Lake Michigan Committee
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Status and Trends of Prey Fish Populations in Lake Michigan, 2018[1,2,3]

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Abstract
The U.S. Geological Survey Great Lakes Science Center has conducted lake-wide surveys of the fish community in Lake Michigan each fall since 1973 using standard 12 m bottom trawls towed along contour at depths of 9 to 110 m at each of seven index transects. The survey provides relative abundance and biomass estimates between the 5 m and 114 m depth contours of the lake for prey fish populations, as well as for burbot and yellow perch. The resulting data are used to estimate various population parameters that are in turn used by state and tribal agencies in managing Lake Michigan fish stocks. All seven established index transects of the survey were completed in 2018, although depths 64 m and greater offshore of Frankfort could not be completed due to excessive dreissenid mussel biomass on our multiple tow attempts. Mean biomass of alewives in 2018 was estimated at 0.54 kg/ha, which was the highest value since 2013, but still only 6.7% of the long-term average (7.96 kg/ha). Age distribution of alewives remained truncated with no alewife age exceeding 5 years. Bloater biomass was 2.60 kg/ha in 2018, relatively unchanged from 2017, but still only 14% of the long-term average. Round goby biomass was 1.25 kg/ha in 2018, the 3rd largest estimate in the time series and 62% higher than the average since they were first sampled in 2003. Rainbow smelt biomass was 0.45 kg/ha, which was the highest since 2006 but only 21% of the long-term average. Likewise, deepwater sculpin biomass was 1.30 kg/ha in 2018, which was the highest since 2007 but only 20% of the long-term average. Slimy sculpin biomass was only 0.07 kg/ha in 2018, and similar to the very low levels estimated since 2012 and only 17% of the long-term average. Ninespine stickleback remained very rare in 2018 (0.004 kg/ha), and only 1% of the long-term average. Overall, the total prey fish biomass (sum of alewife, bloater, rainbow smelt, deepwater sculpin, slimy sculpin, round goby, and ninespine stickleback) in 2018 was 6.22 kg/ha, roughly 65% greater than in 2017 but still only 17% of the long-term average. With respect to other species of interest, burbot biomass was only 0.04 kg/ha in 2018 (18% of the long-term average) and no age-0 yellow perch were caught in 2018, indicating a weak year-class.

[1] Presented at Great Lakes Fishery Commission, Lake Michigan Committee Meeting, Ypsilanti, MI on March 25, 2019

[2] Data release available online. Please use the following citation for the data. "U.S. Geological Survey, Great Lakes Science Center, 2019, Great Lakes Research Vessel Operations 1958-2018. (ver. 3.0, April 2019): U.S. Geological Survey data release, https://doi.org/10.5066/F75M63X0."

[3] All GLSC sampling and handling of fish during research are carried out in accordance with guidelines for the care and use of fishes by the American Fisheries Society (http://fisheries.org/docs/wp/Guidelines-for-Use-of-Fishes.pdf).

The U.S. Geological Survey Great Lakes Science Center (GLSC) has conducted daytime bottom trawl surveys in Lake Michigan during the fall annually since 1973. Estimates from the 1998 survey are not reported because the trawls were towed at non-standard speeds. From these surveys, the relative abundances of the prey fish populations are measured, and estimates of lake-wide biomass available to the bottom trawls (for the region of the main basin between the 5 m and 114 m depth contours) can be generated (Hatch et al. 1981; Brown and Stedman 1995). Such estimates are critical to fisheries managers making decisions on stocking and harvest rates of salmonines and allowable harvests of fish by commercial fishing operations.

The basic unit of sampling in our surveys is a 10 min tow using a bottom trawl (12 m headrope, 25 to 45 mm bar mesh in net body, 6.4 mm bar mesh in cod end) dragged on contour at 9 m (5 fathom) depth increments. At most survey transects, towing depths range from 9 or 18 m to 110 m. Depths shallower than 9 m cannot be sampled at most sites because the draft of the research vessel (i.e., vertical distance between the waterline and the bottom of the hull) prevents safe navigation while trawling. In 2013, however, we began adding tows at deeper depths (i.e., 128 m) to assess the extent to which populations of deepwater sculpins and bloater have migrated outside of our traditional survey range. Since then, we have sampled depths deeper than 110 m (e.g., 128-151 m) for a total of 30 non-standard "deep" tows. To maintain time series consistency, these tows are not included in our time series trends but are specifically noted for some species and included in some maps showing biomass for each tow (Figures 3, 6, 8, 10, 12).

Ages were estimated for alewives (*Alosa pseudoharengus*) using otoliths from our bottom trawl catches (Madenjian et al. 2003). Although our surveys have included as many as nine index transects in any given year, we have consistently conducted the surveys at seven transects, and data from those seven transects are reported herein. These transects are situated off Manistique, Frankfort, Ludington, and Saugatuck, Michigan; Waukegan, Illinois; and Port Washington and Sturgeon Bay, Wisconsin (Figure 1). All seven transects were completed in 2018, although depths 64 m and greater offshore of Frankfort could not be completed due to excessive dreissenid mussel biomass on our multiple tow attempts.

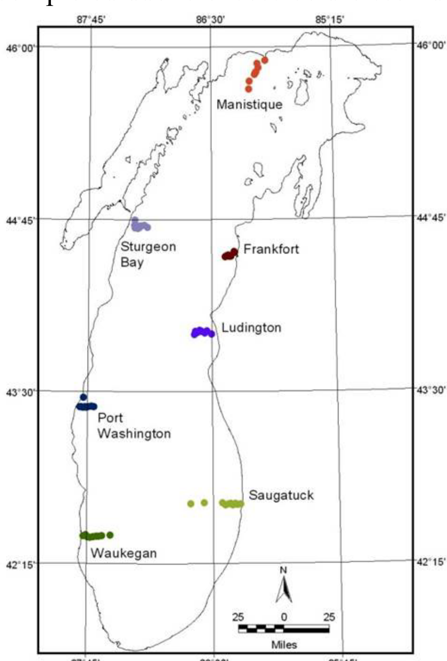

Figure 1. Established sampling locations for GLSC bottom trawls in Lake Michigan.

Indices of biomass or numeric density of fishes vulnerable to the bottom trawl require accurate measures of (1) the surface areas that represent the depths sampled and (2) bottom area swept by the trawl. A complete Geographical Information System (GIS) based on depth soundings at 2-km intervals in Lake Michigan was developed as part of the acoustics study performed by Argyle et al. (1998). This GIS database was used to estimate the surface area for each individual depth zone surveyed by the bottom trawls. In June 2009, we used trawl mensuration gear designed to provide real-time data on net configuration. These results provided specific correction factors for width of the net and actual time on bottom when sampling at 2.1 mph (Madenjian et al. 2010a) that were applied to all years through 2015. The R/V Arcticus replaced the R/V Grayling in 2015. In June 2016, we used mensuration gear to estimate net configuration on the R/V Arcticus, which has a wider beam than the R/V Grayling. A new regression to adjust the width of the net with bottom depth has been used since 2016 (Bunnell et al. 2017). From 2016 to present, we also began directly estimating time on bottom for each tow with a sensor that is attached to the head rope that estimates sensor depth every second. Thus, since 2016, the head-rope sensor and the updated net-width regression relationship are used to estimate area swept by the bottom trawl during each tow.

