Status and Trends of Pelagic and Benthic Prey Fish Populations in Lake Michigan, 2023[1,2]

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[1] The data associated with this report are currently under review and will be publicly available in 2024 (https://doi.org/10.5066/P9XVOLR1). Previous versions of the data may be accessed at 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. Please direct questions to our Data Management Librarian, Sofia Dabrowski, at sdabrowski@usgs.gov.

[2] 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).

Executive Summary

Fall bottom trawl (fall BT) and lakewide acoustic (AC) surveys are conducted annually to generate indices of pelagic and benthic prey fish densities in Lake Michigan. The fall BT survey has been conducted each fall since 1973 using 12-m trawls at depths ranging from 9 to 110 m at fixed locations distributed across seven transects; this survey estimates densities of seven prey fish species [i.e., Alewife (*Alosa pseudoharengus*), Bloater (*Coregonus hoyi*), Rainbow Smelt (*Osmerus mordax*), Deepwater Sculpin (*Myoxocephalus thompsonii*), Slimy Sculpin (*Cottus cognatus*), Round Goby (*Neogobius melanostomus*), Ninespine Stickleback (*Pungitius pungitius*)] as well as age-0 Yellow Perch (*Perca flavescens*) and large (> 350 mm) Burbot (*Lota lota*). The AC survey has been conducted each late summer/early fall since 2004, and the 2023 survey consisted of 20 transects [450 km total (336 miles)] covering bottom depths ranging from 12 to 248 m and 29 midwater trawl tows above bottom depths ranging 16 to 246 m; this survey estimates densities of three prey fish species (i.e., Alewife, Bloater, and Rainbow Smelt). The data generated from these surveys are used to estimate various population parameters that are, in turn, used by state and tribal agencies in managing Lake Michigan fish stocks. A spring bottom trawl survey (spring BT) was implemented across 3 of the transects sampled in the fall and sites ranged in depth from 18 to 164 m. The goal of the spring BT is to explore seasonal differences in biomass density and distributions of key prey species, most notably Alewife. Additionally, we conducted acoustic sampling while bottom trawling to evaluate the vertical distribution of fish relative to the height of the trawl.

The abbreviated spring BT survey results indicated that Alewives were primarily offshore with peak biomass density at the 91 m bottom depth. There was no evidence of higher acoustic density above the trawl at depths of 18, 73, 128, and 146 m. At 91 and 164 m, acoustic density above the trawl was >2x that in the trawl path, but sample size at these two depths was low. For the AC survey, total biomass density of prey fish equaled 14.8 kg/ha, 223% higher than the long-term average (2004-2022) of 4.6 kg/ha and 8.8 kg/ha higher than the 2022 estimate. For the fall BT, total biomass density of prey fish equaled 3.6 kg/ha, about 50% lower than the average value from 2004-2022 (6.9 kg/ha). The 2023 fall BT biomass was an order of magnitude lower than the average over the entirety of the time series (1973-2022; 33.7 kg/ha).

Bloater was the dominant species (by biomass) among prey fishes in the fall BT, while the AC survey reported dominance of Alewife. Mean biomass of yearling and older (YAO) Alewife was 10.3 kg/ha in the AC survey, and 0.7 kg/ha in the fall BT. Since 2014, catchability of YAO Alewives for the fall BT has been substantially lower than the AC survey. While limited in scope, the results of the 2023 spring BT do not suggest that catchability is substantially higher in the spring than the fall, which aligns with the 2022 survey results.

Comparing the AC estimate to previous years, YAO Alewife biomass was 359% higher than the average from 2004-2022. Numeric density of age-0 Alewife from the AC survey was 1,205 fish/ha in 2023, which is the third highest in the time series and well above the long-term mean of 428 fish/ha. Biomass density of large (≥120 mm) Bloater in 2023 was 3.5 kg/ha in the AC survey and 2.1 kg/ha in the fall BT - each at least an order of magnitude lower than what was estimated by the fall BT between 1985 and 1997. Following a record high year in 2021 (1,034 fish/ha), the numeric density of small (<120 mm) Bloater was 142 fish/ha in the AC survey, similar to the long-term mean of 120 fish/ha. Meanwhile, small Bloater density estimated in the fall BT was 2 fish/ha. Biomass density of large Rainbow Smelt (≥90 mm) was <0.05 kg/ha in the

AC and fall BT surveys, continuing the trend of low Rainbow Smelt biomass that has been observed since 2001. Numeric density of small (<90 mm) Rainbow Smelt was 119 fish/ha in the AC survey and 7 fish/ha in the fall BT, indicating a weak year-class. All four prey fish species sampled only by the fall BT indicated below average biomass densities. Deepwater Sculpin biomass density was estimated at 0.4 kg/ha, which makes 13 of the past 14 years when biomass was <1 kg/ha. Slimy Sculpin was estimated at 0.02 kg/ha, only 5% of the long-term average. Round Goby was estimated at 0.3 kg/ha, below the average biomass of 0.85 kg/ha since 2008 but similar to intermittent low values observed throughout the dataset. Ninespine Stickleback density was 1 fish/ha. Only 35 small (<100 mm) Yellow Perch were caught, indicating a weak Yellow Perch year-class in 2023.

Table 1. List of fish species common and scientific names.

Common Name	Scientific Name
Alewife	*Alosa pseudoharengus*
Bloater	*Coregonus hoyi*
Brown Trout	*Salmo trutta*
Burbot	*Lota lota*
Cisco	*Coregonus artedi*
Chinook salmon	*Oncorhynchus tshawytscha*
Coho Salmon	*Oncorhynchus kisutch*
Deepwater Sculpin	*Myoxocephalus thompsonii*
Emerald Shiner	*Notropis atherinoides*
Lake Trout	*Salvelinus namaycush*
Lake Whitefish	*Coregonus clupeaformis*
Ninespine Stickleback	*Pungitius pungitius*
Rainbow Smelt	*Osmerus mordax*
Round Goby	*Neogobius melanostomus*
Sea Lamprey	*Petromyzon marinus*
Slimy Sculpin	*Cottus cognatus*
Smallmouth Bass	*Micropterus dolomieu*
Steelhead	*Oncorhynchus mykiss*
Threespine Stickleback	*Gasterosteus aculeatus*
Yellow Perch	*Perca flavescens*

Introduction

Annual evaluation of prey fish dynamics is critical to understand changes to the Lake Michigan food web during the last 40 years (e.g., Madenjian et al. 2002, 2015) and continued restructuring due to non-native species, changing nutrient inputs, changing climate, and management activities including harvest regulation and fish stocking. Non-native Alewives (*Alosa pseudoharengus*) are a key prey fish in the Lake Michigan food web because they serve as the primary prey for Lake Michigan salmonines (Elliott 1993; Rybicki and Clapp 1996; Warner et al. 2008; Jacobs et al. 2013). Alewife also help structure the food web because they are predators of native larval fish [e.g., Lake Trout (*Salvelinus namaycush*), Emerald Shiner (*Notropis atherinoides*); Madenjian et al. (2008)] and contribute to recruitment bottlenecks. Bloater (*Coregonus hoyi*, commonly known as “chub”) is a native coregonine prey fish that dominated the community biomass in the 1980s and 1990s. Non-native Rainbow Smelt (*Osmerus mordax*) is another abundant planktivorous prey fish species since its introduction into Lake Michigan in the early 20th century. Alewife, Bloater, and Rainbow Smelt supported commercial fisheries in the 1980s, but these fisheries have either been closed (Alewife) or now have limited participation (Bloater, Smelt) owing to low fish catches in recent decades. Key native benthic species include Deepwater and Slimy Sculpin (*Myoxocephalus thompsonii* and *Cottus cognatus*, respectively). Since 2004, non-native benthic Round Goby (*Neogobius melanostomus*) has become abundant in Lake Michigan and another key player in the food web given their importance as prey for Lake Trout (Happel et al. 2018, Leonhardt et al. 2020), Brown Trout (*Salmo trutta,* Leonhardt et al. 2020), and Smallmouth Bass (*Micropterus dolomieu;* Steinhart et al. 2004a), but also for their ability to consume non-native dreissenid mussels (Bunnell et al. 2015). At the same time, Round Goby can potentially have a negative effect on native fishes by consuming their eggs (e.g., Chotkowski and Marsden 1999; Steinhart et al. 2004b).

Lakewide monitoring of prey fish began in 1973 with a fall bottom trawl (fall BT) survey that sampled the bottom ~1.5 m of water over soft or sandy substrates during the daytime. Although many adult prey fishes occupy the bottom of the lake during the day, presumably to avoid predation, scientists recognized that the survey provided a relative (not absolute) density index because some proportion of adult Alewife, Bloater, and Rainbow Smelt remain pelagic during the daytime. In addition, age-0 Alewives are mostly above the thermocline, rather than below, during the day (Brandt 1980). To provide a complementary relative index of prey fish abundance, Lake Michigan scientists began conducting nighttime AC (acoustic) surveys in the early 1990s, and an interagency, lakewide, annual survey was formalized in 2004. Together, these two annual surveys have enabled the development of a stock assessment model for Alewives (Tsehaye et al. 2014) that is used to inform annual agency stocking decisions of Chinook salmon (*Oncorhynchus tshawytscha*), Lake Trout, Steelhead (*Oncorhynchus mykiss*), Brown Trout, and Coho Salmon (*Oncorhynchus kisutch*) in Lake Michigan; each survey provides unique data. The fall BT provides abundance indices for benthic species such as Deepwater Sculpin, Slimy Sculpin, Round Goby, Ninespine Stickleback (*Pungitius pungitius*), and even age-0 Yellow Perch (*Perca flavescens*). The fall BT has also traditionally indexed Burbot (*Lota lota*), a native piscivore. In turn, the AC survey provides abundance indices for age-0 Alewife, which is an early indicator of Alewife year-class strength (Warner et al. 2008), as well as Cisco (*Coregonus artedi*). Both surveys provide relative indices of Bloater, Smelt and yearling and older (YAO) Alewife that can be used as two lines of evidence for tracking density changes over time.

