Fig. 7). These long-term temporal trends were not well explained by predation effects imposed by salmonines (Tsehaye et al., 2014a), and this time series remains a difficult one to interpret (Madenjian et al., 2002, 2014). O'Brien et al. (2014) found that spring precipitation was an important factor regulating rainbow smelt recruitment in Lake Huron, and these researchers proposed that spring precipitation influenced the availability

of stream-spawning habitat for rainbow smelt. However, a similar regression analysis for Lake Michigan revealed that spring precipitation did not significantly affect rainbow smelt recruitment in Lake Michigan (Feiner et al., 2015).

Sculpins

Deepwater sculpin (*Myoxocephalus thompsonii*) biomass density remained at moderately high levels during the 1990s and early 2000s, but then rapidly declined during 2005–2011 (Fig. 7). This rapid decline has been attributed to movement of the bulk of the deepwater sculpin population to waters deeper than 110 m, and coincided with the quagga mussel expansion (Madenjian et al., 2014). If *M. diluviana* did move to deeper waters during the 2000s, then this apparent movement by deepwater sculpins may have been in response to a *M. diluviana* migration. Madenjian and Bunnell (2008) documented a trend toward occupying deeper water for deepwater sculpins beginning in the late 1980s and continuing through the early 2000s, and by 2007 most of the population may have moved outside the range of the bottom trawl survey. Supplementary bottom trawl tows at depths ranging between 128 and 132 m performed during September 2013 supported this contention of movement to deeper waters (Madenjian et al., 2014). Energy density of Lake Michigan deepwater sculpins decreased by 26% during 2001–2009, and this decrease was attributed to decreased importance of *Diporeia* in deepwater sculpin diet (Pothoven et al., 2011). By 2009, *M. diluviana* represented nearly all of the diet of deepwater sculpins, while *Diporeia* greatly declined in diet importance due to its decreasing abundance (Bunnell et al., 2015).

Slimy sculpin (*Cottus cognatus*) biomass density in Lake Michigan appeared to be considerably influenced by predation by juvenile lake trout (*Salvelinus namaycush*) (Madenjian et al., 2005a, 2014). Slimy sculpins are favored prey items for juvenile lake trout. Slimy sculpin abundance decreased when lake trout stocking was focused in nearshore waters during 1965–1985, but slimy sculpin abundance within the waters covered by the bottom trawl survey increased during 1985–2006 when lake trout stocking became more focused on offshore reefs that were not located within the area covered by the survey. The decrease in slimy sculpin biomass density following 2009 was concomitant with a substantial increase in the rate of stocking lake trout into Lake Michigan and an increase in abundance of wild juvenile lake trout in the lake, especially in the southern portion (Lake Trout Working Group, 2014; Madenjian et al., 2014).

Ninespine stickleback

The dreissenid mussel invasions appeared to benefit the ninespine stickleback (*Pungitius pungitius*) population in Lake Michigan, as ninespine stickleback biomass density increased more than fivefold between the 1973–1995 and 1996–2007 periods (Fig. 7). Madenjian et al. (2010a) hypothesized that the increased biomass of green algae *Cladophora* associated with the dreissenid mussel invasions improved spawning habitat for ninespine sticklebacks, thereby facilitating increased abundance. Ninespine sticklebacks are nest builders, and they prefer to use aquatic vegetation in constructing their nests. In support of the Madenjian et al. (2010a) hypothesis, the time series developed by Brooks et al. (2015) for spatial extent of submerged aquatic vegetation (including *Cladophora*) in two areas of Lake Michigan were well synchronized with the GLSC bottom trawl time series for ninespine stickleback biomass density during years 1973–2007. Ninespine stickleback biomass density fell precipitously during 2007–2011, and this sudden drop has been attributed to increased predation from salmonines. Ninespine sticklebacks were not found in the stomachs of Chinook salmon caught during 1994–1996, but accounted for 1.6% of the diet of large Chinook salmon during 2009–2010 (Jacobs et al., 2013). With YAO alewives at very depressed levels of abundance during the late 2000s, apparently Chinook salmon had begun to incorporate ninespine

sticklebacks into their diet. Similarly, the decrease in ninespine stickleback abundance in Lake Superior between the 1978–1999 and 2000–2007 periods was attributed to increased predation by siscowet lake trout (Madenjian et al., 2010a).

Round goby

Round gobies (*Neogobius melanostomus*) invaded Lake Michigan during the 1990s and have been observed in harbors and bays since 1993, with some sightings in the southern main basin of the lake as early as 1997 (Clapp et al., 2001). Round gobies were not captured in the GLSC bottom trawl survey of Lake Michigan until 2003, but round goby biomass density rapidly increased during 2003–2011 (Fig. 7). Round goby biomass density may already have leveled off in Lake Michigan, and signs of predatory control have been detected (Madenjian et al., 2014). Several piscivorous fishes prey upon round gobies in Lake Michigan, and estimates of annual mortality rates for adult round gobies during 2008–2012 ranged from 79 to 85%, which are comparable to the mortality rates currently experienced by Lake Michigan adult alewives (Huo et al., 2014; Tsehaye et al., 2014a).

Salmonines

The salmonines represent the predominant top predators in the Lake Michigan food web (Claramunt et al., 2012; Madenjian et al., 2002). A major salmonine stocking program for Lake Michigan was launched in 1965, and has continued to the present (Madenjian et al., 2002; Tsehaye et al., 2014b). The five species currently stocked are lake trout, Chinook salmon, coho salmon (*Oncorhynchus kisutch*), rainbow trout (*Oncorhynchus mykiss*), and brown trout (*Salmo trutta*). On average, Chinook salmon accounted for roughly 40% of the total salmonine biomass, while lake trout and rainbow trout each contributed about 25% to the total salmonine biomass (Tsehaye et al., 2014b). During the 2000s, about 60% of the Chinook salmon caught in Lake Michigan were wild, rather than hatchery, fish (Williams, 2012). In contrast, natural reproduction by lake trout in Lake Michigan has been limited (Lake Trout Working Group, 2014). Although the percentage of wild lake trout taken in the spring gillnet surveys increased during 2005–2013, the percentage remained under 10% on a lake-wide basis. The recent increase in lake trout natural reproduction was most likely due to the recently depressed levels of adult alewife abundance in the lake; alewives can impair lake trout natural reproduction via predation on lake trout fry and via thiamine deficiency (Fitzsimons et al., 1999; Lake Trout Working Group, 2014; Madenjian et al., 2008). A diet rich in alewives can lead to thiamine deficiency in lake trout, and a sufficiently low thiamine level in lake trout eggs can lead to reduced egg survival.

Lake-wide salmonine biomass, as estimated from the modeling effort by Tsehaye et al. (2014b), increased steadily and rapidly during 1965–1978, and then peaked in 1986 at 27.4 kilotons (kt, 1 kt = 1000 metric tons) (Fig. 8). Salmonine biomass declined by about 25% during 1986–1990 but then increased during 1994–2007. This slight depression in salmonine biomass during the late 1980s and early 1990s was attributable to the bacterial kidney disease (BKD) outbreak in the Chinook salmon population (Madenjian et al., 2002). Overall, salmonine biomass had reached a relatively high level by 1980 and has remained at relatively high levels to the present time.