We estimate both numeric (fish per hectare [ha]) and biomass (kg/ha) density, although we display graphical trends mostly in biomass for brevity. A weighted mean density over the entire range of depths sampled (within the 5 m to 114 m depth contours) was estimated by first calculating mean density for each depth zone, and then weighting mean density for each depth zone by the proportion of lake surface area assigned to that depth zone. Standard error (SE) of mean density was estimated by weighting the variances of fish density in each of the depth zones by the appropriate weight (squared proportion of surface area in the depth zone), averaging the weighted variances over all depth zones, and taking the square root of the result.

NUMERIC AND BIOMASS DENSITY BY SPECIES

By convention, we classify "adult" prey fish as age 1 or older, based on total length (TL): alewives ≥ 100 mm, rainbow smelt (*Osmerus mordax*) ≥ 90 mm, bloaters ≥ 120 mm, and yellow perch (*Perca flavescens*) ≥ 100 mm. We assume all fish smaller than the above length cut-offs are age-0, and this assumption is aided by age-length distributions for the case of alewife. Bloaters are also aged but these data are not provided in this report. Catches of age-0 alewife are not reliable indicators of future year-class strength (Madenjian et al. 2005a), because their position in the water column makes them less vulnerable to bottom trawls. Catches of age-0 bloater, though biased low, can be used as an index of relative abundance given the positive correlation between density of age-0 bloater and density of age-3 bloater (the age at which catch curves reveal full recruitment to our gear, Bunnell et al. 2006a, 2010). Catch of age-0 (< 100 mm TL) yellow perch is likely a good indicator of year-class strength, given that large catches in the bottom trawl during the 1980s corresponded to the strong yellow perch fishery. At the end of this report, we also present densities of age-0 yellow perch and other bottom-dwelling species such as burbot (*Lota lota*) that are not necessarily "prey fish" but are caught in sufficient numbers to index. Unfortunately lake whitefish (*Coregonus clupeaformis*) are only rarely sampled in our trawl and the resultant trends are not meaningful. Since 1999, dreissenid mussels sampled in the trawl have also been sorted and weighed (but not counted), and their biomass is reported in the Appendix.

<u>Alewife</u> – Since its establishment in the 1950s, the alewife has become a key member of the fish community. As a predator on larval fish, adult alewife can depress recruitment of native fishes, including burbot, deepwater sculpin (*Myoxocephalus thompsonii*), emerald shiner (*Notropis atherinoides*), lake trout (*Salvelinus namaycush*), and yellow perch (Smith 1970; Wells and McLain 1973; Madenjian et al. 2005b, 2008; Bunnell et al. 2006b). Additionally, alewife has remained the most important constituent of salmonine diet in Lake Michigan for the last 45 years (Jude et al. 1987; Stewart and Ibarra 1991; Warner et al. 2008; Jacobs et al. 2013). Most of the alewives consumed by salmonines in Lake Michigan are eaten by Chinook salmon (*Oncorhynchus tshawytscha*, Madenjian et al. 2002; Tsehaye et al. 2014). A commercial harvest was established in Wisconsin waters of Lake Michigan in the 1960s to make use of the then extremely abundant alewife that had become a nuisance and health hazard along the lakeshore. In 1986, a quota was implemented, and as a result of these restrictions, the estimated annual alewife harvest declined from about 7,600 metric tons in 1985 to an incidental harvest of only 12 metric tons after 1990 (Mike Toneys, Wisconsin Department of Natural Resources, Sturgeon Bay, personal communication). Lake Michigan currently has no commercial fishery for alewives.

According to the bottom trawl survey results in 2018, adult alewife biomass density equaled 0.54 kg/ha (Figure 2a) and numeric density equaled 29.4 fish/ha (Figure 2b). For the 2nd time in 4 years, no age-0 alewives were captured during the survey, indicating these fish occupy the bottom of the lake during the day less than in previous years. Alewives were caught at all ports other than Saugatuck during 2018 (Figure 3), and the average densities were influenced by a substantial catch of nearly 46 kg/ha (1776 alewife) at the 46 m Sturgeon Bay site (Figure 3).

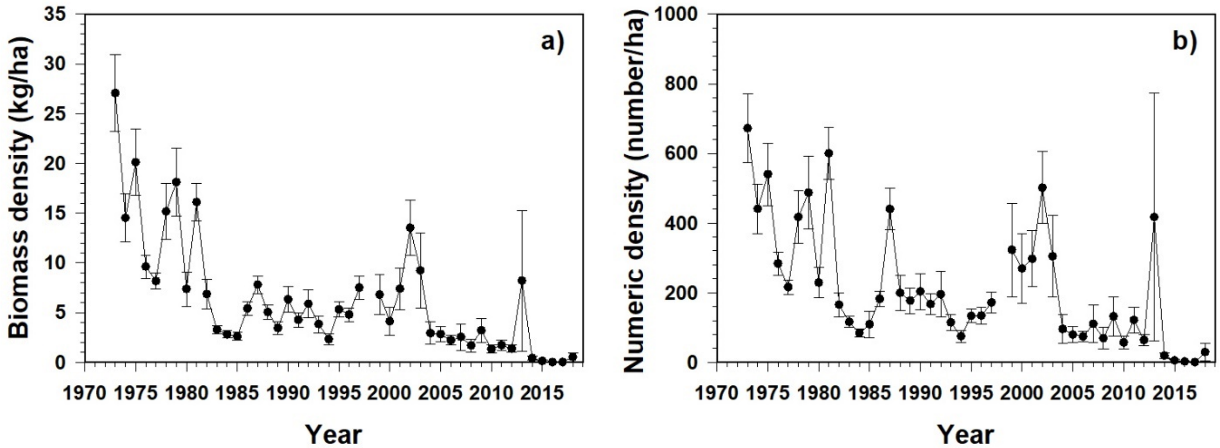

Figure 2. Density of adult alewives as biomass (a) and number (b) per ha (+/- standard error) in Lake Michigan, 1973-2018.

Since 2013, alewives have been sampled in 15 of the 30 non-standard "deep" tows. However, mean alewife biomass density at sites 128 m and deeper was only 0.12 kg/ha, which was lower than the mean of all other depths except 27 m. Over this time period, the depth with the highest mean alewife biomass (e.g., 12.57 kg/ha) was 9 m. Thus, these data do not support a hypothesis that the bottom trawl survey has underestimated alewife biomass because alewife have shifted to deeper waters than typically sampled by the bottom trawl survey (i.e., > 110 m).

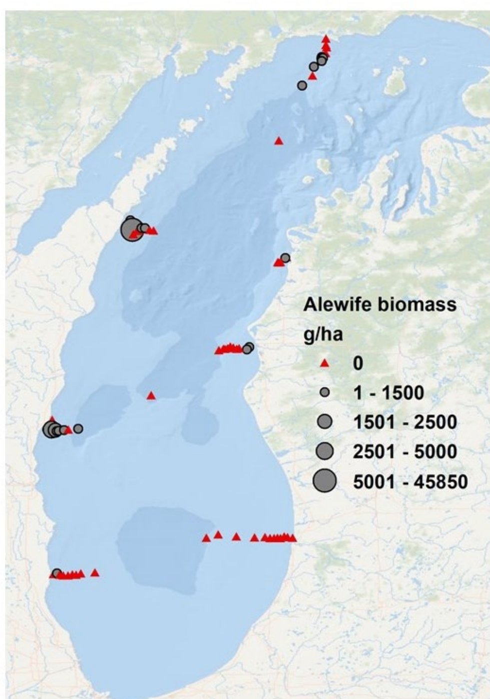

Figure 3. Scaled-symbol plot showing the biomass of alewife sampled during each of the 2018 bottom trawl sites.