Prior to 2023, biomass indices for Alewife and other key prey fishes declined in Lake Michigan to historically low levels as compared to the 1970s and 1980s (Warner et al. 2022). This overall reduction in biomass density is related to top-down (e.g., predation by salmonids) and bottom-up controls (e.g., declines in pelagic primary productivity and dreissenid mussel establishment), and possibly also a long-term shift in depth distribution of Deepwater Sculpins. The decline in YAO Alewife biomass indices from the fall BT has been accompanied by a divergence from the AC survey estimates, which have been an order of magnitude higher in recent years (Warner et al. 2022). Scientists and managers alike have questioned whether changes in fish habitat use (e.g., less use of benthic habitats in the autumn) are at least partially responsible for the divergence in prey fish indices (Bunnell et al. 2018). This discrepancy and potential change in behavior has led to the need to explore whether an additional spring bottom trawl survey (spring BT) may provide a more informative measure of biomass for Alewife (see Tingley et al. 2023 for more details).

We have combined the results of the fall BT and AC survey in one report since 2019 and have included the spring BT since 2022. Our goal is to provide a synthetic and concise report that emphasizes the complementarity of the two standard surveys and provides additional insight on prey fish populations that can be gained from the spring survey. For methodological details, we invite readers to consult the previous separate survey reports (see Bunnell et al. 2019; Warner et al. 2019; Tingley et al. 2023). We provide a high-level overview of all methods below.

Methods

The standard unit of sampling for both bottom trawl surveys is a 10-min tow using a “Yankee” trawl (12-m headrope, 25- to 45-mm bar mesh in net body, 6.4-mm bar mesh in cod end). In the fall BT, the trawl is dragged along depth contours 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, we began adding tows at deeper depths (i.e., 128 m) to assess the extent to which some species (e.g., Deepwater Sculpin, Bloater) have migrated outside of our traditional survey range. In 2023, we also sampled three deepwater tows at 146 m (Ludington and Sturgeon Bay) and 164 m (Frankfort). During each fall BT survey, seven transects are sampled offshore of Manistique, Frankfort, Ludington, and Saugatuck, Michigan (MI); Waukegan, Illinois (IL); and Port Washington and Sturgeon Bay, Wisconsin (WI; Fig. 1). Since 2016, we have directly estimated time on bottom for each tow with a head-rope depth sensor that provides a more accurate estimate of area (ha) swept.

We estimate both numeric (fish per hectare [fish/ha]) and biomass (kg/ha) density with lakewide means and variances calculated using a stratified design (fall BT) and a stratified cluster design (AC).

For the AC survey, split beam transducers with a nominal frequency of 120 kHz (range 120-129) are used to estimate numeric fish density along each of the 20 transects sampled in 2023 (Fig. 1). While sampling those transects, midwater trawls are deployed to sample fish, enabling estimation of species and size composition of fish for the numeric fish density data. Trawl deployment is generally driven by the presence or absence of fish. Acoustic estimates for the upper part of the water column (<40 m) were derived using the NearD method (Yule et al. 2013). Briefly, numeric fish density estimates were generated with consideration of the six geographic strata (north nearshore east, north nearshore west, north offshore, south nearshore, south offshore, west nearshore; see Warner et al. 2019) and vertical depth layer. Numeric fish density estimates were apportioned to species and size groups using the midwater catch data target strength. Fish density in the <40 m layer was apportioned to fish categories (age or size groups within species) using the catch from the nearest trawl (Euclidean distance). Fish density in the >40 m layer was apportioned to fish categories (age or size groups within species) using acoustic target strength (TS) and prior information about the composition of midwater trawl catch in this layer (Warner et al. 2012). For additional details regarding assignment assumptions in this deep layer see Warner et al. (2019). Lakewide average numeric and biomass density are estimated by calculating the

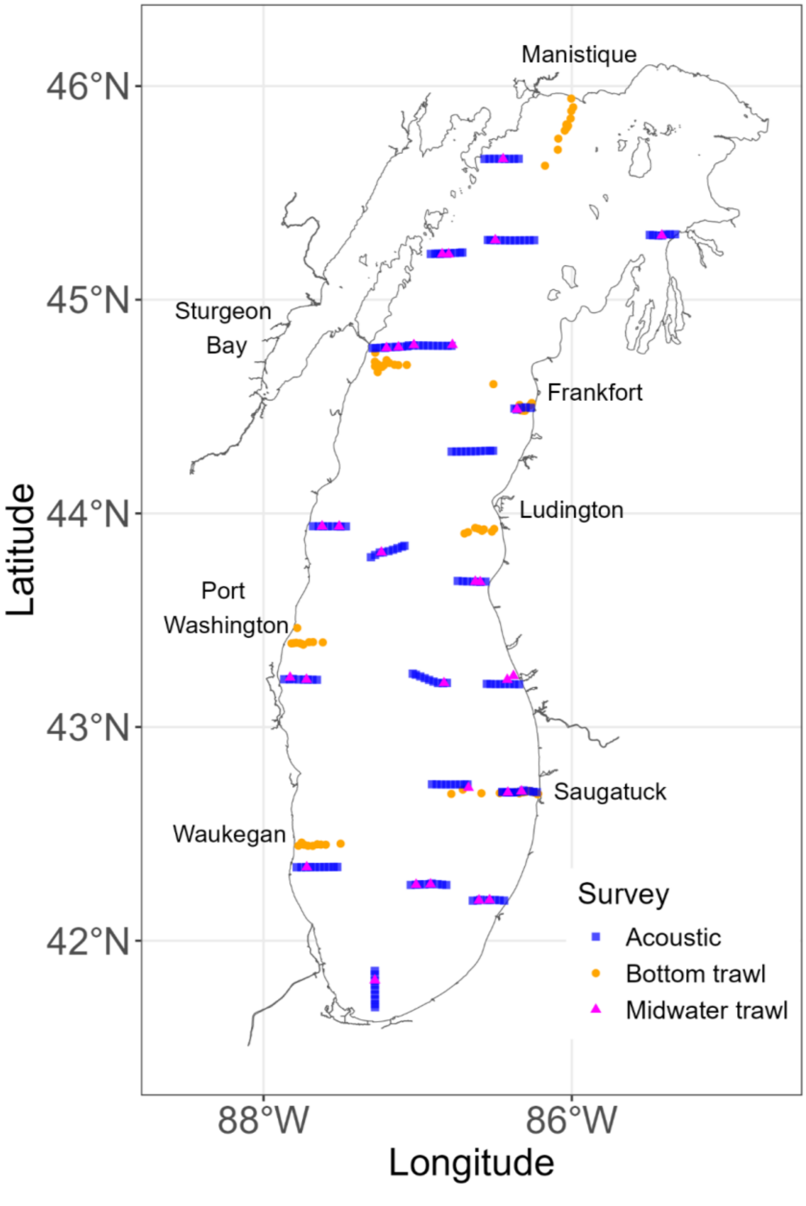

Figure 1. Map of sampling locations for the Lake Michigan bottom trawl and acoustic surveys in 2023. Blue squares represent acoustic transects, magenta triangles represent midwater trawl locations, and orange circles represent bottom trawl tows conducted in the fall. A subset of sites from the fall bottom trawl were also sampled in the spring outside of Frankfort, Ludington, and Sturgeon Bay.

population mean for a single stage stratified cluster estimator with known stratum areas.

In spring of 2023, vessel-related constraints limited our ability to conduct a full spring BT. With the approval of the Lake Michigan Committee, we implemented a 16-tow bottom trawl survey paired with hydroacoustic sampling and midwater tows to assess whether there was evidence of substantial numbers of alewife being “missed” by the bottom trawl because they are occupying areas higher in the water column. This research direction arose after we found that while Alewife biomass estimated during the 2022 spring BT was higher than that in the fall BT (0.38 vs. 0.10 kg/ha), it was still an order of magnitude lower than that in the acoustic survey (3.0 kg/ha; Tingley et al. 2023). Given we appear to effectively sample lake depths where Alewives are aggregated in April (~125-175 m; Tingley et al. 2023), gear bias associated with bottom trawling could be an alternative reason for low density estimates. Prior to each bottom trawl, we conducted a ~30-minute acoustic transect that included the bottom trawl transect. If fish were observed in the water column, we deployed a midwater trawl to determine species composition, then completed the bottom trawl. The initial study design included tows at 18 m and 110 – 164 m sites at Frankfort, Sturgeon Bay, and Ludington, but tows at Sturgeon Bay and Ludington were adjusted to include 73 m and 91 m sites, and to omit 146 m and 164 m sites, due to patterns in Alewife distribution observed at Frankfort (see results section). Hydroacoustic data were segmented into 500 m sections and total fish/ha was calculated in the path of the trawl (up to 1.5 m off bottom) and above it (>1.5 m through the water column) then averaged by tow depth to examine differences in abundance across zones. Calculations of fish/ha were done using an assumed mean backscattering cross section equivalent to a target strength of -43 dB [roughly a 100 mm fish, (Warner et al. 2002)].