Alewives have served as the mainstay of the diet of salmonines in Lake Michigan since 1965 (Madenjian et al., 2002). Alewives constituted about 70% of the biomass of prey consumed by salmonines during 1965–1995. By the late 1990s, the percentage of alewife biomass in salmonine diet increased to about 80%. Annual consumption of alewives by salmonines increased from an average of 56 kt during 1980–1995 to an average of 72 kt during 1996–2011 (Fig. 8). Thus, on average, predation exerted by salmonines on alewives increased between the

time periods. As previously mentioned, activation of a new source of Chinook salmon recruitment to Lake Michigan during the late 1990s, increased importance of alewives in Chinook salmon diet, and a reduction in adult alewife energy density during the late 1990s or early 2000s contributed to this increased predation on alewives. Due to decreased adult alewife energy density, salmonines have to consume a greater amount of alewife biomass during the low-energy-density era than the high-energy-density era to attain equal amounts of growth during both eras (Madenjian et al., 2006). Moreover, after allowing for the alewife 1998 year-class to pass through the predatory gauntlet, this increased predation could account for the unusually low YAO alewife abundances during 2004–2011. The 1998 year-class was the largest alewife year-class produced in Lake Michigan since 1970 (Tsehaye et al., 2014a), but the abundance of the year-class had been greatly reduced via salmonine predation by 2004. The predator–prey statistical age-structured model developed by Tsehaye et al. (2014a) predicted both the increased predation on alewives during 1996–2011 and the unusually low YAO alewife abundance during 2004–2011. These simulation modeling results clearly indicated that alewives have been under top-down control by salmonines since the 1980s. The only bottom-up effect included in the Tsehaye et al. (2014a) model was the decrease in adult alewife energy density presumably brought about by reduced importance of *Diporeia* in adult alewife diet. In addition, results from linear regression modeling, using GLSC bottom trawl estimates for alewife biomass, have also indicated top-down control of salmonines on alewives (Madenjian et al., 2005b; Collingsworth et al., 2014).

Lake whitefish

The lake whitefish (*C. clupeaformis*) population in Lake Michigan has supported the most important commercial fishery operating in the lake for the past 3 decades (Brenden et al., 2013; Ebener et al., 2008). Lake whitefish can be characterized as a benthivore with feeding habits primarily targeting benthic macroinvertebrates (Scott and Crossman, 1973). Historically, the diet of lake whitefish in Lake Michigan was predominantly *Diporeia* and *M. diluviana*, but the diet underwent substantial changes after the dreissenid mussel invasions, with much of the *Diporeia* component being replaced by dreissenid mussels during the late 1990s and early 2000s (Pothoven and Madenjian, 2008). Lake whitefish diet in Lake Michigan shifted yet again during the late 2000s, with part of the dreissenid mussel component being replaced by round gobies (S. Hansen, Wisconsin Department of Natural Resources, personal communication, 3/13/2014; Lehrer-Brey and Kornis, 2014; Pothoven and Madenjian, 2013). The Lake Michigan lake whitefish population continues to show great plasticity in its diet. Similar shifts in lake whitefish diets have also been observed in the main basin of Lake Huron (He et al., 2015; Pothoven and Madenjian, 2013). Stable isotopic signatures for carbon and nitrogen have also been used to infer changes in Lake Huron lake whitefish diet over time (Rennie et al., 2009). The carbon isotopic signature can be used to distinguish between isotopically distinct energy sources, such as littoral or nearshore versus pelagic or profundal sources. Turschak et al. (2014) proposed that a shift to greater use of nearshore benthic energy sources by fish in association with the dreissenid mussel invasions of Lake Michigan, as revealed by carbon isotopic signatures, may be due to transport of *Cladophora* and associated periphytic diatoms from the nearshore zone to the offshore zone, and Bootsma et al. (2015) provided further evidence to support this contention.

The dreissenid mussel invasions did not yet appear to have a negative effect on lake whitefish abundance in Lake Michigan. In fact, as best we can estimate, lake whitefish abundances in Lake Michigan during the 2000s were among the highest lake whitefish abundances occurring in the lake since 1890. Commercial harvest of lake whitefish from Lake Michigan during 1990–2009 was higher than any other 20-year period since 1890, when the historical records began (Brenden et al., 2013; Wells and McLain, 1973). According to

results from the statistical catch-at-age (SCA) modeling applied to Lake Michigan lake whitefish (Ebener et al., 2005; Madenjian et al., 2010b), lake-wide biomass of age-3 and older lake whitefish in Lake Michigan peaked in 2005 at an estimated value of 57 kt, but then decreased to 38 kt by 2011 (Fig. 11). Overall, lake whitefish lake-wide biomass was greater, on average, during 2000–2011 than during 1990–1999 or during the late 1980s. Of additional note is that dreissenid mussels have negatively affected the ability of commercial fishers to catch lake whitefish in Lake Michigan (Ebener et al., 2008). Average depth of fishing has increased in response to the dreissenid mussel invasions, presumably due to increased bathymetric distribution of lake whitefish as a consequence of increased light penetration in the water column (due to mussels' filtering activity) and reduced *Diporeia* abundance. Moreover, beginning as early as 1994, *Cladophora* has fouled both gill nets and trap nets used to catch lake whitefish to such a degree that fishing efficiency was severely reduced at times. As previously mentioned, increased abundance of *Cladophora* was associated with the dreissenid mussel invasions. In addition, dreissenid mussels themselves fouled gill nets and trap nets, thereby reducing the fishing efficiency of these gear.

The dreissenid mussel invasions have led to a reduction in lake whitefish growth and condition during the late 1990s (Madenjian et al., 2002; Pothoven et al., 2001), and these reductions have been attributed, in part, to the above-mentioned diet shift (Pothoven and Madenjian, 2008). Density-dependent effects also contributed to these reductions (DeBruyne et al., 2008). Lake whitefish condition continued to slowly decline through the early 2000s before leveling off (Fig. 11).

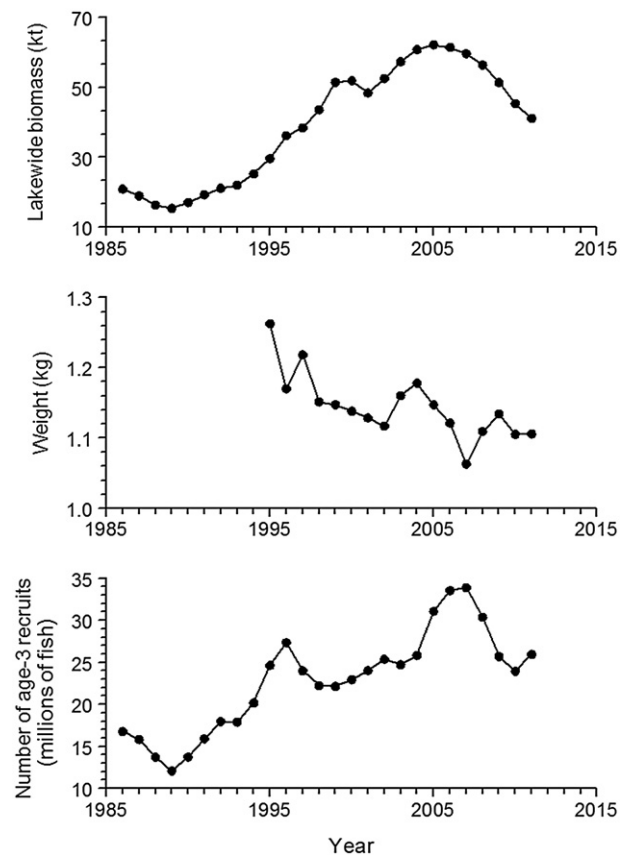


Fig. 11. Lake-wide biomass of age-3 and older lake whitefish in Lake Michigan (upper panel), wet weight of a 500-mm (total length) lake whitefish in Lake Michigan (middle panel), and number of age-3 recruits to the lake whitefish population in Lake Michigan, during 1986–2011. Lake-wide lake whitefish population biomass and recruitment were estimated via application of statistical catch-at-age (SCA) models (Ebener et al., 2005; Madenjian et al., 2010b). Weight of a 500-mm lake whitefish was estimated via application of length–weight regression analysis to data used in the SCA model applications.

Thus, the incorporation of round gobies into the diet of lake whitefish did not result in an increase in lake whitefish condition. Similarly, lake whitefish condition did not significantly increase in both northern and southern Lake Huron when lake whitefish began to feed on round gobies (Pothoven and Madenjian, 2013). Perhaps the incorporation of round gobies into the diet of Lake Michigan lake whitefish prevented further decreases in lake whitefish condition.