The long-term temporal trends in adult alewife biomass, as well as in alewife recruitment to age 3, in Lake Michigan are attributable to consumption of alewives by salmonines (Madenjian et al. 2002, 2005a; Tsehaye et al. 2014). Several factors have likely maintained this high predation pressure in the 2000s including: a relatively high abundance of wild Chinook salmon in Lake Michigan (Williams 2012; Tsehaye et al. 2014), increased migration of Chinook salmon from Lake Huron in search of alewives (Adlerstein et al. 2007; Clark et al. 2017), increased importance of alewives in the diet of Chinook salmon in Lake Michigan (Jacobs et al. 2013), a decrease in the energy density of adult alewives (Madenjian et al. 2006), and increases in lake trout abundance due to increased rates of stocking and natural reproduction (FWS/GLFC 2017; Lake Michigan LTWG 2017). As adults, there is no evidence for starvation among alewives despite declining prey resources. The average weight of a 175 mm alewife has actually trended slightly upward ($F_{1,21}$=4.81; P = 0.04) since 1996 when alewife condition dropped to its lowest level (Madenjian et al. 2003).

In 2018, 189 "adult" (i.e., >100 TL) alewives from the survey were aged to construct an age-length distribution. Similar to 2017, the age composition was dominated by age-1 (33%, 2017 year-class) and age-2 (62%, 2016 year-class) fish. Age-3 (2015 year-class), age-4 (2014 year-class), and age-5 (2013 year-class) fish represented 4%, 0.4% and 0.3%, respectively, of the remaining adults, (Figure 4). No alewives older than age 5 were caught in the survey; thus, the recent trend of age truncation in the alewife population continued through 2018. Likewise, no alewives older than age 5 were caught in the acoustics survey in 2018. Prior to 2009, age-8 alewives were routinely captured in the bottom trawl survey.

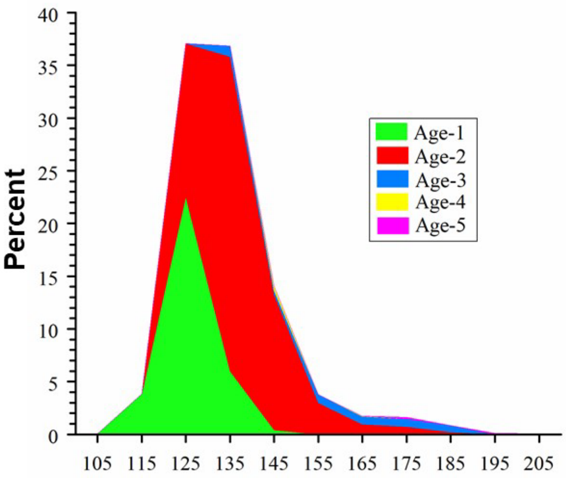

Figure 4. Age-length distribution of alewives > 100 mm total length caught in the bottom trawls in Lake Michigan, 2018.

Both the acoustic and bottom trawl survey time series for total alewife biomass are in general agreement, indicating that biomass during 2004-2018 was relatively low compared with biomass during 1994-1996 (Warner et al. 2019). Across the 22 years, however, the acoustic estimate has been higher than the bottom trawl survey estimate 82% of the time. The discrepancy between the two estimates has increased between 2014 and 2018, with the acoustic estimate ranging from 10 to nearly 200 times higher during this 4-year period. In 2018, the estimate for adult alewife biomass in the acoustic survey was 10 times higher than the estimate for the bottom trawl survey. Given that alewife historically have not fully recruited to the bottom trawl until age 3 (Madenjian et al. 2006) and the majority of the alewife population we sampled was age-1 and 2, it is not surprising that the acoustic survey estimates a higher number of alewives. Thus, the recent higher discrepancy between the two surveys may partially be explained by the alewife population becoming younger in recent years.

Bloater - Bloaters are eaten by salmonines in Lake Michigan, but are far less prevalent in salmonine diets

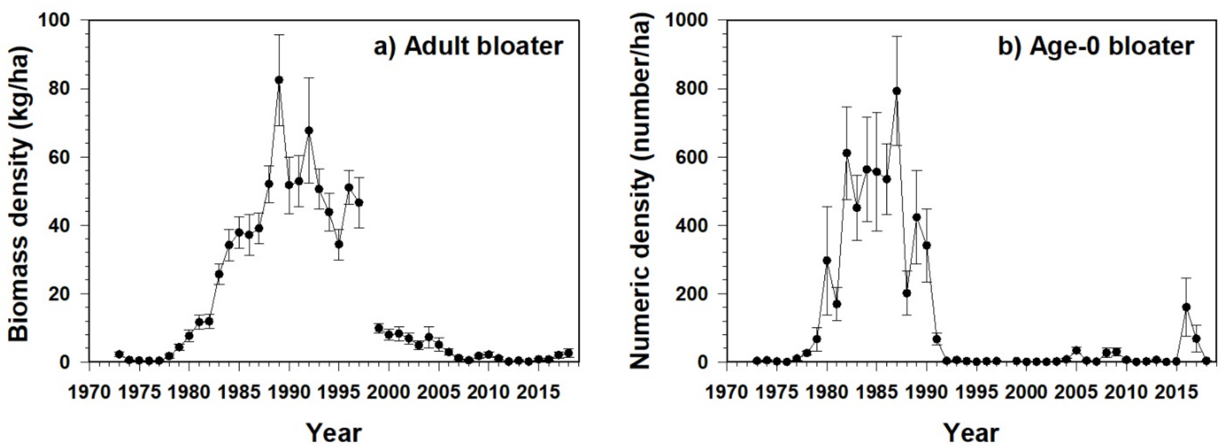

Figure 5. Density per ha (+/- standard error) of adult bloater (a, in terms of biomass) and age-0 bloater (b, in terms of number) in Lake Michigan, 1973-2018.

than alewives (Warner et al. 2008; Jacobs et al. 2010, 2013). For large (≥ 600 mm) lake trout, over 30% of the diets offshore of Saugatuck and on Sheboygan Reef were composed of adult bloaters during 1994-1995, although adult bloaters were a minor component of lake trout diet at Sturgeon Bay (Madenjian et al. 1998). For Chinook salmon, the importance of bloater (by wet weight) in the diets has declined between 1994-

1995 and 2009-2010. For small (< 500 mm) Chinook salmon the proportion declined from 9% to 6% and for large Chinook salmon the proportion declined from 14% to <1% (Jacobs et al. 2013). The bloater population in Lake Michigan also supports a valuable commercial fishery, although its yield has declined sharply since the late 1990s.