Given the importance of the Alewife age distribution for the stock assessment model, sagittal otoliths were removed from Alewives in all surveys. Otoliths were mounted and the number of annual rings was read independently up to three times by two readers. If consensus on the number of annual rings could not be reached, the otolith age was determined to be unknown. In 2023, ages from 198 and 459 otoliths were successfully obtained from Alewife sampled in the spring and fall BT surveys, respectively, and ages from 209 otoliths were successfully estimated from Alewife sampled in the AC survey. Two age-length keys were developed; one for the spring BT and one for the AC survey and fall BT.

By convention, we classified Alewife, Bloater, Rainbow Smelt, and Yellow Perch caught in the fall BT and AC surveys as either “small” or “large” based on total length (TL) cutoffs: Alewife = 100 mm, Bloater = 120 mm, Smelt = 90 mm, Yellow Perch = 100 mm. For Alewife, this cutoff can reliably be used to estimate YAO densities in a given sample year. However, recent examination of Bloater age-length frequencies from 2016-2018 indicates that annual variability in growth results in a proportion of age-1 and age-2 fish being <120 mm. Further, no recent Rainbow Smelt and Yellow Perch aging data are available. Therefore, we reserve the term YAO for Alewife only. The numeric density of age-0 Alewife is only reported for the AC survey and was estimated using aged fish. We did not implement any length cutoffs when summarizing the spring BT data, as 2023 year-classes for the aforementioned species would not yet be present at the time of the survey. For ease of interpretation, we refer to spring BT indices using the same nomenclature as the fall BT and acoustic surveys (e.g., YAO Alewife, large Bloater).

Results

Alewife

Biomass density of YAO Alewife in 2023 was 10.3 kg/ha in the AC survey and 0.74 kg/ha in the fall BT (Fig. 2). During the spring BT, Alewife densities were highest at the 91-110 m depths, which are slightly shallower than those in the previous two seasons (2021, 2022; Fig. 3). YAO Alewife were most common along the western shoreline of Lake Michigan in the fall BT and the AC survey (Fig. 4b,4c), but were found in higher densities throughout the lake during the AC survey.

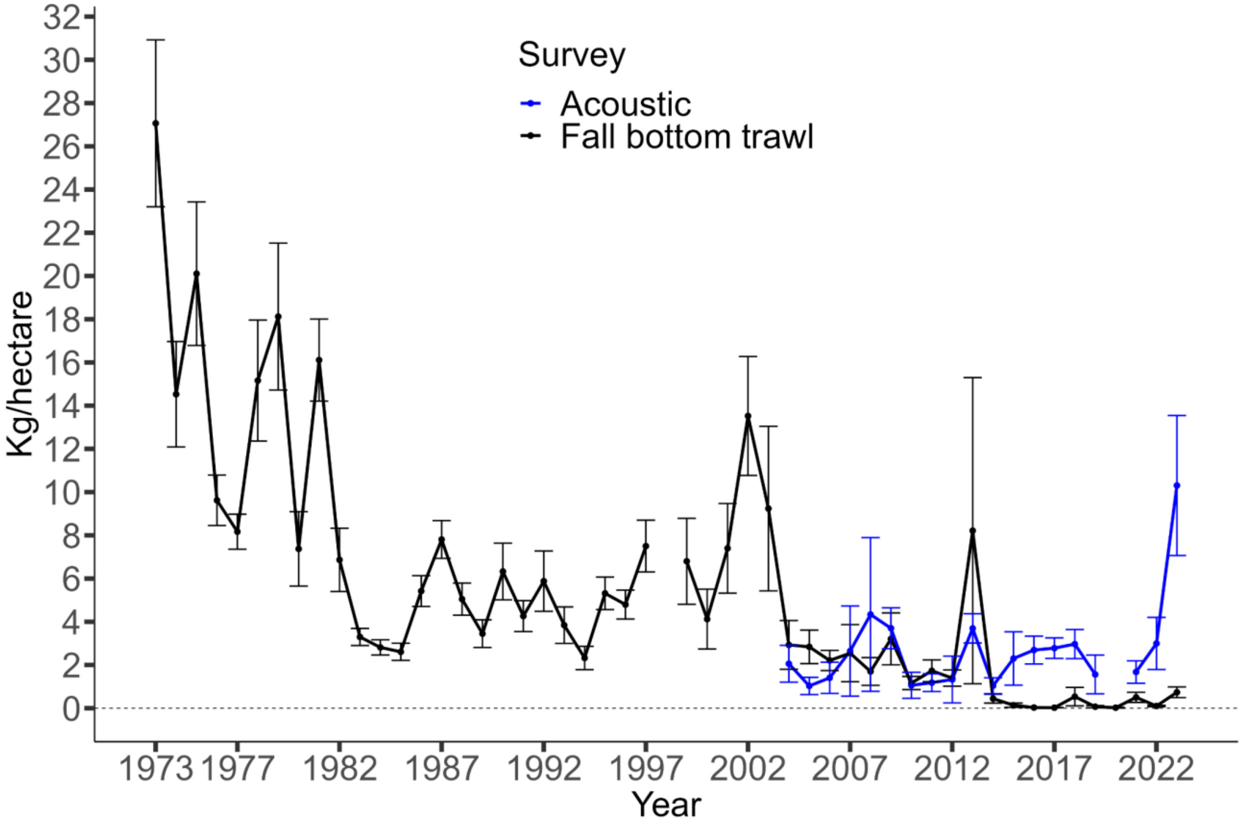

Figure 2. Yearling and older (YAO) Alewives, *Alosa pseudoharengus*, (≥100 mm) as biomass density for the fall bottom trawl and acoustic survey from 1973-2023 in Lake Michigan. Error bars are +/- standard error.

Between 2004 and 2013 standard error (SE) bars for the fall BT and AC survey overlapped each year except in 2005 (BT higher) and 2008 (AC higher; Fig. 2). However, from 2014-2023, the SE bars never overlapped. Standard error bars did not overlap between the two surveys in 2023 and the AC survey estimate was an order of magnitude higher than the fall BT. Even assuming the AC survey more accurately indexes YAO Alewife biomass, estimates from the AC survey during the last five years sampled (averaging 3.9 kg/ha) are still markedly lower than acoustic estimates in 1987 [9.6 kg/ha, (Argyle 1992)], 1995 and 1996 [8.3 and 10.0 kg/ha respectively, (Argyle et al. 1998)], which were calculated by dividing the number of kg reported by 5,396,683 ha, the area covered by the acoustic survey. Similarly, except for 2023, recent AC estimates are below the mean biomass estimated by the fall BT in the 1970s (16.1 kg/ha), 1980s (6.1 kg/ha), and 1990s (6.0 kg/ha). In the AC time series, the 2023 AC estimate is 7.2 kg/ha higher than that in 2022 and 8.0 kg/ha higher than the mean from 2004-2022.

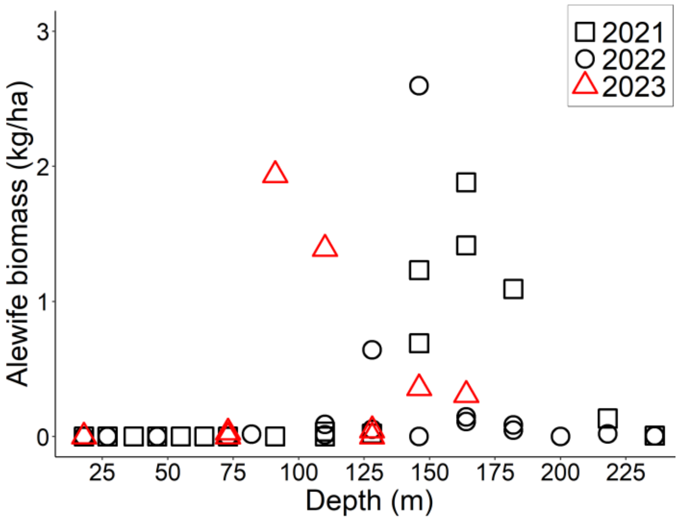

Figure 3. Density of yearling and older alewife (kg/ha) collected in the abbreviated 2023 spring trawl survey and previous spring surveys (2021, 2022) at sites sampled in 2023 (Sturgeon Bay, Ludington, Frankfort).

Numeric density of age-0 Alewives estimated from the AC survey was 1,205 fish/ha in 2023, a strong year-class and the third highest in the acoustic time series (Fig. 4). This 2023 estimate is well above the mean over the entire time series (469 fish/ha) and follows a weak year-class in 2022. Age-0 Alewife was highest in the northwest section of the lake near the Door Peninsula (Fig. 5d). Fish density from the spring acoustic data was generally low in all parts of the water column. Evidence of consistently higher fish density above the bottom trawl was observed at only one site (164 m bottom depth) with small sample size. However, the difference between fish density in the trawl path and above the trawl path was too small to account for the differences between the BT survey and AC survey estimates of biomass densities.