The dreissenid mussel invasions did not yet appear to negatively influence lake whitefish recruitment. Muir et al. (2010) concluded that declines in growth and condition of lake whitefish did not translate into decreased recruitment potential, and Claramunt et al. (2010a,b) determined that mechanisms influencing recruitment of lake whitefish to the juvenile stage were independent of dreissenid mussel effects. Moreover, according to the SCA modeling results, lake whitefish recruitment at age 3 nearly tripled during 1989–2007, peaked in 2007, and then just slightly (23%) decreased during 2007–2011 (Fig. 11). Thus, recruitment of lake whitefish was apparently not impaired by a reduction in condition, as was also the case for alewives.

Burbot

Lake trout and burbot are the two native, coldwater top predators in Lake Michigan (Wells and McLain, 1973). During the 1980s and early 1990s, the burbot population in Lake Michigan exhibited a strong recovery, which has been attributed to control of both sea lamprey and alewives (Madenjian et al., 2002), but burbot biomass density substantially decreased during 1997–2011 (Fig. 12). One plausible explanation for the initial part of this decrease would be that burbot population biomass had simply exceeded the carrying capacity of the Lake Michigan ecosystem by the early 1990s, and this resulted in a negative feedback on burbot recruitment. The continued decrease in burbot biomass density after 2007 may possibly have been due to a portion of the burbot population moving to waters deeper than 110 m in response to a movement of deepwater sculpins, a favored prey of burbot, to deeper waters (Madenjian et al., 2014). In shallower waters, burbot had begun to incorporate round gobies into their diet as early as 2006, or perhaps even earlier (Jacobs et al., 2010).

Yellow perch

The yellow perch population attained its highest biomass during the late 1980s and early 1990s, owing to several unusually strong year-classes in the 1980s (Clapp and Dettmers, 2004). The abrupt decline in yellow perch recruitment, beginning in the late 1980s, eventually led to the formation of the Yellow Perch Task Group in 1994, and a large group of scientists set out to test five hypotheses related to this decline (Clapp and Dettmers, 2004). Dreissenid mussels

were indirectly implicated in one of these hypotheses that postulated that relatively low zooplankton density was limiting larval yellow perch survival after 1990. Some resultant empirical work suggested that larval survival was, in fact, relatively low in the early 1990s (Marsden and Robillard, 2004), and a positive correlation between age-0 yellow perch abundance in the fall and nearshore zooplankton density the previous June when larvae are first feeding provided corroborative support (Dettmers et al., 2003; Clapp and Dettmers, 2004). At the same time, several other factors were believed to underlie population declines, including overfishing that limited the spawning stock biomass (Wilberg et al., 2005), and negative effects of alewife, via predation on yellow perch larvae (Shroyer and McComish, 2000; Redman et al., 2011). Although complete understanding of the factors limiting yellow perch recruitment remains elusive, a recent “summit” hosted by the Lake Michigan Committee of the Great Lakes Fishery Commission concluded that, at present, the greatest impediment to a recovery of yellow perch was a changing lake ecosystem, with lower primary productivity and higher water clarity (affecting yellow perch habitat selection), rather than overfishing (Lake Michigan Committee, 2014). Dreissenid mussels, alone, were not the cause of the yellow perch population decline, but likely were a contributing factor if the mussels did indeed contribute to nearshore declines in zooplankton abundance.

Discussion

Even though the negative effect of dreissenid mussels on primary production has prompted some ecologists to view the dreissenid mussel invasions as serving as a trigger for bottom-up effects throughout the entire food web, changes in the Lake Michigan food web following the dreissenid mussel invasions were inconsistent with classic bottom-up theory. According to this theory, a reduction in primary production would yield a decrease in the population biomass of first-order consumers, which in turn would yield a decrease in the population biomass of second-order consumers, which in turn would cause a reduction in top predator population biomass of the food web (Crowder et al., 1988; Hall et al., 1970; Menge, 1992). Primary production in Lake Michigan has declined following the dreissenid mussel invasions, and this decline has been attributed primarily to grazing control by the quagga mussel expansion. However, the dreissenid mussel invasions were not accompanied by a decrease in the population biomass of the first-order consumers, in large part because huge biomasses of dreissenid mussels far outweighed any reductions in other first-order consumers. Thus, first-order consumer biomass substantially increased following the dreissenid mussel invasions. For simplicity, we will consider zooplankton and benthic macroinvertebrates as first-order consumers. Zooplankton biomass in the offshore waters of Lake Michigan has trended neither upward nor downward in response to the dreissenid mussel invasions, whereas total zooplankton biomass in the nearshore waters may have undergone a decrease due to the quagga mussel expansion. Benthic macroinvertebrate biomass during the late 2000s exceeded benthic macroinvertebrate biomass during the 1980s by threefold or more, due to the huge increase in dreissenid mussel biomass. The apparent decrease in lakewide total zooplankton biomass was more than compensated by the relatively large increase in benthic macroinvertebrate biomass (primarily dreissenid mussel biomass) following the dreissenid mussel invasions. Across depths ranging from 15 to 110 m, total zooplankton biomass at the Muskegon transect averaged about 1.5 g/m² during 2007–2012 (Pothoven and Fahnenstiel, 2015). Even assuming an average lakewide total zooplankton biomass of 3 g/m² prior to the quagga mussel expansion, this proposed decrease of 1.5 g/m² in total zooplankton biomass would be dwarfed by the 14 g/m² increase in benthic macroinvertebrate biomass accompanying the dreissenid mussel invasions. The net result was a substantial increase in first-order consumer biomass. Responses of the second-order consumers to the dreissenid mussel

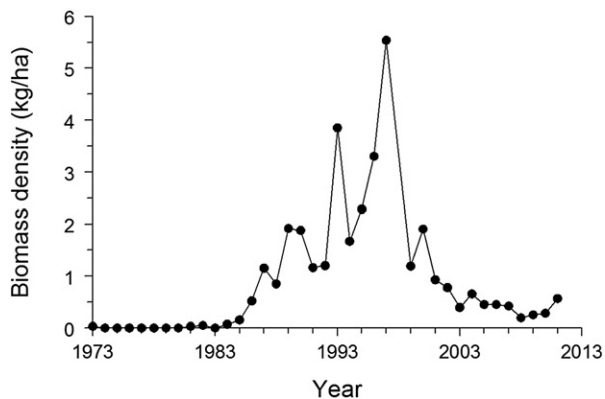


Fig. 12. Biomass densities (wet-weight basis) of burbot in Lake Michigan during 1973–2011, based on the U. S. Geological Survey (USGS) Great Lakes Science Center (GLSC) annual bottom trawl survey (Madenjian et al., 2014).

invasions were mixed. *M. diluviana* abundance, to date, did not appear to be negatively affected by the dreissenid mussel invasions. Lake-wide biomass of lake whitefish has remained at historically high levels in the face of extremely high densities of quagga mussels. Although total prey fish biomass, based on the GLSC bottom trawl survey, declined by about tenfold during 1993–2011, factors other than reduced primary production were at least partly responsible for this decline. Reduction in YAO alewife abundance can be accounted for as the direct result of increased predation by salmonines (Tsehaye et al., 2014a). The decrease in deepwater sculpin abundance during 2006–2011 was most likely due to movement of the bulk of the population to waters deeper than those sampled by the bottom trawl survey, perhaps in response to an apparent movement of *M. diluviana* to deeper waters. Reasons for the prolonged period of apparently low bloater recruitment during 1992–2011 remain unknown, but are not believed to be caused by bottom-up effects related to dreissenid mussels. Recent declines in abundances of slimy sculpin and ninespine stickleback abundances were most likely due to predation effects. Lake-wide biomass of the top predators (third-order consumers), namely the salmonines, has been relatively stable during 1995–2011, in the face of extremely high quagga mussel densities and declining prey fish biomass. Thus, the top predators of the food web appeared unaffected by the dreissenid mussel invasions. In sum, a classic bottom-up response is an inaccurate characterization of the changes in the Lake Michigan food web following the dreissenid mussel invasions, to date.