Adult bloater biomass density in our survey has been < 10 kg/ha since 1999 (Figure 5a). Nevertheless, adult bloater biomass has exceeded 2 kg/ha since 2017, a nearly fivefold increase over the record-low levels measured from 2012-2016. This increase in adult bloater biomass was attributable to the relatively strong 2016 and 2017 year-classes (Figure 5b). In 2018, however, densities of age-0 bloater were only 3 fish/ha, more comparable to the low levels of recruitment observed from 2010-2015. Bloaters were sampled in all ports in 2018 except Frankfort where deeper tows could not be completed (Figure 6). The highest mean biomass was at Port Washington at 55 and 64 m.

Since 2013, bloaters have been sampled in 11 of 30 deep tows. However, mean bloater biomass density at sites 128 m and deeper was only 0.15 kg/ha, which was lower than the mean biomass of each of the depths from 46 to 110 m. The depth with the highest mean biomass since 2013 was 64 m (e.g., 3.89 kg/ha). Thus, the data do not support a hypothesis that the bottom trawl survey has underestimated bloater biomass because it does not sample a large proportion of the bloater population that occupies the bottom of the lake in depths deeper than 110 m.

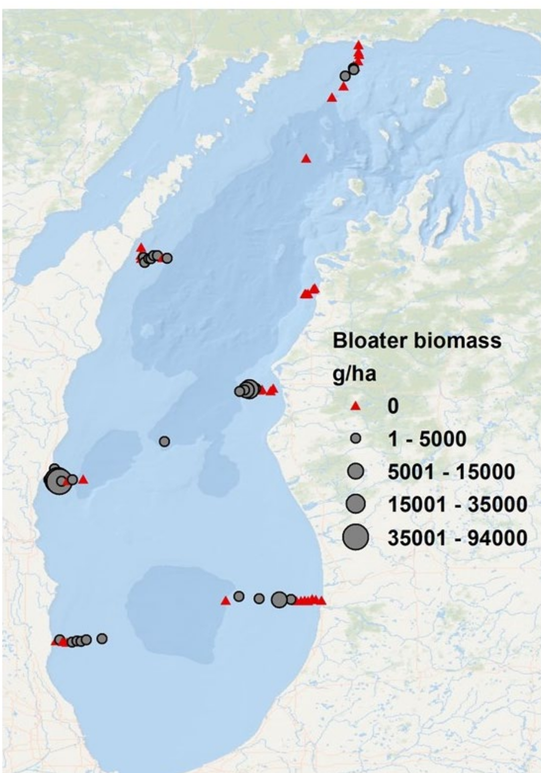

Figure 6. Scaled-symbol plot showing the biomass of bloater sampled during each of the 2018 bottom trawl sites, including the non-standard deep ones.

The exact mechanisms underlying the apparently poor bloater recruitment from 1992-2015 period (Figure 5b), and the low biomass of adult bloater since 2007 (Figure 5a), remain unknown. Madenjian et al. (2002) proposed that the Lake Michigan bloater population may be cycling in abundance, with a period of about 30 years, although the exact mechanism by which recruitment is regulated remains unknown. Of the mechanisms that have been recently evaluated, reductions in fecundity associated with poorer condition (Bunnell et al. 2009) and egg predation by slimy and deepwater sculpins (Bunnell et al. 2014a) may be contributing to the reduced bloater recruitment, but neither one is the primary regulating factor.

An important consideration when interpreting the bottom trawl survey results is that bloater catchability may have decreased in recent years, in response to the proliferation of quagga mussels and the associated increased water clarity and decreased *Diporeia* spp. densities, which could be responsible for a shift to the more pelagic calanoid copepods in their diets (Bunnell et al. 2015). Hence, one hypothesis is that bloaters are less vulnerable to our daytime bottom trawls either because of behavioral changes (more pelagic during the day) or increased ability to avoid the net while on the bottom (due to clearer water). Further, vulnerability of bloaters to our bottom trawl survey may have decreased more for large bloaters than for small bloaters. In recent years, nearly all of the bloaters captured by our bottom trawls were less than 240 mm in TL, whereas commercial fishers using gill nets continue to harvest bloaters well over 300 mm in TL. Perhaps, in recent years, bloaters have become more pelagic and/or better able to avoid the net as they grow.

Both the acoustic and bottom trawl survey have assessed that bloater biomass was more than an order of magnitude higher during 1992-1996 than during 2001-2018. A comparison of the two surveys during 1992-2006 revealed that the biomass estimate from the bottom trawl survey was always higher (about 3 times higher, on average) than the acoustic survey estimate. Since 2007, either survey was just as likely to yield the higher estimate as the other survey. In 2018, total biomass density estimated for bloater from the bottom trawl survey (2.60 kg/ha) was relatively similar to that from the acoustic survey (2.93 kg/ha, Warner et al. 2019).

Rainbow smelt – Adult rainbow smelt have been an important part of the diet for intermediate-sized (400 to 600 mm) lake trout in the nearshore waters of Lake Michigan (Stewart et al. 1983; Madenjian et al. 1998; Jacobs et al. 2010). For Chinook salmon, rainbow smelt comprised as much as 18% in the diets of small

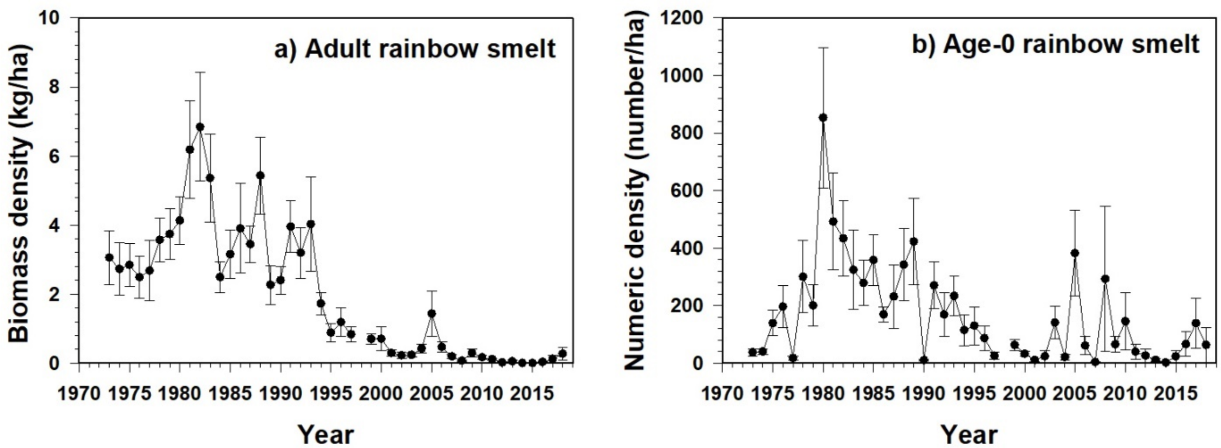

Figure 7. Density per ha (+/- standard error) of adult rainbow smelt (a, in terms of biomass) and age-0 rainbow smelt (b, in terms of number) in Lake Michigan, 1973-2018.

individuals in 1994-1996, but that dropped precipitously to 2% in 2009-2010. Rainbow smelt has been consistently rare in the diets of larger Chinook salmon since 1994 (Jacobs et al. 2013). The rainbow smelt population has traditionally supported commercial fisheries in Wisconsin and Michigan waters (e.g., Belonger et al. 1998), but its yields have also declined through time. Between 1971 and 1999, more than 1.3 million pounds were annually harvested on average. Between 2000 and 2011, the annual average dropped to about 375,000 pounds. Since 2013, less than 2,000 pounds have been harvested per year.