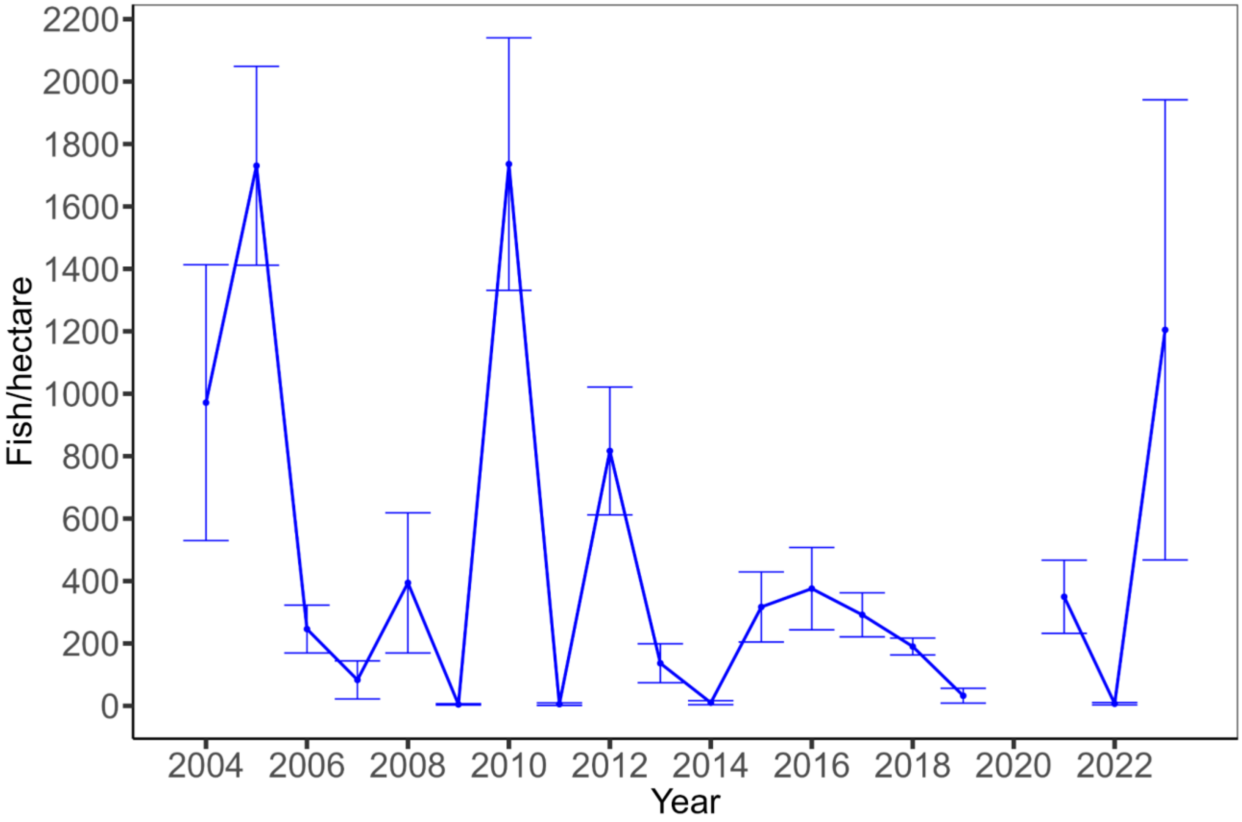

Figure 4. Age-0 Alewives (*Alosa pseudoharengus*) as numeric density for the acoustic survey from 2004-2023 in Lake Michigan. Error bars are +/- standard error.

Spring BT Alewife catch was 24% yearlings and 65% age-2, with all other ages accounting for about 11% (Fig. 6, upper panel). The AC survey trawl catch was predominately age-0 (50%) and age-2 fish (36%; Fig. 6, middle panel). The 2020 year-class made up 9% of the catch, while other ages made up the remaining 5%. Age-2 fish were 49% of the fall BT catch, age-3 fish were 18%, and age-0 fish were 23% (Fig. 6, bottom panel). Fish older than age-5 made up <1% of the

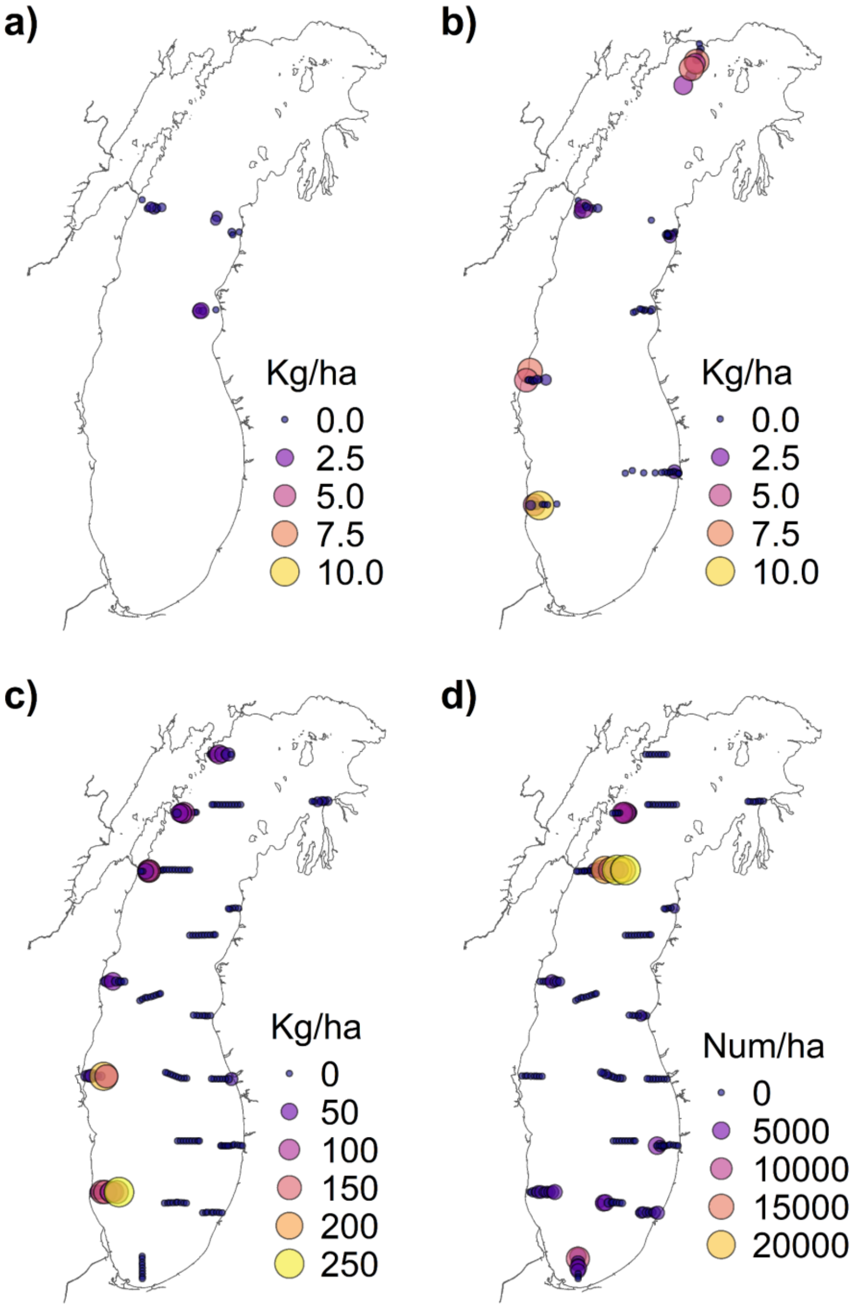

Figure 5. Alewife (*Alosa pseudoharengus)* biomass density (kg/ha) collected during the abbreviated spring bottom trawl (a), YAO Alewife (≥ 100 mm) collected in the fall bottom trawl (b) and acoustic survey (c), and the numeric density of age-0 Alewife from the acoustic survey (d) in 2023. Note the scale difference between maps.

catch. Evidence from the two annual surveys and the spring BT continues to point towards age truncation in the Alewife population, likely due to high predation pressure (see Warner et al. 2022 and prior reports for a full summary).