Although the Lake Michigan food web did not exhibit a classic bottom-up response to the dreissenid mussel invasions, signs of both bottom-up and top-down interactions operating within the food web were apparent. For example, total zooplankton biomass in the near-shore waters of Lake Michigan appeared to decline in response to the quagga mussel expansion, and such a decline signaled a bottom-up effect on total zooplankton biomass. Another bottom-up example was the decline in *D. thomasi* biomass density in offshore waters accompanying the quagga mussel expansion, due in part to lowered microzooplankton biomass density owing to water filtering by quagga mussels. With regard to top-down examples, the population of the invasive cladoceran *B. longimanus* appeared to apply some predatory control over certain herbivorous cladocerans in offshore waters (Vanderploeg et al., 2012). At times, large alewife year-classes were likely responsible for top-down effects on not only the *B. longimanus* population but also on total zooplankton biomass in offshore waters (Pothoven et al., 2007; Vanderploeg et al., 2012).

We must also point out that reductions in growth, condition, and/or energy density do not necessarily imply reductions in population abundance or biomass. In fact, population abundance or biomass may actually increase while growth, condition, and energy density of individual fish in the population are decreasing. For example, lake whitefish condition and growth declined during the 1990s and early 2000s, while population size and biomass substantially increased. These decreases in growth and condition were partly attributable to dreissenid mussel effects stemming from reduced *Diporeia* abundance, but were also partly attributable to density-dependent effects. The alewife population offers a somewhat different example. Alewife condition, growth, and energy density declined beginning in 1995 via dreissenid mussel effects stemming from decreased *Diporeia* abundance, despite an overall decrease in alewife population biomass during 1995–2011. The decrease in YAO alewife abundance between the 1990s and the late 2000s was most likely attributable to increased predation by salmonines. As previously discussed, the decreases in growth and condition of alewives and lake whitefish did not appear to impair the ability of both populations to reproduce.

We recommend that Lake Superior be treated as an unaffected lake, for comparison purposes, when attempting to disentangle the effects of dreissenid mussels from other effects on the Lake Michigan food web. To date, Lake Superior has not been invaded by dreissenid mussels on a lake-wide basis (Grigorovich et al., 2003; Vanderploeg et al., 2002),

rather the dreissenid mussel distribution in Lake Superior is limited to just a few harbors, bays, and coastal areas (Grigorovich et al., 2003). This failure to invade Lake Superior was most likely due to calcium levels not being sufficiently high to support dreissenid mussel growth. *Diporeia* abundance in Lake Superior did not decrease during the 1990s or early 2000s, further supporting the contention that dreissenid mussel invasions are responsible for decreased *Diporeia* abundance in the lower four Great Lakes (Nalepa et al., 2005). Madenjian et al. (2010a) treated Lake Superior as a control when assessing the effects of the dreissenid mussel invasion on ninespine stickleback abundance in Lake Michigan. Similarly, Madenjian et al. (2008) treated Lake Superior as a control to evaluate the adverse effects of alewives on Great Lakes fish communities, because alewives never became well established in Lake Superior but did become well established in Lakes Ontario, Michigan, and Huron.

Substantially more research will be needed to identify and quantify the effects of dreissenid mussel invasions on abundances of many of the populations of plants and animals comprising the Lake Michigan food web, including some of the fish populations. To address these research needs, surveillance of these populations must continue into the future. In some cases, survey effort may have to be increased, or perhaps new surveillance techniques may be needed, to improve the accuracy of the lakewide estimate of population abundance or biomass. For example, deepwater sculpins in Lake Michigan may have moved to deeper waters in recent years. This movement appeared to have been triggered by the quagga mussel expansion. Perhaps bloaters have also moved to deeper waters in response to the quagga mussel expansion. To obtain more accurate estimates of the lake-wide biomasses of this fish, the bottom trawl survey would need to be expanded to deeper waters, and the effect of increased water clarity would need to be understood. In addition to continued surveillance in Lake Michigan, researchers should continue to compare the dynamics of the Lake Superior food web with Lake Michigan food web dynamics, as well as the food web dynamics of other Great Lakes. In addition, use of stable isotope analysis and food web modeling may provide other clues for identifying the effects of the dreissenid mussel invasions on the Lake Michigan food web (Rogers et al., 2014; Turschak et al., 2014). Moreover, investigations on the mechanisms driving the microbial food web may reveal key insights into the dynamics of the entire Lake Michigan food web (Carrick et al., 1991, 2015).

Part of the difficulty in assessing the effects of dreissenid mussels on the Lake Michigan food web is our incomplete understanding of: (1) certain dreissenid mussel processes (Mosley and Bootsma, 2015; Tang et al., 2014), (2) basic structure and function of the food web (Carrick et al., 2015), (3) spatial connections among food web components (Vanderploeg et al., 2015), and (4) the effects of ecosystem engineering, especially increased light intensity, on food web processes (Vanderploeg et al., 2002, 2012). Some progress has been made on feeding preferences by dreissenid mussels (Lavrentyev et al., 2014; Tang et al., 2014; Vanderploeg et al., 2010). However, the effects of dreissenid mussels on phosphorus cycling are poorly understood (Mosley and Bootsma, 2015; Johengen et al., 2013; Vanderploeg et al., 2010). Both the GLNPO and GLERL annual surveys of the lower food web have focused on nutrients, chlorophyll, and crustacean zooplankton, with some work done on phytoplankton. Consequently, the old paradigm of nutrients → phytoplankton → zooplankton → fish has been emphasized (Carrick et al., 2015). However, the microbial food web plays a major role in converting phytoplankton into a food source for crustacean zooplankton (Bundy et al., 2005; Carrick et al., 1991). Understanding the role of this under-sampled pathway is critical to better understanding the dynamics of the entire food web. This knowledge gap is particularly important now that picoplankton (<2 μm) has become the dominant size fraction of the Lake Michigan plankton, reversing the trend of nanoplankton (2–20 μm) and microplankton (20–200 μm) dominance (Carrick et al., 2015). Finally, phytoplankton, zooplankton, and fish can nowadays show high spatial overlap in

the vertical dimension, which, along with increased light intensity, could compensate for lowered primary production and phytoplankton biomass (Vanderploeg et al., 2015).

Our synthesis provided additional insights into the workings of the Lake Michigan food web beyond the findings of Bunnell et al. (2014), who pooled the food web components into trophic-level communities and then examined changes in community indices over time. Using this trophic-level community approach, Bunnell et al. (2014) addressed changing ecosystem dynamics in all five Laurentian Great Lakes, and they focused their analyses on data sets that provided adequate long-term coverage and were generated from lake-wide surveys conducted across all five lakes. As a result, they were not able to fully characterize changes in the Lake Michigan food web following the dreissenid mussel invasions. For example, because only four years of lake-wide survey data were available for dreissenid mussels in Lake Michigan, dreissenid mussel biomass was not included in their analyses, and consequently the grazing effect exerted by benthic macroinvertebrates on phytoplankton was not evaluated. Likewise, to assess changes in phytoplankton and zooplankton biomass, Bunnell et al. (2014) limited their data to the GLNPO time series for offshore waters, whereas we also made use of the GLERL time series for offshore waters, which provides greater seasonal resolution than the GLNPO time series, as well as the available data for nearshore waters. In addition, we found that lake whitefish abundance and lake-wide biomass appeared to be unaffected by the dreissenid mussel invasions, to date, but changes in the lake whitefish population were not addressed in the Bunnell et al. (2014) analyses. All of these limitations were discussed by Bunnell et al. (2014). Nonetheless, both the Bunnell et al. (2014) study and our study provided evidence for bottom-up and top-down interactions occurring within the Lake Michigan food web.

We are not claiming that the dreissenid mussel invasions have not had any effects on fish abundances in Lake Michigan. Rather, we are contending that much more research work will be required to identify and quantify those effects on certain fish population abundances. The bottom trawl time series indicated a positive effect of the dreissenid mussel invasions on ninespine stickleback abundance in Lake Michigan. Most likely, the dreissenid mussel invasions have had negative effects on some of the other fish population abundances. But, more research work will be needed to disentangle the effects of dreissenid mussels from effects of other factors influencing the Lake Michigan food web.

Given the time course of the dreissenid mussel invasion in Lake Ontario, we may expect that lake-wide biomass of quagga mussels in Lake Michigan will soon peak and then decrease. Dreissenid mussel abundance in Lake Ontario appeared to peak in 2003 and then decreased (Birkett et al., 2015; Bunnell et al., 2014; Nalepa et al., 2014a). A reduction in Lake Michigan quagga mussel biomass density should lead to a reduction in the effects of dreissenid mussels on the food web.