Similar to the commercial yields, adult rainbow smelt biomass density in the bottom trawl has remained at low levels since 2001, aside from a relatively high estimate in 2005 (Figure 7a). Biomass in 2018 was 0.27 kg/ha, more than double the mean from 2017 and the highest estimate since 2009. This recent uptick was due to the high densities of age-0 (< 90 mm TL) rainbow smelt sampled in 2016 and 2017 (Figure 7b), and the 2018 estimate (63 fish/ha) was also relatively high compared to 2011-2015. Rainbow smelt were sampled at all seven ports in 2017 (Figure 8), with the highest mean biomass densities at 18 m at Port Washington, Ludington, Waukegan. Rainbow smelt have only been sampled in 2 of the 30 non-standard deep tows since 2013. Their highest mean biomass over this period has been at 18 m. Causes for the long-term decline in rainbow smelt biomass since 1993 remain unclear. Consumption of rainbow smelt by salmonines was higher in the mid-1980s than during the 1990s (Madenjian et al. 2002), yet adult and age-0 rainbow smelt abundance remained high during the 1980s (Figure 7b). Results from a recent population modeling exercise suggested that predation by salmonines was not the primary driver of long-term temporal trends in Lake Michigan rainbow smelt abundance (Tsehaye et al. 2014). Furthermore, a recent analysis of our time series suggested that the productivity of the population has actually increased since 2000 (relative to 1982-1999), yet those recruits do not appear to be surviving as well to the adult population (Feiner et al. 2015).

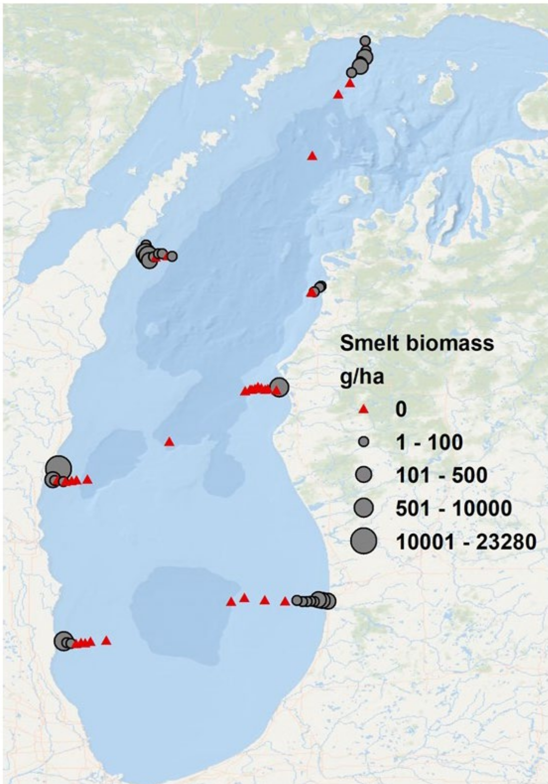

Figure 8. Scaled-symbol plot showing the biomass of rainbow smelt sampled during each of the 2018 bottom trawl sites, including the non-standard deep ones.

The bottom trawl and acoustic surveys detected similar temporal trends, with total (age-0 and adult pooled) rainbow smelt biomass densities more than 7 times higher, on average, during 1992-1996 than during 2001-2017. A comparison of the two survey estimates revealed that the acoustic survey estimate generally exceeds that of the bottom trawl survey, on average by a factor of about 6. This difference is not surprising given that rainbow smelt tend to be more pelagic than other prey species during the day. In 2018, however, the total biomass estimate for all rainbow smelt was 0.09 kg/ha for the acoustic survey (Warner et al. 2019), which was actually lower than the bottom trawl survey estimate of (0.45 kg/ha).

Sculpins – From a biomass perspective, the cottid populations in Lake Michigan have been dominated by deepwater sculpins, and to a lesser degree, slimy sculpins (*Cottus cognatus*). Spoonhead sculpins (*Cottus ricei*), once fairly common, suffered declines to become rare to absent by the mid-1970s (Eck and Wells 1987). Spoonhead sculpins were encountered in small numbers in our survey between 1990 and 1999 (e.g., Potter and Fleischer 1992), but have not been sampled since 1999.

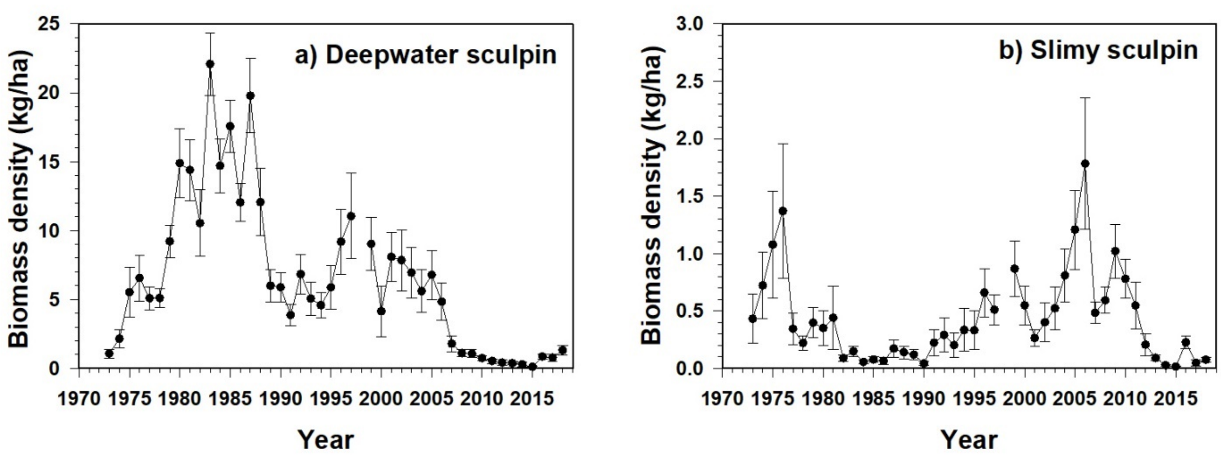

Figure 9. Biomass density (+/- standard error) for deepwater sculpin (a) and slimy sculpin (b) in Lake Michigan, 1973-2018.

Slimy sculpin is a favored prey of juvenile lake trout in Lake Michigan (Stewart et al. 1983; Madenjian et al. 1998), but is only a minor part of adult lake trout diets. When abundant, deepwater sculpin can be an important diet constituent for burbot in Lake Michigan, especially in deeper waters (Van Oosten and Deason 1938; Brown and Stedman 1995; Fratt et al. 1997).