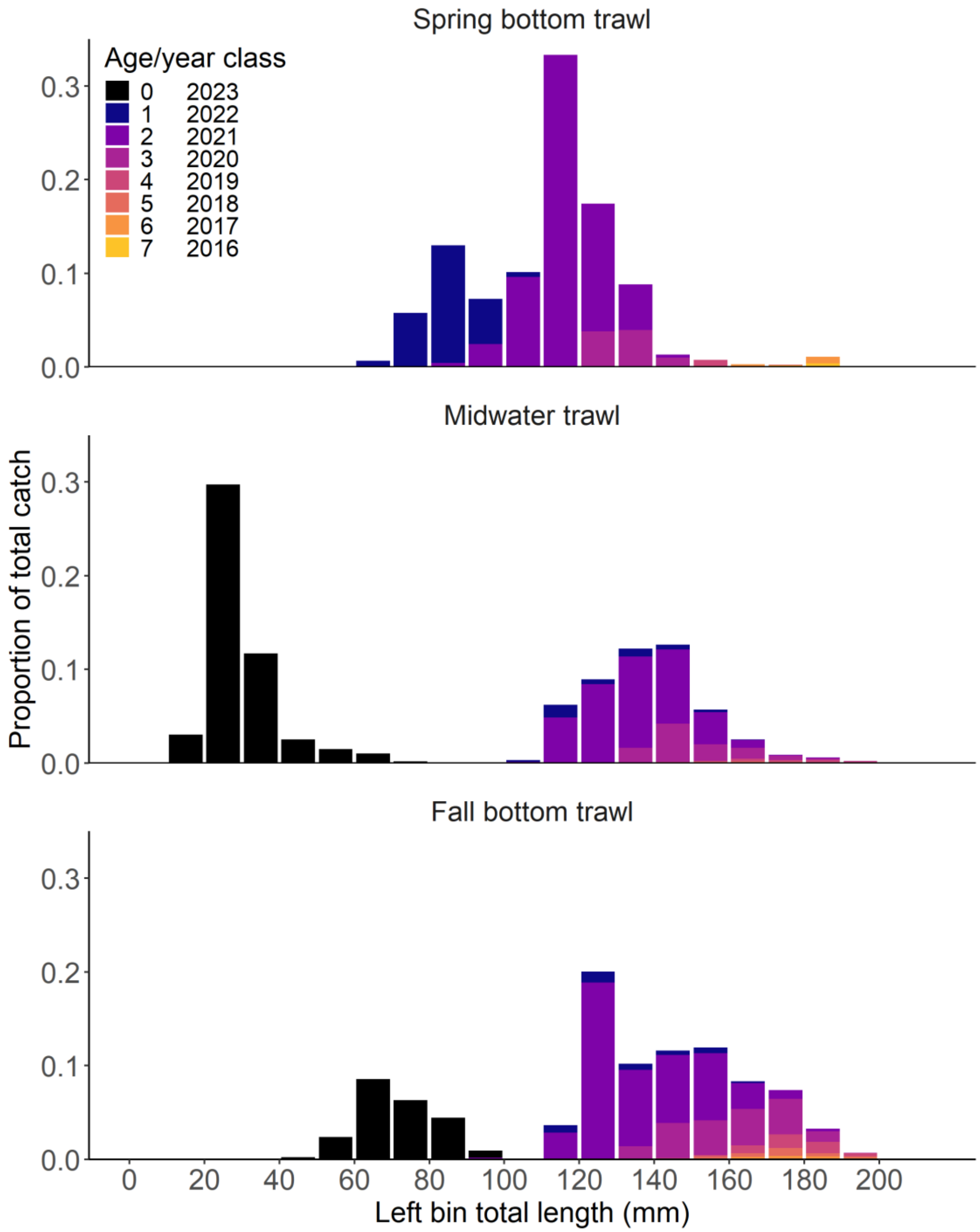

Figure 6. Age-at-length composition of Lake Michigan Alewife (*Alosa pseudoharengus*), as indexed by the spring bottom trawl (top panel), midwater trawl (from the acoustic survey, center panel), and fall bottom trawl (bottom panel) surveys in 2023.

Bloater

Biomass density of large Bloater in 2023 was 3.5 kg/ha in the AC survey and 2.1 kg/ha in the fall BT (Fig. 7a). Standard error bars from each survey overlapped for the second consecutive year and the fourth time since 2018. Regardless, the maximum biomass density measured from any survey during 2004-2021 was 7.3 kg/ha, which is an order of magnitude lower than the maximum biomass density measured during 1981-1997.

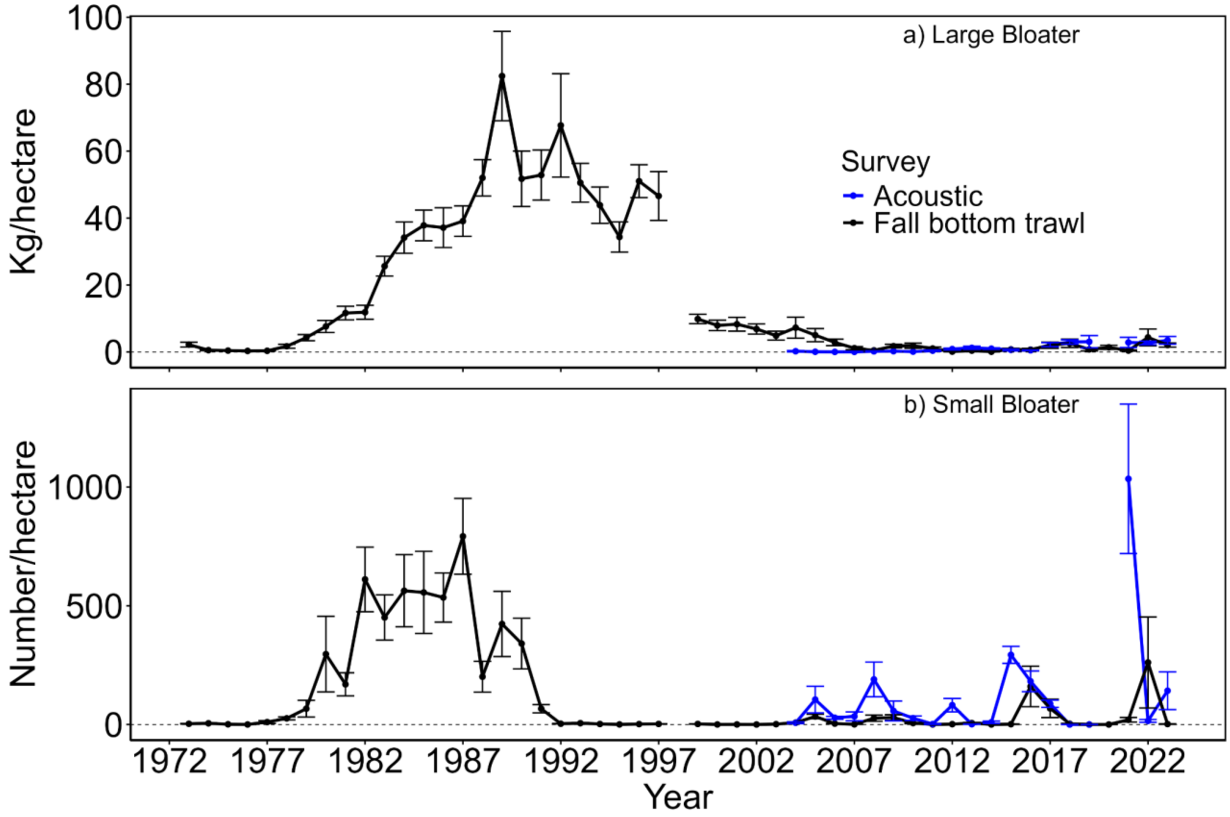

Figure 7. Density of large Bloater, *Coregonus hoyi,* (≥120 mm) as biomass density (a) and of small Bloater (<120 mm) as numeric density (b) in Lake Michigan as indexed by the fall bottom trawl and acoustic survey. Error bars in both panels are +/- standard error.

Following a historically high estimate in 2021 (1,035 fish/ha), the small Bloater (<120 mm) numeric density estimate from the AC survey was only 142 fish/ha in 2023, similar to the average over the time series (121 fish/ha; Fig. 7b). Conversely, the fall BT numeric density estimate of small Bloater was 2 fish/ha, well below the long-term mean of 117 fish/ha. Continued efforts to age Bloater from the past several years of surveys will provide insight into observed lags in small Bloater density peaks between the acoustic survey and the fall BT (e.g., 2021, 2022).

Catches of large Bloater in the 2023 fall BT survey were relatively sporadic, with the highest density occurring at 110 m outside of Frankfort (Fig. 8a). Densities of large Bloater in the AC survey were high throughout the southern and central portion of Lake Michigan (Fig. 8a). Small Bloater from the AC survey were primarily observed in the southern basin in deeper waters (Fig. 8b).

The exact mechanisms underlying poor Bloater recruitment from 1992-2004 period remain 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. 2014) may be contributing to the reduced Bloater recruitment, but neither one is the primary regulating factor. Further, these two species are at all-time low abundance. Based on the fall BT, the buildup of adult biomass during the 1980s and 1990s was due to 11 consecutive years of age-0 Bloater density > 100 fish/ha from 1980-1990. Following 13 years of weak production (i.e., <10 fish/ha) from 1992-2004, six year-classes with more than 100 age-0 Bloater/ha were detected by at least one of the surveys between 2005 and 2016. In 2018 and 2019, Lake Michigan produced two year-classes with near record lows of age-0 Bloater production prior to the historically high value in 2021. The large Bloater index appears trending upward in the AC survey (mean from 2004-2016: 0.43 kg/ha vs. 2017-2023: 2.9 kg/ha) and the fall BT appears to track similar biomass density estimates over time.