Our study results suggested that the effects of dreissenid mussel invasions on the Lake Michigan food web are quite complex, more subtle than once believed, and difficult to predict. Similarly, Strayer et al. (2004, 2014a,b) concluded that the food web changes, especially those changes for fish growth and populations sizes, in the Hudson River ecosystem in response to the zebra mussel invasion were both complex and subtle, as well as being nearly impossible to predict. Not only did responses by fish populations to the zebra mussel invasion of the Hudson River vary by species and occupied habitats, but the responses changed over time. In response to the dreissenid mussel invasions of Lake Michigan, some consumer populations decreased in abundance whereas other consumer populations did not. For example, the amphipod *Diporeia* exhibited a drastic decline in abundance following the dreissenid mussel invasions. The cyclopoid copepod *D. thomasi* population showed a substantial decrease in biomass immediately following the quagga mussel expansion beginning in 2004. Vanderploeg et al. (2012) attributed this decrease, in part, to declines in the prey abundance of *D. thomasi* brought about by the quagga mussel

expansion. Protozoan microzooplankton, particularly ciliates, are favored prey of quagga mussels. Further, *D. thomasi* is totally dependent on moving prey, namely microzooplankton, for food. Thus, the response of the *D. thomasi* population to this apparent decrease in microzooplankton abundance brought about by the quagga mussel expansion has been a substantial decline in its own abundance. In stark contrast, population biomass of lake whitefish and Chinook salmon have remained at historically high levels in the 2000s, despite establishment of the zebra mussel population in the early 1990s, establishment of the quagga mussel population in the early 2000s, and the quagga mussel expansion in the late 2000s.

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References

- Adlerstein, S.A., Rutherford, E.S., Clapp, D., Clevenger, J.A., Johnson, J.E., 2007. Estimating seasonal movements of Chinook salmon in Lake Huron from efficiency analysis of coded wire tag recoveries in recreational fisheries. *N. Am. J. Fish. Manag.* 27, 792–803.
- Barbiero, R.P., Lesht, B.M., Warren, G.J., 2012. Convergence of trophic state and the lower food web in Lakes Huron Michigan and Superior. *J. Great Lakes Res.* 38, 368–380.
- Birkett, K., Lozano, S.J., Rudstam, L.G., 2015. Long-term trends in Lake Ontario's benthic macroinvertebrate community from 1994–2008. *Aquat. Ecosyst. Health Manag.* 18, 76–88.
- Bootsma, H.A., Rowe, M.D., Brooks, C.N., Vanderploeg, H.A., 2015. Commentary: The need for model development related to *Cladophora* and nutrient management in Lake Michigan. *J. Great Lakes Res.* 41 (Supplement 3), 7–15.
- Brenden, T.O., Brown, R.W., Ebener, M.P., Reid, K., Newcomb, T.J., 2013. Great Lakes commercial fisheries: historical overview and prognoses for the future. In: Taylor, W.W., Lynch, A.J., Leonard, N.J. (Eds.), *Great Lakes Fisheries Policy and Management: A Binational Perspective*, 2nd edition Michigan State University Press, East Lansing, pp. 339–397.
- Brooks, C., Grimm, A., Shuchman, R., Sayers, M., 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.
- Bundy, M.H., Vanderploeg, H.A., Lavrentyev, P.J., Kovalcik, P.A., 2005. The importance of microzooplankton versus phytoplankton to copepod populations during late winter and early spring in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 62, 2371–2385.
- Bunnell, D.B., Madenjian, C.P., Holuszko, J.D., Adams, J.V., French III, J.R.P., 2009. Expansion of *Dreissena* into offshore waters of Lake Michigan and potential impacts on fish populations. *J. Great Lakes Res.* 35, 74–80.
- Bunnell, D.B., Adams, J.V., Gorman, O.T., Madenjian, C.P., Riley, S.C., Roseman, E.F., Schaeffer, J.S., 2010. Population synchrony of a native fish across three Laurentian Great Lakes: evaluating the effects of dispersal and climate. *Oecologia* 162, 641–651.
- Bunnell, D.B., Barbiero, R.P., Ludsins, 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., Weidel, B.C., 2014. Changing ecosystem dynamics in the Laurentian Great Lakes: bottom-up and top-down regulation. *Bioscience* 64, 26–39.
- Bunnell, D.B., Davis, B.M., Chriscinske, M.A., Keeler, K.M., 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 (Supplement 3), 161–171.
- Carrick, H.J., Fahnenstiel, G.L., Stoermer, E.F., Wetzel, R.G., 1991. The importance of zooplankton–protozoan trophic couplings in Lake Michigan. *Limnol. Oceanogr.* 36, 1335–1345.
- Carrick, H.J., Butts, E., Daniels, D., Fehringer, M., Frazier, C., Fahnenstiel, G.L., Pothoven, S.A., Vanderploeg, H.A., 2015. Variation in the abundance of pico, nano, and microplankton in Lake Michigan: Historical and basin-wide comparisons. *J. Great Lakes Res.* 41 (Supplement 3), 66–74.
- Chipps, S.R., Bennett, D.H., 1996. Comparison of net mesh sizes for estimating abundance of the opossum shrimp *Mysis relicta* from vertical hauls. *N. Am. J. Fish. Manag.* 16, 689–692.
- Clapp, D.F., Dettmers, J.M., 2004. Yellow perch research and management in Lake Michigan: evaluating progress in a cooperative effort, 1997–2001. *Fisheries* 29 (11), 11–19.
- Clapp, D.F., Schneeberger, P.J., Jude, D.J., Madison, G., Pistis, C., 2001. Monitoring round goby (*Neogobius melanostomus*) population expansion in eastern and northern Lake Michigan. *J. Great Lakes Res.* 27, 335–341.