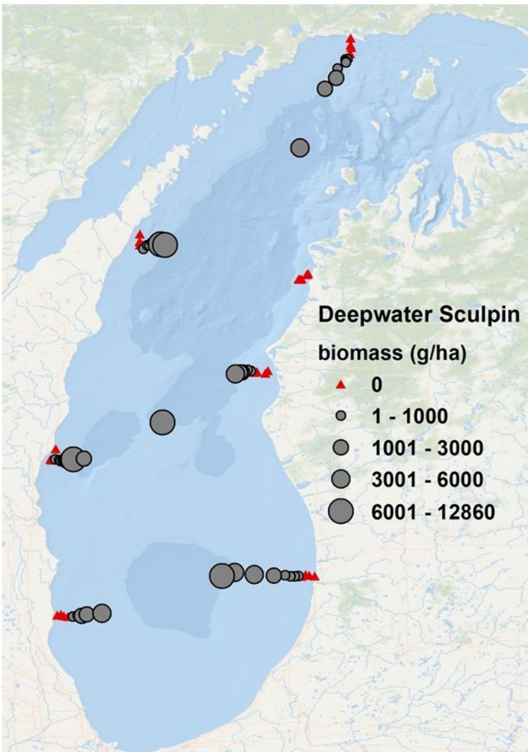

Figure 10. Scaled-symbol plot showing the biomass of deepwater sculpin sampled during each of the 2018 bottom trawl sites, including the non-standard deep ones.

Deepwater sculpin biomass density in 2018 was 1.30 kg/ha, the highest biomass estimated since 2007 (Figure 9a), and a continuation of increasing biomass since 2015. Relative to historical values from 1979-1988 (mean = 14.7 kg/ha) and 1989-2006 (mean = 6.3 kg/ha), however, deepwater sculpin remain at relatively low levels since 2007 (mean = 0.78 kg/ha). Previous analysis of the time series indicated deepwater sculpin density is negatively influenced by alewife (predation on sculpin larvae) and burbot (predation on juvenile and adult sculpin, Madenjian et al. 2005b). Madenjian and Bunnell (2008) demonstrated that deepwater sculpins have been captured at increasingly greater depths since the 1980s. Therefore, one potential explanation for the decline since 2007 is an increasing proportion of the population occupying depths deeper than those sampled by our survey (i.e., 9-110 m), perhaps in response to the decline of *Diporeia* and proliferation of dreissenid mussels. Our sampling at deeper depths since 2013 has been supportive of this hypothesis given that deepwater sculpins have been sampled in all 30 deep tows. Moreover, among these years the mean biomass density increased with depth out to the sites 128 m and deeper, and Figure 10 illustrates this pattern. Hence, the hypothesis that the bulk of the deepwater sculpin population in Lake Michigan now occupies waters deeper than 110 m is supported by our data and the long-term trend of declining deepwater sculpin biomass illustrated in the survey may be an artifact of our standard sampling out to only 110 m.

Slimy sculpin biomass density in 2018 was 0.07 kg/ha, similar to the extremely low densities estimated in 2013-2015 and 2017. Overall, slimy sculpin biomass density has substantially declined since 2009 (Figure 9b). Slimy sculpin abundance in Lake Michigan is regulated, at least in part, by predation from juvenile lake trout (Madenjian et al. 2005b). We attribute the slimy sculpin recovery that occurred during the 1990s to, in part, the 1986 decision to emphasize stocking lake trout on offshore reefs (as opposed to the areas closer to shore where our survey samples, Madenjian et al. 2002). Likewise, the slimy sculpin decline that began in 2009 coincided with a substantial increase in the rate of stocking juvenile lake trout into Lake Michigan and an increase in natural reproduction by lake trout (FWS/GLFC 2017; Lake Michigan LTWG 2017). Since 2013, slimy sculpins have been sampled in 15 out of 30 deep tows. However, mean biomass density at sites 128 m and deeper (e.g., 0.02 kg/ha) were an order of magnitude lower than the biomass estimated at 73, 82, 91, and 110 m sites. Since 2013, the highest mean biomass has been estimated at 82 m (e.g., 0.18 kg/ha). These results suggest that a relatively small proportion of the population resides in waters deeper than 110 m.

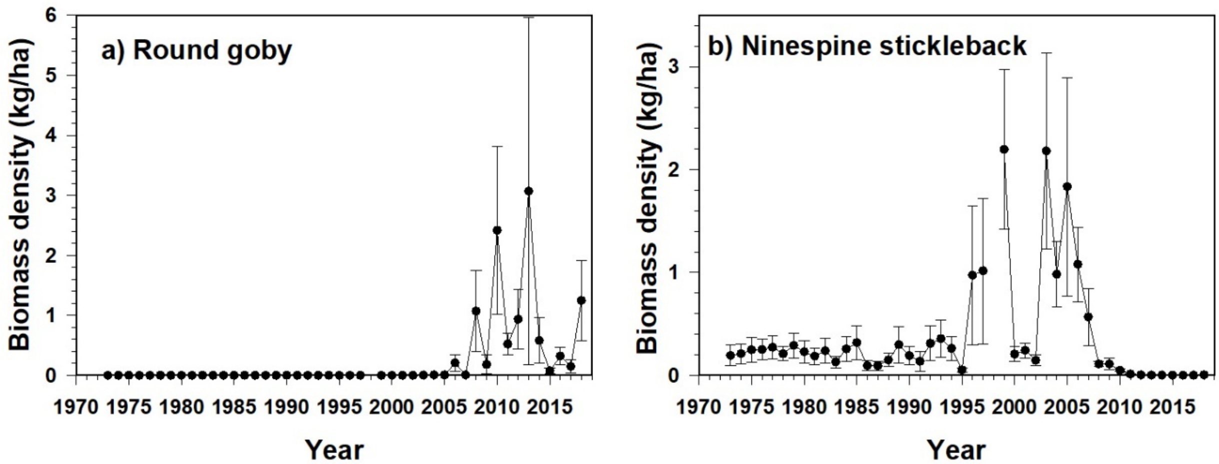

Figure 11. Biomass density (+/- standard error) of round goby (a) and ninespine stickleback (b) in Lake Michigan, 1973-2018.

Round goby – The round goby (*Neogobius melanostomus*) is an invader from the Black and Caspian Seas. Round gobies have been observed in bays and harbors of Lake Michigan since 1993 and were captured in the southern main basin of the lake as early as 1997 (Clapp et al. 2001). Round gobies were not captured in the bottom trawl survey until 2003; our survey likely markedly underestimates round goby abundance given their preferred habitat includes rocky and inshore (i.e., < 9 m bottom depth) areas that we do not sample. By 2002, round gobies had become an integral component of yellow perch diets at nearshore sites (i.e., < 15 m depth) in southern Lake Michigan. Recent studies have revealed round gobies are an important constituent of the diets of Lake Michigan burbot (Hensler et al. 2008; Jacobs et al. 2010), yellow perch (Truemper et al. 2006), smallmouth bass (*Micropterus dolomieu*, T. Galarowicz, Central Michigan University, personal communication), lake trout (Happel et al. 2018), lake whitefish (S. Hansen, Wisconsin DNR, personal communication), and even cisco (*Coregonus artedi*, J. Jonas, Michigan DNR, personal communication).