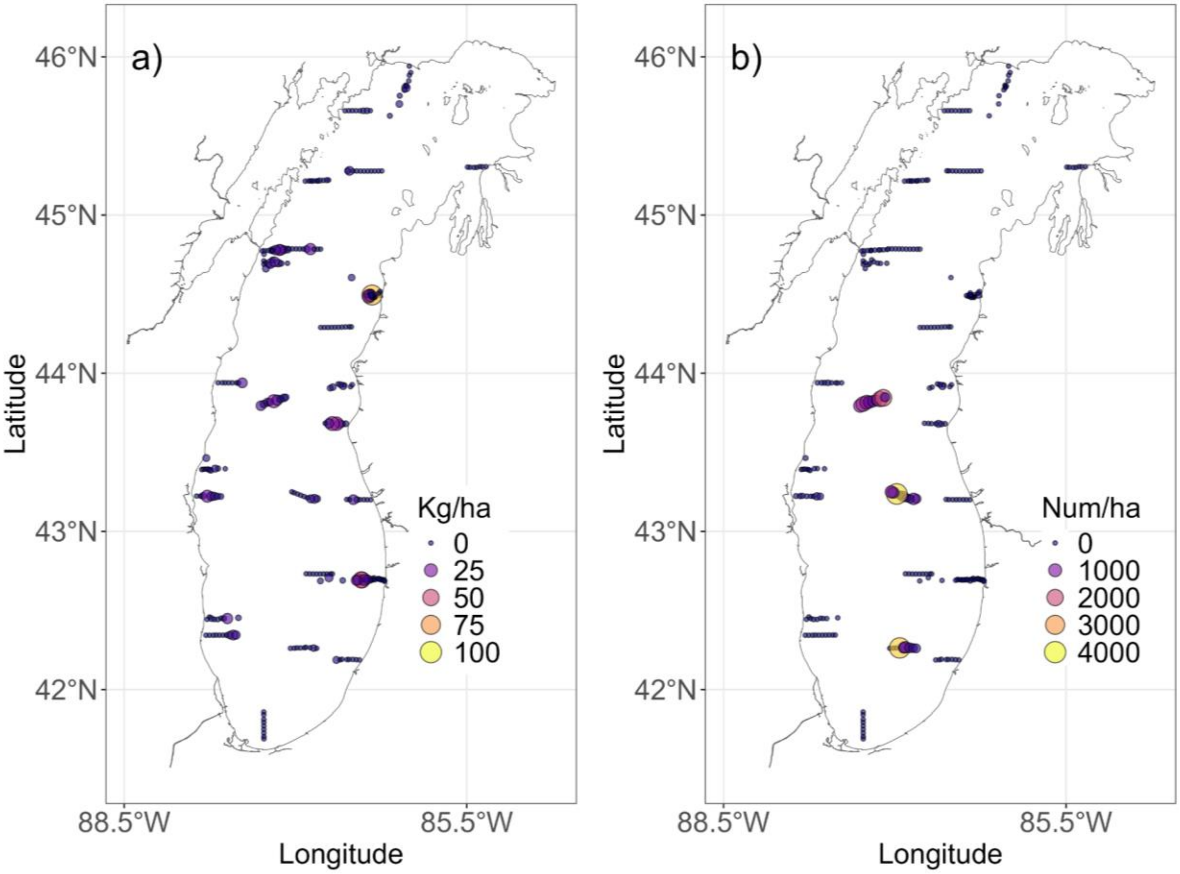

Figure 8. Large Bloater (≥ 120 mm) biomass in the fall bottom trawl and acoustic surveys (a) and small Bloater density (<120 mm) from the same surveys (b) in 2023. Note the scale difference between maps.

Rainbow Smelt

The 2023 index of large Rainbow Smelt biomass density was < 0.05 kg/ha in both the AC survey and the fall BT survey (Fig. 9a). Fall BT and AC survey estimates have been similar in most of the previous 19 years as the SE bars for the two surveys overlapped; in 2023, density decreased from 2022 in both surveys. Biomass density of large Rainbow Smelt has been <2 kg/ha since 1994, following the 1973-1993 era when Rainbow Smelt density averaged 3.7 kg/ha.

Numeric density of small Rainbow Smelt estimated by the 2023 AC survey was 119 fish/ha compared with 7 fish/ha by the fall BT (Fig. 9b). The value indexed by the AC survey in 2023 was the third highest in the period 2004-2022, while the fall BT has now indexed <10 fish/ha for small Rainbow Smelt each year since 2019. The highest biomass densities of Rainbow Smelt in the 2023 fall BT survey were collected in shallow waters (5, 18 m) outside of Saugatuck, while Rainbow Smelt densities were highest in the northern half of the lake during the AC survey (Fig. 10a). The highest numeric densities of small Rainbow Smelt in the AC survey were observed in the southern region of Lake Michigan (494 fish/ha; Fig. 10b). 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 abundance remained high. Results from a recent analysis suggested that predation by salmonines was not the primary driver of long-term temporal trends in Lake Michigan abundance (Tsehaye et al. 2014). Furthermore, a time series analysis through 2012 suggested that the production of age-0 fish relative to the number of spawners had increased since 2000 (relative to 1982-1999), yet those age-0 fish do not appear to be surviving to adulthood (Feiner et al. 2015).

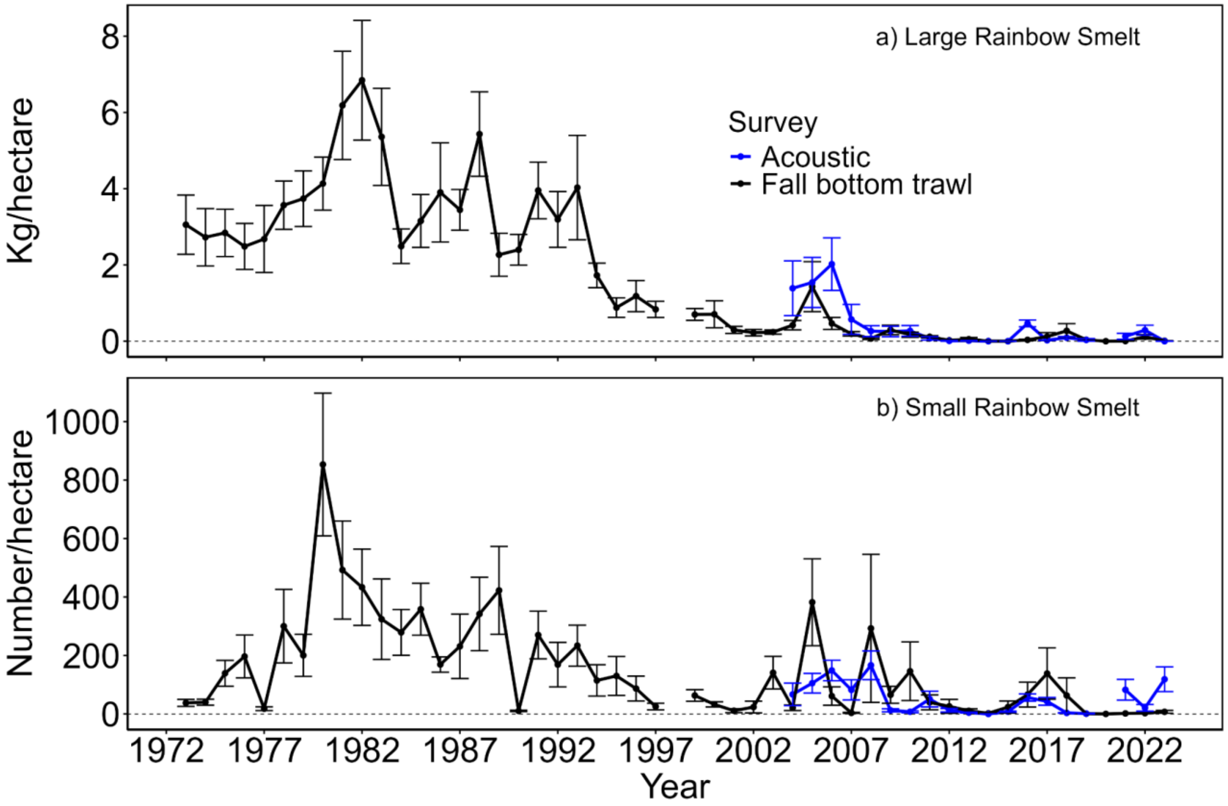

Figure 9. Density of large Rainbow Smelt, *Osmerus mordax*, (≥90 mm) as biomass density (a) and of small Rainbow Smelt (<90 mm) as numeric density (b) in Lake Michigan as indexed by the fall bottom trawl and acoustic survey. Error bars in both panels are +/- standard error.

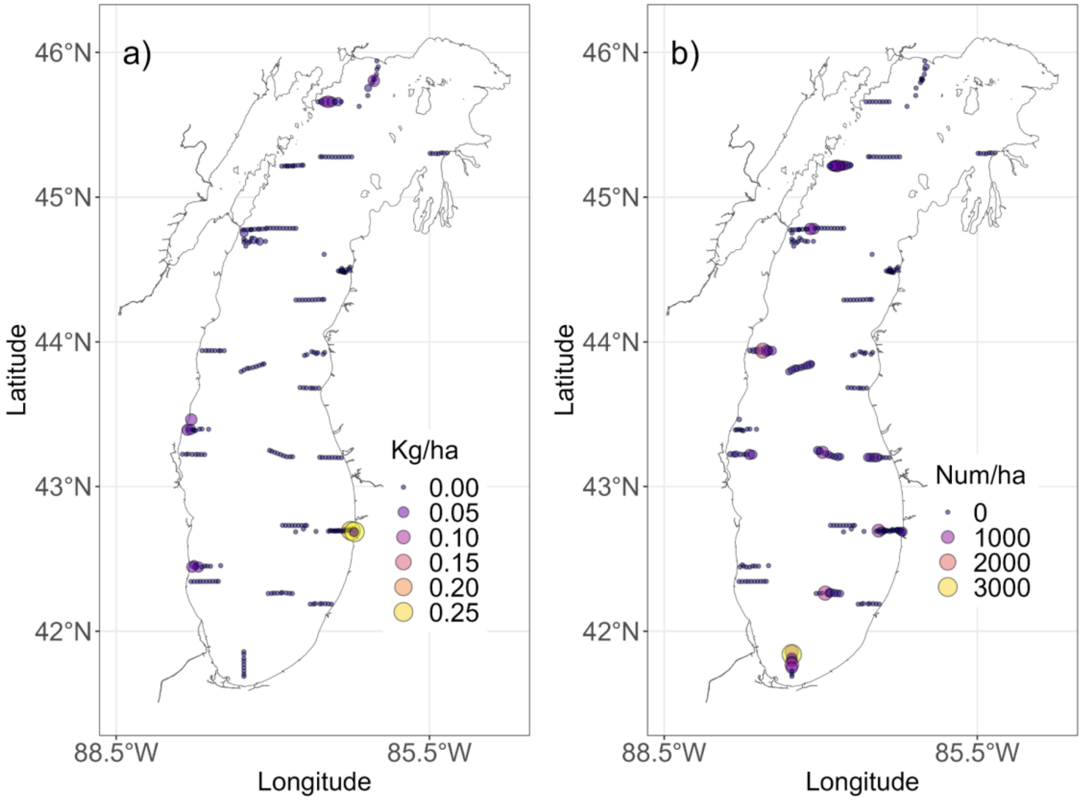

Figure 10. Large Rainbow Smelt (≥ 90 mm) (*Osmerus mordax*) biomass density (kg/ha) collected from the fall bottom trawl and acoustic survey (a), and the numeric density of small Rainbow Smelt (<90 mm) in both surveys (b) in 2023. Note the scale difference between maps.