- Claramunt, R.M., Muir, A.M., Johnson, J., Sutton, T.M., 2010a. Spatio-temporal trends in the food habits of age-0 lake whitefish. *J. Great Lakes Res.* 36 (Supplement 1), 66–72.
- Claramunt, R.M., Muir, A.M., Sutton, T.M., Peeters, P.J., Ebener, M.P., Fitzsimons, J.D., Koops, M.A., 2010b. Measures of larval lake whitefish length and abundance as early predictors of year-class strength in Lake Michigan. *J. Great Lakes Res.* 36 (Supplement 1), 84–91.
- Claramunt, R.M., Madenjian, C.P., Clapp, D.F., 2012. Pacific salmonines in the Great Lakes basin. In: Taylor, W.W., Lynch, A.J., Leonard, N.J. (Eds.), *Great Lakes Fisheries Policy and Management: A Binational Perspective*, 2nd ed. Michigan State University Press, East Lansing, pp. 609–650.
- Collingsworth, P.D., Bunnell, D.B., Madenjian, C.P., Riley, S.C., 2014. Comparative recruitment dynamics of alewife and bloater in Lakes Michigan and Huron. *Trans. Am. Fish. Soc.* 143, 294–309.
- Crowder, L.B., Drenner, R.W., Kerfoot, W.C., McQueen, D.J., Mills, E.L., Sommer, U., Spencer, C.N., Vanni, M.J., 1988. Food web interactions in lakes. In: Carpenter, S.R. (Ed.), *Complex Interactions in Lake Communities*. Springer-Verlag, New York, pp. 141–160.
- Davis, B.M., Savino, J.F., Ogilvie, L.M., 2007. Diet niches of major forage fish in Lake Michigan. In: Jankun, M., Brzuzan, P., Hliwa, P., Luczynski, M. (Eds.), *Biology and Management of Coregonid Fishes – 2005, Advances in Limnology 60*. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, pp. 261–275.
- DeBruyne, R.L., Galarowicz, T.L., Claramunt, R.M., Clapp, D.F., 2008. Lake whitefish relative abundance, length-at-age, and condition in Lake Michigan as indicated by fishery-independent surveys. *J. Great Lakes Res.* 34, 235–244.
- Dettmers, J.M., Raffenberg, M.J., Weis, A.K., 2003. Exploring zooplankton changes in southern Lake Michigan: implications for yellow perch recruitment. *J. Great Lakes Res.* 29, 355–364.
- Dunlop, E.S., Riley, S.C., 2013. The contribution of cold winter temperatures to the 2003 alewife population collapse in Lake Huron. *J. Great Lakes Res.* 39, 682–689.
- Ebener, M.P., Bence, J.R., Newman, K.R., Schneeberger, P.J., 2005. Application of statistical catch-at-age models to assess lake whitefish stocks in the 1836 treaty-ceded waters of the upper Great Lakes. In: Mohr, L.C., Nalepa, T.F. (Eds.), *Proceedings of a Workshop on the Dynamics of Lake Whitefish (*Coregonus clupeaformis*) and the Amphipod *Diporeia* spp. in the Great Lakes*, Great Lakes Fishery Commission Technical Report 66, Ann Arbor, pp. 271–309.
- Ebener, M.P., Kinnunen, R.E., Schneeberger, P.J., Mohr, L.C., Hoyle, J.A., Peeters, P., 2008. Management of commercial fisheries for lake whitefish in the Laurentian Great Lakes of North America. In: Schechter, M.G., Taylor, W.W., Leonard, N.J. (Eds.), *International Governance of Fisheries Ecosystems: Learning From the Past, Finding Solutions for the Future*. American Fisheries Society, Bethesda, pp. 99–143.
- Eck, G.W., Brown Jr., E.H., 1985. Lake Michigan's capacity to support lake trout (*Salvelinus namaycush*) and other salmonines: an estimate based on the status of prey populations in the 1970s. *Can. J. Fish. Aquat. Sci.* 42, 449–454.
- Fahnenstiel, G., Nalepa, T., Pothoven, S., Carrick, H., Scavia, D., 2010a. Lake Michigan lower food web: long-term observations and *Dreissena* impact. *J. Great Lakes Res.* 36 (Supplement 3), 1–4.
- Fahnenstiel, G., Pothoven, S., Vanderploeg, H., Klarer, D., Nalepa, T., Scavia, D., 2010b. Recent changes in primary production and phytoplankton in the offshore region of southeastern Lake Michigan. *J. Great Lakes Res.* 36 (Supplement 3), 20–29.
- Feiner, Z.S., Bunnell, D.B., Höök, T.O., Madenjian, C.P., Warner, D.M., Collingsworth, P.D., 2015. Non-stationary recruitment dynamics of rainbow smelt: the influence of environmental variables and variation in size structure and length-at-maturation. *J. Great Lakes Res.* 41, 246–258.
- Fitzsimons, J.D., Brown, S.B., Honeyfield, D.C., Hnath, J.G., 1999. A review of early mortality syndrome (EMS) in Great Lakes salmonids: relationship with thiamine deficiency. *Ambio* 28, 9–15.
- Gal, G., Loew, E.R., Rudstam, L.G., Mohammadian, A.M., 1999. Light and diel vertical migration: spectral sensitivity and light avoidance by *Mysis relicta*. *Can. J. Fish. Aquat. Sci.* 56, 311–322.
- Grigorovich, I.A., Kornushin, A.V., Gray, D.K., Duggan, I.C., Colautti, R.I., MacIsaac, H.J., 2003. Lake Superior: an invasion coldspot? *Hydrobiologia* 499, 191–210.
- Hall, D.J., Cooper, W.E., Werner, E.E., 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol. Oceanogr.* 15, 939, 928.
- He, J.X., Bence, J.R., Madenjian, C.P., Pothoven, S.A., Dobiesz, N.E., Fielder, D.G., Johnson, J.E., Ebener, M.P., Cottrill, R.A., Mohr, L.C., Koproski, S.R., 2015. Coupling age-structured stock assessment and fish bioenergetics models: a system of time-varying models for quantifying piscivory patterns during the rapid trophic shift in the main basin of Lake Huron. *Can. J. Fish. Aquat. Sci.* 72, 7–23.
- Hondorp, D.W., Pothoven, S.A., 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, 588–601.
- Huo, B., Madenjian, C.P., Xie, C.X., Zhao, Y., O'Brien, T.P., Czesny, S.J., 2014. Age and growth of round gobies in Lake Michigan, with preliminary mortality estimation. *J. Great Lakes Res.* 40, 712–720.
- Jacobs, G.R., Madenjian, C.P., Bunnell, D.B., Holuszko, J.D., 2010. Diet of lake trout and burbot in Northern Lake Michigan during spring: evidence of ecological interaction. *J. Great Lakes Res.* 36, 312–317.
- Jacobs, G.R., Madenjian, C.P., Bunnell, D.B., Warner, D.M., Claramunt, R.M., 2013. Chinook salmon foraging patterns in a changing Lake Michigan. *Trans. Am. Fish. Soc.* 142, 362–372.
- Johengen, T.H., Vanderploeg, H.A., Liebig, J.R., 2013. Effects of algal composition, seston stoichiometry, and feeding rate on zebra mussel (*Dreissena polymorpha*) nutrient excretion in two Laurentian Great Lakes. In: Nalepa, T.F., Schloesser, D.W. (Eds.), *Quagga and Zebra Mussels: Biology, Impacts, and Control*, 2nd edition CRC Press, Boca Raton, pp. 445–459.