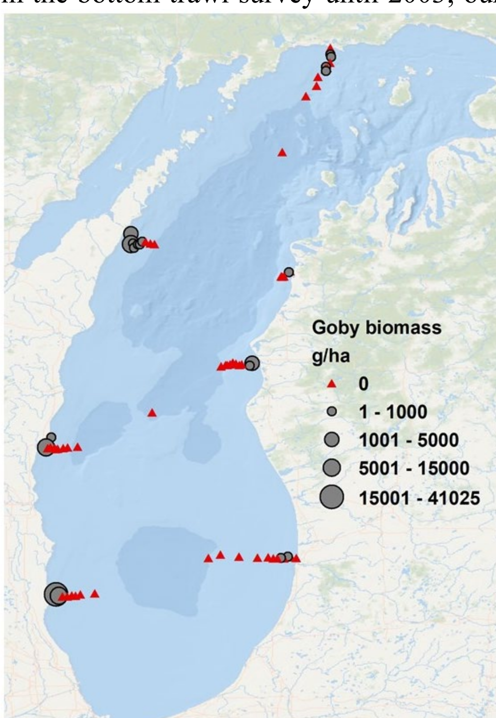

Figure 12. Scaled-symbol plot showing the biomass of round goby sampled during each of the 2018 bottom trawl sites, including the non-standard deep ones.

Round goby biomass density equaled 1.25 kg/ha in 2018 (Figure 11a), the 3rd highest estimate of the time series. Round gobies were sampled at all seven ports in 2018 (Figure 12), with the highest mean biomass densities near the western shoreline which generally has rockier habitat. We hypothesize that round goby abundance in Lake Michigan is controlled by predation. This hypothesis was supported by annual mortality rates of between 79 and 84% estimated in 2008-2012 (Huo et al. 2014), which are comparable to the mortality rates currently experienced by Lake Michigan adult alewives (Tsehaye et al. 2014).

Ninespine stickleback – Two stickleback species occur in Lake Michigan. Ninespine stickleback (*Pungitius pungitius*) is native, whereas threespine stickleback (*Gasterosteus aculeatus*) is non-native and was first collected in the GLSC bottom trawl survey during 1984 (Stedman and Bowen 1985), but has been extremely rare in recent sampling years. Biomass density of ninespine stickleback in 2017 was only 4.5 g per ha, continuing a trend of very low biomass since 2011 (Figure 11b). Biomass of ninespine stickleback remained fairly low from 1973-1995 and then increased dramatically through 2007, perhaps attributable to dreissenid mussels enhancing ninespine stickleback spawning and nursery habitat through proliferation of *Cladophora* (Madenjian et al. 2010b). One plausible explanation for the low ninespine stickleback abundance since 2011 is that piscivores began to incorporate ninespine sticklebacks into their diets as the abundance of alewives declined to a lower level. For example, Jacobs et al. (2013) found ninespine sticklebacks in large Chinook salmon diets (i.e., 2% occurrence) during 2009-2010 after 0% occurrence in 1994-1996.

COMMUNITY TRENDS

The prey fish community includes alewife, bloater, rainbow smelt, deepwater sculpin, slimy sculpin, ninespine stickleback, and round goby. In 2018, we estimated a total biomass density of prey fish available to the bottom trawl equal to 6.22 kg/ha (Figure 13a, Appendix 1), which is a 65% increase relative to 2017 but still far below the long-term average total biomass of 36.9 kg/ha. Total biomass density has trended downward since 1989, primarily due to a dramatic decrease in bloater biomass (Figure 13a). Total biomass density first dropped below 13 kg/ha in 2007 and has since remained below that level with the exception of 2013 (when the biomass estimates for alewife and round goby were highly uncertain). In previous reports, we have reported "lake-wide" biomass of preyfish in terms of kilotonnes, but we now have ceased usage of this term in the report to reduce confusion. To be clear, the bottom trawl survey has never sampled lake-wide, but since 2014 a new predator-prey model (see Tsehaye et al. 2014) has been developed that uses information from this bottom trawl prey fish survey, the acoustic prey fish survey, and a predator consumption model to provide a more realistic "lake-wide" biomass for alewife, a key prey fish.

For the fourth straight year, the composition of the 2018 prey fish community (as assessed by the bottom trawl) was dominated by bloater (42%, Figure 13b). Deepwater sculpin (21.7%) and round goby (20%) each made considerable contributions to the biomass, whereas alewife (9%), rainbow smelt (7%), slimy sculpin (1%), and ninespine stickleback (<1%) each comprised less than 10% of the community.

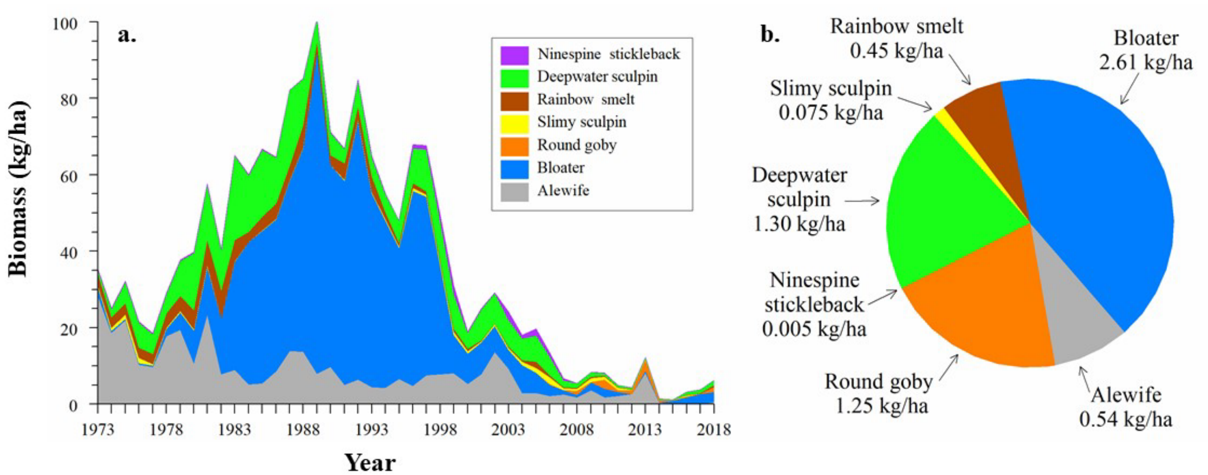

Figure 13. Estimated biomass of prey fishes in the region sampled by the bottom trawl (i.e., 5-114 m depth) in Lake Michigan, 1973-2018 (a) and species composition in 2018 (b).

OTHER SPECIES OF INTEREST

Burbot – Burbot and lake trout represent the native top predators in Lake Michigan. The decline in burbot abundance in Lake Michigan during the 1950s has been attributed to sea lamprey predation (Wells and McLain 1973). Sea lamprey control was a necessary condition for recovery of the burbot population in Lake Michigan, however Eshenroder and Burnham-Curtis (1999) proposed that a reduction in alewife abundance was an additional prerequisite for burbot recovery.