Slimy Sculpin

Slimy Sculpin biomass indexed by the 2023 fall BT survey was 0.02 kg/ha, making it the 12th consecutive survey year with values below 0.25 kg/ha (Fig 11a). Slimy Sculpin abundance is regulated, at least in part, by predation from juvenile Lake Trout (Madenjian et al. 2005). In fact, Slimy Sculpin biomass began declining in 2010, which coincides 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 2019). The decline in Slimy Sculpin biomass does not appear to be an artifact of only sampling to a depth of 110 m for our standard tows. Comparisons of mean depth at capture and changes in biomass density with and without 128 m sites sampled 2013-2021 do not support the hypothesis that shifts of Slimy Sculpin distributions to depths outside our standard coverage have impacted density estimates (Madenjian et al. 2022). capture and biomass density are significantly higher when 128 m sites are included in recent biomass density estimates (Madenjian et al. 2022).

Deepwater Sculpin

Biomass density of Deepwater Sculpin in 2023 indexed by the fall BT was 0.36 kg/ha. Deepwater Sculpin have remained at relatively low levels since 2007 (mean = 0.67 kg/ha; Fig. 11b). 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. 2005); because neither of these species have increased since 2007, these mechanisms likely do not underlie the long-term downward trend. A likely explanation is that some proportion of the Deepwater Sculpin population has shifted to waters deeper than 110 m (the deepest depth for the standard trawling sites). In support of this, Madenjian and Bunnell (2008) found that Deepwater Sculpins have been captured at increasingly greater depths since the 1980s. Further, depth at

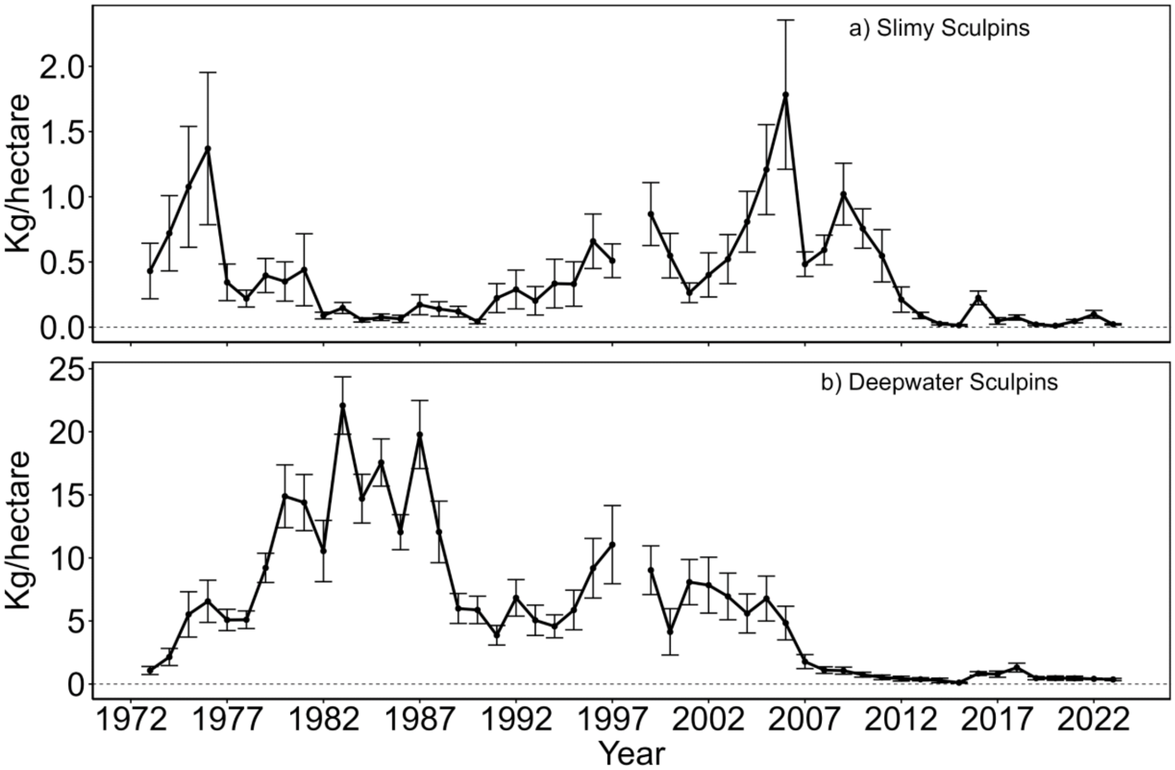

Figure 11. Biomass density of a) Slimy Sculpin and b) Deepwater Sculpin in Lake Michigan, 1973-2023, as measured by the fall bottom trawl survey. Error bars in both panels are +/- standard error. Refer to Table 1 for scientific names of fish species.

Ninespine Stickleback

Two stickleback species occur in Lake Michigan. Ninespine Stickleback is native, whereas Threespine Stickleback (*Gasterosteus aculeatus*) is non-native and was first collected in the fall BT survey during 1984 (Stedman and Bowen 1985) but has been rare in recent sampling years. Biomass density of Ninespine Stickleback has also been low (i.e., <0.1 kg/ha) since 2010. The density in 2023 was <0.01 kg/ha in the fall BT (Fig. 12a). Biomass of Ninespine Stickleback remained 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* (Fig. 12a; Madenjian et al. 2010). Since 2009, Ninespine Stickleback have declined, likely because piscivores began to incorporate them into their diets as Alewives declined. Jacobs et al. (2013) found Ninespine Sticklebacks in large Chinook Salmon diets (2% occurrence) during 2009-2010 after 0% occurrence in 1994-1996.

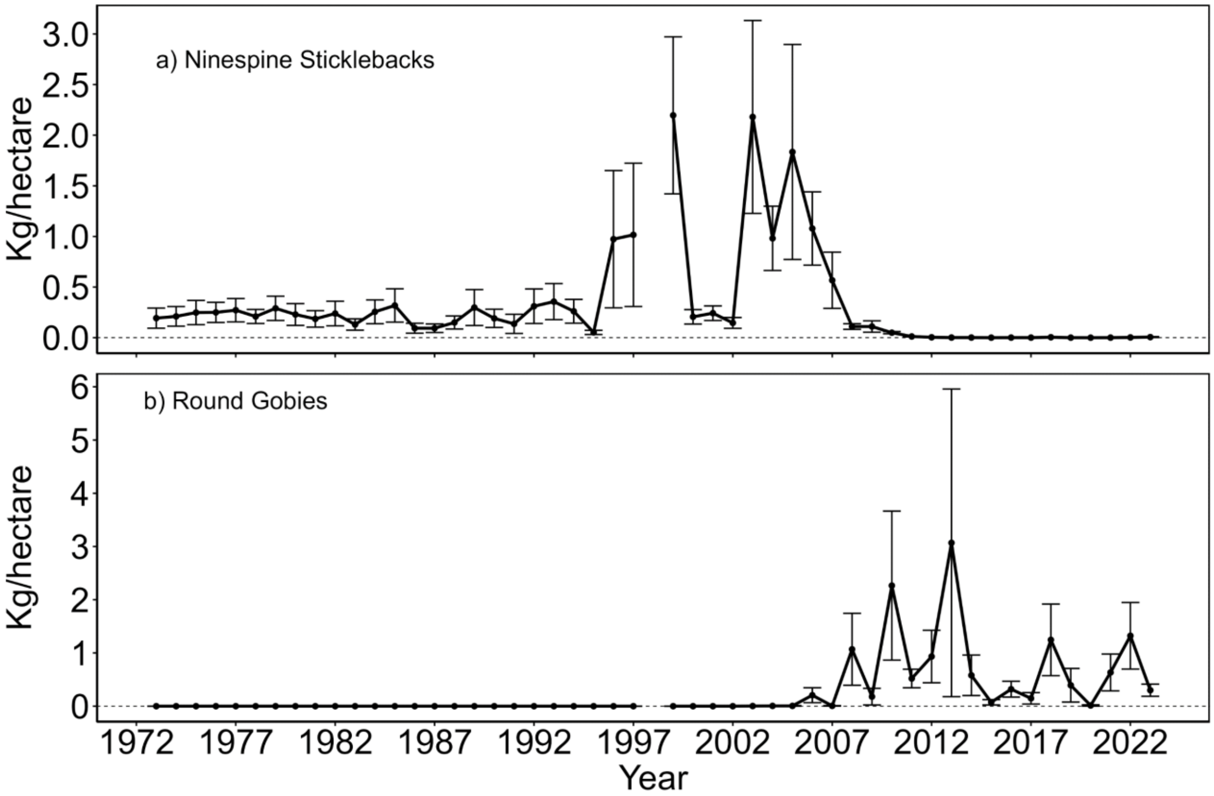

Figure 12. Biomass density of a) Ninespine Stickleback and b) Round Goby in Lake Michigan, 1973-2023, as measured by the fall bottom trawl survey. Error bars in both panels are +/- standard error. Refer to Table 1 for scientific names of fish species.