- Lake Michigan Committee, 2014. Lake Michigan yellow perch summit summary report Available online: http://glfc.org/lakecom/lmc/Lake_Michigan_Yellow_Perch_Summit_Report_2014.pdf.
- Lake Trout Working Group, 2014. 2013 Lake Michigan Lake Trout Working Group report. A Report to the Great Lakes Fishery Commission. Lake Michigan Committee, Windsor, Ontario (March 26, 2014).
- Lavrentyev, P.J., Vanderploeg, H.A., Franzé, G., Chacin, D.H., Liebig, J.R., 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 (Supplement 1), 95–105.
- Lehman, J.T., Bowers, J.A., Gensemer, R.W., Warren, G.J., Branstrator, D.K., 1990. *Mysis relicta* in Lake Michigan: abundances and relationships with their potential prey, *Daphnia*. *Can. J. Fish. Aquat. Sci.* 47, 977–983.
- Lehrer-Brey, G., Kornis, M.S., 2014. Winter distributional overlap facilitates lake whitefish (*Coregonus clupeaformis*) piscivory on invasive round gobies (*Neogobius melanostomus*) in Green Bay, Lake Michigan. *J. Freshw. Ecol.* 29, 153–156.
- Lesht, B.M., Barbiero, R.P., Warren, G.J., 2013. A band-ratio algorithm for retrieving open-lake chlorophyll values from satellite observations of the Great Lakes. *J. Great Lakes Res.* 39, 138–152.
- Madenjian, C.P., Bunnell, D.B., 2008. Depth distribution dynamics of the sculpin community in Lake Michigan. *Trans. Am. Fish. Soc.* 137, 1346–1357.
- Madenjian, C.P., Fahnenstiel, G.L., Johengen, T.H., Nalepa, T.F., Vanderploeg, H.A., Fleischer, G.W., Schneeberger, P.J., Benjamin, D.M., Smith, E.B., Bence, J.R., Rutherford, E.S., Lavis, D.S., Robertson, D.M., Jude, D.J., Ebener, M.P., 2002. Dynamics of the Lake Michigan food web, 1970–2000. *Can. J. Fish. Aquat. Sci.* 59, 736–753.
- Madenjian, C.P., Holuszko, J.D., Desorcie, T.J., 2003. Growth and condition of alewives in Lake Michigan, 1984–2001. *Trans. Am. Fish. Soc.* 132, 1104–1116.
- Madenjian, C.P., Hondorp, D.W., Desorcie, T.J., Holuszko, J.D., 2005a. Sculpin community dynamics in Lake Michigan. *J. Great Lakes Res.* 31, 267–276.
- Madenjian, C.P., Höök, T.O., Rutherford, E.S., Mason, D.M., Croley II, T.E., Szalai, E.B., Bence, J.R., 2005b. Recruitment variability of alewives in Lake Michigan. *Trans. Am. Fish. Soc.* 134, 218–230.
- Madenjian, C.P., Pothoven, S.A., Dettmers, J.M., 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, 891–902.
- Madenjian, C.P., O'Gorman, R., Bunnell, D.B., Argyle, R.L., Roseman, E.F., Warner, D.M., Stockwell, J.D., Stapanian, M.A., 2008. Adverse effects of alewives on Laurentian Great Lakes fish communities. *N. Am. J. Fish. Manag.* 28, 263–282.
- Madenjian, C.P., Bunnell, D.B., Gorman, O.T., 2010a. Ninespine stickleback abundance in Lake Michigan increases after invasion of dreissenid mussels. *Trans. Am. Fish. Soc.* 139, 11–20.
- Madenjian, C.P., Pothoven, S.A., Schneeberger, P.J., Ebener, M.P., Mohr, L.C., Nalepa, T.F., Bence, J.R., 2010b. Dreissenid mussels are not a “dead end” in Great Lakes food webs. *J. Great Lakes Res.* 36 (Supplement 1), 73–77.
- Madenjian, C.P., Bunnell, D.B., Desorcie, T.J., Kostich, M.J., Armenio, P.M., Adams, J.V., 2014. Status and trends of prey fish populations in Lake Michigan, 2013. Compiled Reports to the Great Lakes Fishery Commission of the Annual Bottom Trawl and Acoustics Surveys, 2013. Great Lakes Fishery Commission, Ann Arbor, pp. 46–61.
- Marsden, J.E., 1992. The zebra mussel invasion. *Aquaticus* 23, 19–27.
- Marsden, J.E., Robillard, S.R., 2004. Decline of yellow perch in southwestern Lake Michigan, 1987–1997. *N. Am. J. Fish. Manag.* 24, 952–966.
- Menge, B.A., 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores? *Ecology* 73, 755–765.
- Mida, J.L., Scavia, D., Fahnenstiel, G.L., Pothoven, S.A., Vanderploeg, H.A., Dolan, D.M., 2010. Long-term and recent changes in southern Lake Michigan water quality with implications for present trophic status. *J. Great Lakes Res.* 36 (Supplement 3), 42–49.
- Mosley, C.M., Bootsma, H.A., 2015. Phosphorus cycling and grazing by profunda quagga mussels (*Dreissena rostriformis bugensis*) in Lake Michigan. *J. Great Lakes Res.* 41 (Supplement 3), 38–48.
- Muir, A.M., Sutton, T.M., Arts, M.T., Claramunt, R.M., Ebener, M.P., Fitzsimons, J.D., Johnson, T.B., Kinnunen, R.E., Koops, M.A., Sepúlveda, M.S., 2010. Does condition of lake whitefish spawners affect physiological condition of juveniles? *J. Great Lakes Res.* 36 (Supplement 1), 92–99.
- Nalepa, T.F., Hartson, D.J., Fanslow, D.L., Lang, G.A., Lozano, S.J., 1998. Declines in benthic macroinvertebrate populations in southern Lake Michigan, 1980–1993. *Can. J. Fish. Aquat. Sci.* 55, 2402–2413.
- Nalepa, T.F., Fanslow, D.L., Lang, G.A., 2000. Trends in benthic macroinvertebrate populations in southern Lake Michigan over the past several decades. *Int. Ver. Theor. Angew. Limnol. Verh.* 27, 2540–2545.
- Nalepa, T.F., Schloesser, D.W., Pothoven, S.A., Hondorp, D.W., Fanslow, D.L., Tuchman, M.L., Fleischer, G.W., 2001. First finding of the amphipod *Echinogammarus ischnus* and the mussel *Dreissena bugensis* in Lake Michigan. *J. Great Lakes Res.* 27, 384–391.
- Nalepa, T.F., Mohr, L.C., Henderson, B.A., Madenjian, C.P., Schneeberger, P.J., 2005. Lake whitefish and *Diporeia* spp. in the Great Lakes: an overview. In: Mohr, L.C., Nalepa, T.F. (Eds.), *Proceedings of a Workshop on the Dynamics of Lake Whitefish (*Coregonus clupeaformis*) and the Amphipod *Diporeia* spp. in the Great Lakes*, Great Lakes Fishery Commission Technical Report 66, Ann Arbor, pp. 3–19.
- Nalepa, T.F., Fanslow, D.L., Lang, G.A., 2009. Transformation of the offshore benthic community in Lake Michigan: recent shift from the native amphipod *Diporeia* spp. to the invasive mussel *Dreissena rostriformis bugensis*. *Freshw. Biol.* 54, 466–479.
- Nalepa, T.F., Fanslow, D.L., Pothoven, S.A., 2010. Recent changes in density, biomass, recruitment, size structure, and nutritional state of *Dreissena* populations in southern Lake Michigan. *J. Great Lakes Res.* 36 (Supplement 3), 5–19.
- Nalepa, T.F., Pavlova, V., Wong, W.H., Janssen, J., Houghton, J.S., Mabrey, K., 2013. Variation in the quagga mussel (*Dreissena rostriformis bugensis*) with emphasis on the deepwater morphotype in Lake Michigan. In: Nalepa, T.F., Schloesser, D.W. (Eds.), *Quagga*