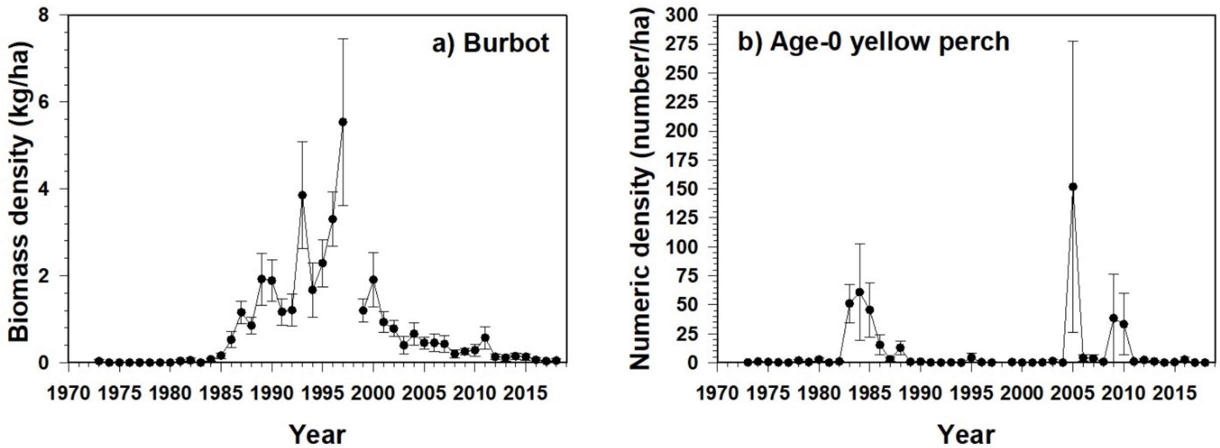

Figure 14. Biomass density (+/- standard error) of burbot (a) and numeric density (+/- standard error) of age-0 yellow perch (b) in Lake Michigan, 1973-2018.

Burbot collected in the bottom trawls are typically large individuals (>350 mm TL); juvenile burbot apparently inhabit areas not usually covered by the bottom trawl survey. Burbot biomass density was 0.04 kg/ha in 2018, consistent with extremely low estimates since 2012. After a period of low biomass density in the 1970s, burbot showed a strong recovery in the 1980s (Figure 14a). Densities increased through 1997 but declined thereafter. It is unclear why burbot catches in the bottom trawl survey have declined in the face of relatively low alewife densities.

Age-0 yellow perch – The yellow perch population in Lake Michigan has supported valuable recreational and commercial fisheries (Wells 1977). GLSC bottom trawl surveys provide an index of age-0 yellow perch numeric density, which serves as an indication of yellow perch recruitment success. The 2005 year-class of yellow perch was the largest ever recorded (Figure 14b) and the 2009 and 2010 year-classes also were higher than average. In 2018, no age-0 yellow perch were caught, indicating a weak year-class.

CONCLUSIONS

In 2018, total prey fish biomass was estimated to be 6.22 kg/ha, which is a 65% increase over 2017 and a five-fold increase over the record-low estimate from 2015. Every species was estimated to attain a higher biomass density in 2018 than in 2017, with round goby providing the largest percentage increase. Relative to the long-term average of 36.9 kg/ha, however, the 2018 estimate indicates relatively low biomass densities of prey fish in Lake Michigan.

This low level of prey fish biomass can be attributable to a suite of factors, two of which can be clearly identified: (1) a prolonged period of poor bloater recruitment during 1992-2015 and (2) intensified predation on alewives by salmonines during the 2000s and 2010s. Adult alewife density has been maintained at a relatively low level over the last 15 years and the age distribution of the adult alewife population has become especially truncated in recent years. As recent as 2007, alewives as old as age 9 were sampled in this survey, whereas the oldest alewife sampled since 2013 has been age 6 or younger, with age 5 being the oldest in 2013, 2014, 2017, and 2018.

We also note that the striking decrease in deepwater sculpin biomass after 2006 appears to have been due, at least in part, to a substantial portion of the population moving to waters deeper than 110 m. Results from the deep tows that we have conducted since 2013 corroborate the contention that the bulk of the deepwater sculpin population in Lake Michigan now inhabits waters deeper than 110 m.

In addition to the importance of top-down forces, prey fishes also may be negatively influenced by reduced prey resources (i.e., "bottom-up" effects). For example, several data sets are indicating a reduction in the base of the food web, particularly for offshore total phosphorus and phytoplankton, as a consequence of long-term declines in phosphorus inputs and the proliferation of dreissenid mussels (Evans et al. 2011; Bunnell et al. 2014b). Grazing of phytoplankton by dreissenid mussels and reduced availability of phosphorus in offshore waters appeared to be the primary drivers of the 35% decline in primary production in offshore waters between the 1983-1987 and 2007-2011 periods (Madenjian et al. 2015; Rowe et al. 2017). The quagga mussel expansion into deeper waters may have been partly responsible for this reduced availability of phosphorus in offshore waters. The evidence for declines in "fish food" (e.g., zooplankton and benthic invertebrates) in offshore waters of Lake Michigan is somewhat less clear. *Diporeia* has undoubtedly declined in abundance (Nalepa et al. 2014), but whether or not crustacean zooplankton and mysids have declined depends on which data set is examined (e.g., Pothoven et al. 2010; Bunnell et al. 2014b; Madenjian et al. 2015). Crustacean zooplankton biomass density in nearshore waters appeared to decrease during 1998-2010, likely due to a reduction in primary production mainly stemming from grazing of phytoplankton by dreissenid mussels. The above-mentioned decline in *Diporeia* abundance appeared to have led to reductions in growth, condition, and/or energy density of lake whitefish, alewives, bloaters, and deepwater sculpins during the 1990s and 2000s (Pothoven et al. 2011, 2012; Madenjian et al. 2015). Of course, decreases in growth, condition, and energy density do not necessarily cause declines in fish abundance. The challenge remains to quantify bottom-up effects on prey fish abundances and biomasses in Lake Michigan. Given the complexities of the food web, disentangling the effects of the dreissenid mussel invasions and the reduction in nutrient loadings from other factors influencing the Lake Michigan food web will require a substantial amount of ecological detective work.

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Appendix 1. Mean numeric and biomass density estimates, based on the bottom trawl survey, for various fishes and dreissenid mussels in Lake Michigan during 2018. Estimates represented the weighted mean density over the range of depths sampled, weighting by the corresponding surface area of the lake assigned to the depth zone. Depth zones ranged between the 5 m and 114 m depth contours. See main text for more details. Standard error enclosed in parentheses. NA denotes that estimate is not available.

Taxon	Numeric density (fish/ha)	Biomass density (kg/ha)
age-0 alewife	0 (0)	0 (0)
adult alewife	29.38 (25.26)	0.536 (0.428)
age-0 bloater	3.18 (1.43)	0.024 (0.488)
adult bloater	97.40 (46.35)	2.586 (1.236)
age-0 rainbow smelt	63.11 (60.30)	0.176 (0.172)
adult rainbow smelt	52.62 (40.78)	0.272 (0.191)
deepwater sculpin	159.77 (37.36)	1.303 (0.349)
slimy sculpin	16.70 (3.86)	0.075 (0.020)
ninespine stickleback	2.41 (2.10)	0.004 (0.004)
burbot	0.02 (0.02)	0.043 (0.043)
age-0 yellow perch	0 (0)	0 (0)
round goby	152.29 (84.64)	1.246 (0.672)
dreissenid mussels	NA	13.697 (5.479)