- and Zebra Mussels: Biology, Impacts, and Control, 2nd edition CRC Press, Boca Raton, pp. 315–329.
- Nalepa, T.F., Dermott, R., Madenjian, C., Schloesser, S.W., 2014a. Dreissenid mussels – zebra and quagga mussels. Environment Canada and the U. S. Environmental Protection Agency, State of the Great Lakes 2011, Cat No. En161-3/1-2011E-PDF, EPA 950-R-13-002, pp. 226–234 (Available at <http://binational.net>).
- Nalepa, T.F., Fanslow, D.L., Lang, G.A., Mabrey, K., Rowe, M., 2014b. Lake-wide benthic surveys in Lake Michigan in 1994–1995, 2000, 2005, and 2010: abundances of the amphipod *Diporeia* spp. and abundances and biomass of mussels *Dreissena polymorpha* and *Dreissena rostriformis bugensis*. NOAA Technical Memorandum GLERL-164, Ann Arbor.
- O'Brien, T.P., Taylor, W.W., Roseman, E.F., Madenjian, C.P., Riley, S.C., 2014. Ecological factors affecting rainbow smelt recruitment in the main basin of Lake Huron, 1976–2010. *Trans. Am. Fish. Soc.* 143, 784–795.
- O'Gorman, R., Schneider, C.P., 1986. Dynamics of alewives in Lake Ontario following a mass mortality. *Trans. Am. Fish. Soc.* 115, 1–14.
- Pangle, K.L., Peacor, S.D., 2006. Non-lethal effect of the invasive predator *Bythotrephes longimanus* on *Daphnia mendotae*. *Freshw. Biol.* 51, 1070–1078.
- Pothoven, S.A., Fahnenstiel, G.L., 2013. Recent change in summer chlorophyll *a* dynamics of southeastern Lake Michigan. *J. Great Lakes Res.* 39, 287–294.
- Pothoven, S.A., Fahnenstiel, G.L., 2015. Spatial and temporal trends in zooplankton assemblages along a nearshore to offshore transect in southeastern Lake Michigan from 2007–2012. *J. Great Lakes Res.* 41 (Supplement 3), 95–103.
- Pothoven, S.A., 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. Manag.* 28, 308–320.
- Pothoven, S.A., Madenjian, C.P., 2013. Increased piscivory by lake whitefish in Lake Huron. *N. Am. J. Fish. Manag.* 33, 1194–1202.
- Pothoven, S.A., Nalepa, T.F., Schneeberger, P.J., 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. Manag.* 21, 876–883.
- Pothoven, S.A., Fahnenstiel, G.L., Vanderploeg, H.A., 2004. Spatial distribution, biomass and population dynamics of *Mysis relicta* in Lake Michigan. *Hydrobiologia* 522, 291–299.
- Pothoven, S.A., Vanderploeg, H.A., Cavaletto, J.F., Krueger, D.M., Mason, D.M., Brandt, S.B., 2007. Alewife planktivory controls the abundance of two invasive predatory cladocera in Lake Michigan. *Freshw. Biol.* 52, 561–573.
- Pothoven, S.A., Fahnenstiel, G.L., Vanderploeg, H.A., 2010. Temporal trends in *Mysis relicta* abundance, production, and life-history characteristics in southeastern Lake Michigan. *J. Great Lakes Res.* 36 (Supplement 3), 60–64.
- Pothoven, S.A., Hondorp, D.W., 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. Freshw. Fish* 20, 14–22.
- Pothoven, S.A., Bunnell, D.B., Madenjian, C.P., Gorman, O.T., Roseman, E.F., 2012a. Energy density of bloaters in the upper Great Lakes. *Trans. Am. Fish. Soc.* 141, 772–780.
- Pothoven, S.A., Fanslow, D.L., Fahnenstiel, G.L., 2012b. Lipid content of *Mysis diluviana* in the offshore region of southeastern Lake Michigan in 2009–2010. *J. Great Lakes Res.* 38, 561–568.
- Redman, R.A., Czesny, S.J., Dettmers, J.M., Weber, M.J., Makauskas, D., 2011. Old tales in recent context: current perspective on yellow perch recruitment in Lake Michigan. *Trans. Am. Fish. Soc.* 140, 1277–1289.
- Rennie, M.D., Sprules, W.G., Johnson, T.B., 2009. Resource switching in fish following a major food web disruption. *Oecologia* 159, 789–802.
- Ridgway, M.S., Hurley, D.A., Scott, K.A., 1990. Effects of winter temperature and predation on the abundance of alewife (*Alosa pseudoharengus*) in the Bay of Quinte, Lake Ontario. *J. Great Lakes Res.* 16, 11–20.
- Riley, S.C., Roseman, E.F., Chrisinske, M.A., Tucker, T.R., Ross, J.E., Armenio, P.M., Watson, N., Woelmer, W., 2014. Status and trends of the Lake Huron offshore demersal fish community, 1976–2013. Compiled Reports to the Great Lakes Fishery Commission of the Annual Bottom Trawl and Acoustics Surveys, 2013. Great Lakes Fishery Commission, Ann Arbor, pp. 88–100.
- Rogers, M.W., Bunnell, D.B., Madenjian, C.P., Warner, D.M., 2014. Lake Michigan offshore ecosystem structure and food web changes from 1987 to 2008. *Can. J. Fish. Aquat. Sci.* 71, 1072–1086.
- Rudstam, L.G., Binkowski, F.P., Miller, M.A., 1994. A bioenergetics model for analysis of food consumption patterns of bloater in Lake Michigan. *Trans. Am. Fish. Soc.* 123, 344–357.
- Schelske, C.L., Stoermer, E.F., 1971. Eutrophication, silica, and predicted changes in algal quality in Lake Michigan. *Science* (Washington, D.C.) 173, 423–424.
- Schelske, C.L., Rothman, E.D., Stoermer, E.F., Santiago, M.A., 1974. Responses of phosphorus limited Lake Michigan phytoplankton to factorial enrichments with nitrogen and phosphorus. *Limnol. Oceanogr.* 19, 409–419.
- Scott, W.B., Crossman, E.J., 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin 184.
- Shroyer, S.M., McComish, T.S., 2000. Relationship between alewife abundance and yellow perch recruitment in southern Lake Michigan. *N. Am. J. Fish. Manag.* 20, 220–225.
- Stanley, J.G., Colby, P.J., 1971. Effects of temperature on electrolyte balance and osmoregulation in the alewife (*Alosa pseudoharengus*) in fresh and sea water. *Trans. Am. Fish. Soc.* 100, 624–638.
- Strayer, D.L., Hattala, K.A., Kahnle, A.W., 2004. Effects of an invasive bivalve (*Dreissena polymorpha*) on fish in the Hudson River estuary. *Can. J. Fish. Aquat. Sci.* 61, 924–941.
- Strayer, D.L., Cole, J.J., Findlay, S.E.G., Fischer, D.T., Gephart, J.A., Malcom, H.M., Pace, M.L., Rosi-Marshall, E.J., 2014a. Decadal-scale change in a large-river ecosystem. *Bioscience* 64, 496–510.
- Strayer, D.L., Hattala, K.A., Kahnle, A.W., Adams, R.D., 2014b. Has the Hudson River fish community recovered from the zebra mussel invasion along with its forage base? *Can. J. Fish. Aquat. Sci.* 71, 1146–1157.
- Tang, H., Vanderploeg, H.A., Johengen, T.H., Liebig, J.R., 2014. Quagga mussel (*Dreissena rostriformis bugensis*) selective feeding of phytoplankton in Saginaw Bay. *J. Great Lakes Res.* 40 (Supplement 1), 83–94.
- Tsehaye, I., Jones, M.L., Bence, J.R., Brenden, T.O., Madenjian, C.P., Warner, D.M., 2014a. 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, 627–644.
- Tsehaye, I., Jones, M.L., Brenden, T.O., Bence, J.R., Claramunt, R.M., 2014b. Changes in the salmonine community of Lake Michigan and their implications for predator–prey balance. *Trans. Am. Fish. Soc.* 143, 420–437.
- Turschak, B.A., Bunnell, D., Czesny, S., Höök, T.O., Janssen, J., Warner, D., Bootsma, H.A., 2014. Nearshore energy subsidies support Lake Michigan fishes and invertebrates following major changes in food web structure. *Ecology* 95, 1243–1252.
- Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., Mills, E.L., Holeck, K.T., Liebig, J.R., Grigorovich, I.A., 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., Pothoven, S.A., 2010. *Dreissena* and the disappearance of the spring phytoplankton bloom in Lake Michigan. *J. Great Lakes Res.* 36 (Supplement 3), 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., 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.
- Vanderploeg, H.A., Pothoven, S.A., Krueger, D., Mason, D.M., Liebig, J.R., Cavaletto, J.F., Ruberg, S.A., Lang, G.A., Ptáčiková, R., 2015. Spatial and predatory interactions of visually preying nonindigenous zooplankton and fish in Lake Michigan during midsummer. *J. Great Lakes Res.* 41 (Supplement 3), 125–142.
- Warner, D.M., Kiley, C.S., Claramunt, R.M., Clapp, D.F., 2008. The influence of alewife year-class strength on prey selection and abundance of age-1 Chinook salmon in Lake Michigan. *Trans. Am. Fish. Soc.* 137, 1683–1700.
- Warner, D.M., Farha, S.H., O'Brien, T.P., Ogilvie, L., Claramunt, R.M., Hanson, D., 2014. Status of pelagic prey fishes in Lake Michigan, 2013. Compiled Reports to the Great Lakes Fishery Commission of the Annual Bottom Trawl and Acoustics Surveys, 2013. Great Lakes Fishery Commission, Ann Arbor, pp. 62–73.
- Wells, L., 1980. Food of Alewives, Yellow Perch, Spottail Shiners, Trout-perch, and Slimy and Fourhorn Sculpins in Southeastern Lake Michigan. U. S. Fish and Wildlife Service Technical Paper 98.
- Wells, L., McLain, A.L., 1973. Lake Michigan – man's effects on native fish stocks and other biota. Great Lakes Fishery Commission Technical Report 20.
- Wilberg, M.J., Bence, J.R., Eggold, B.T., Makauskas, D., Clapp, D.F., 2005. Yellow perch dynamics in southwestern Lake Michigan during 1986–2002. *N. Am. J. Fish. Manag.* 25, 1130–1152.
- Williams, M.C., 2012. Spatial, Temporal, and Cohort-related Patterns in the Contribution of Wild Chinook Salmon (*Oncorhynchus tshawytscha*) to Total Chinook Harvest in Lake Michigan (Thesis) Michigan State University.
- Yousef, F., Kerfoot, W.C., Shuchman, R., Fahnenstiel, G., 2014. Bio-optical properties and primary production of Lake Michigan: insights from 13-years of SeaWiFS imagery. *J. Great Lakes Res.* 40, 317–324.