Round goby

Non-native Round Gobies were first detected in bays and harbors of Lake Michigan in 1993 (Clapp et al. 2001) but were not widespread enough to be sampled in the fall BT until 2003. By 2008, Round Goby were well established in the fall BT. However, as our survey samples only soft substrates ≥ 9 m in depth, our index is biased low because we are not sampling their preferred habitat in September (rocky substrate and shallow [< 9 m] depths). Round Goby biomass density was 0.30 kg/ha in the fall 2023 BT survey, continuing the pattern of large yearly fluctuations in density estimates (Fig. 12b). Densities were highest on the western side of the lake (Fig. 13), a common result and one that is attributed to rockier habitat relative to the eastern side of the lake (Janssen et al. 2005). Round Goby are consumed by a diverse array of fishes including Smallmouth Bass (Crane and Einhouse, 2016), Yellow Perch (Truemper et al. 2006), Burbot (Jacobs et al. 2010), Lake Trout (Luo et al. 2019), Lake Whitefish (*Coregonus clupeaformis*, Pothoven and Madenjian, 2013), and Cisco (Breaker et al, 2020), as well as Brown Trout, Steelhead, Coho

Salmon, and Chinook Salmon (Turschak et al. 2022). We hypothesize that Round Goby abundance in Lake Michigan is controlled by predation, given that annual mortality rate estimates range from 79 to 84% (Huo et al. 2014), comparable to adult Alewives (Tsehaye et al. 2014).

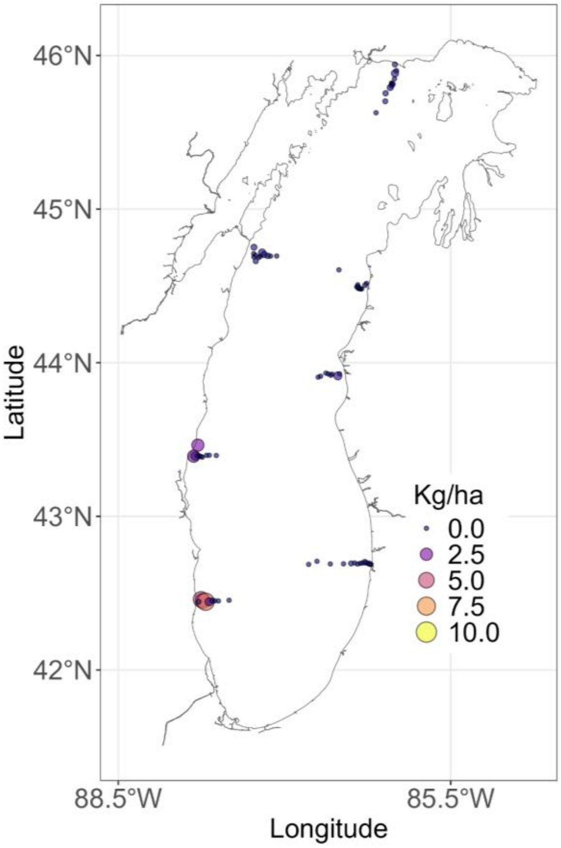

Figure 13. Map of Round Goby (*Neogobius melanostomus*) biomass estimates in Lake Michigan as measured by the 2023 fall bottom trawl survey.

Prey fish community trends

The prey fish community sampled by both BT surveys includes Alewife, Bloater, Rainbow Smelt, Deepwater Sculpin, Slimy Sculpin, Ninespine Stickleback, and Round Goby. Total prey fish biomass density from the fall BT was equal to 3.6 kg/ha, less than half the value observed in 2022. The reduction of total prey fish biomass was due to a decline in Bloater density from 2022. In 2023, Bloater still accounted for 58% of total biomass while Alewife accounted for 22% (Fig. 14a). Total fall BT biomass was still well below the long-term average of 33.8 kg/ha. Total biomass density first dropped below 10 kg/ha in 2007 and has since remained below that level except in 2013, when the biomass estimates for Alewife and Round Goby were uncertain.

The prey fish community sampled by the AC survey includes Alewife, Bloater, Rainbow Smelt, and Cisco. In 2023, this survey estimated a total biomass density of 14.8 kg/ha (Fig. 14b), the highest since 2004 but only 20% of the mean of the 1987, 1995, and 1996 surveys [72.4 kg/ha, Argyle 1992; Argyle et al. 1998)]. Alewife accounted for the large increase in total prey fish biomass density between 2022 and 2023 (Fig. 14b), as Alewife represented 76% of the total biomass in 2023.

Other species of interest

Burbot - Burbot and Lake Trout represent the native top predators in Lake Michigan. The recovery of Burbot during the 1980s was attributable to reduced Sea Lamprey (*Petromyzon marinus*; Wells and McLain 1973) abundance and perhaps a reduction in abundance of Alewife, which has been hypothesized to feed on Burbot larvae (Eshenroder and Burnham-Curtis 1999; Madenjian et al. 2008). Burbot collected in the fall BT are typically large individuals (>350 mm TL); juvenile Burbot typically do not inhabit areas sampled during the fall BT. Burbot biomass indexed by the 2023 fall BT was 0.16 kg/ha. This fall BT index is consistent with low estimates since 2012 (Fig. 15a). While it is unclear why Burbot catches in the fall BT survey have remained low in the face of relatively low densities of Sea Lamprey and Alewife over the past decade, Madenjian et al. (2022) hypothesized that a proportion of the Burbot population may have followed the Deepwater Sculpin population into deeper waters of Lake Michigan. This is partially supported by Burbot densities increasing between 91 and 110 m (averaged from 2013-2021) and because over 10% of mean biomass occurs at the 128 m sites (Madenjian et al. 2022).

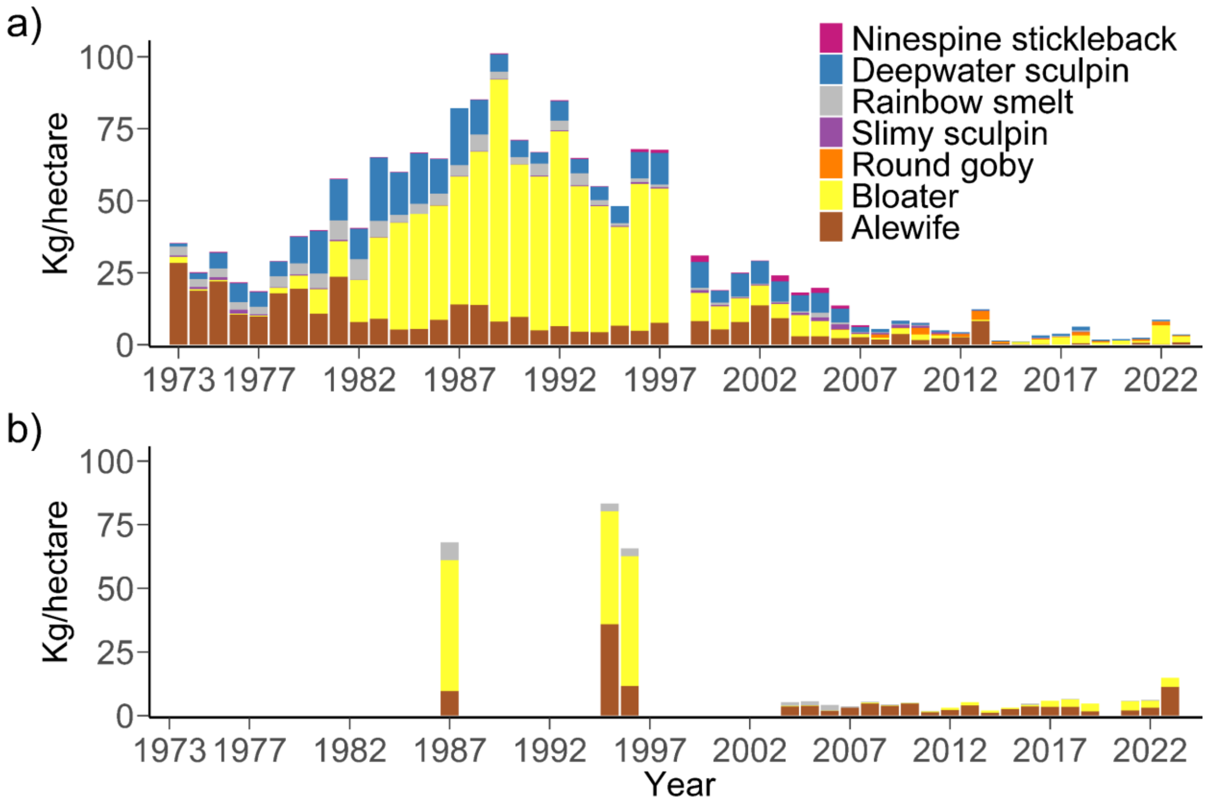

Figure 14. Estimated biomass of prey fishes sampled in the fall bottom trawl survey, 1973-2023 (a) and the estimated biomass of prey fishes sampled by the acoustic survey, 2004-2023, with historic estimates included (b). Refer to Table 1 for scientific names of fish species.

<ins>Small Yellow Perch</ins> - The Yellow Perch population in Lake Michigan has supported valuable recreational and commercial fisheries (Wells 1977). The fall BT survey provides an index of small (<100 mm) Yellow Perch numeric density, which serves as an indication of recruitment success. The 2005 year-class of Yellow Perch was the largest recorded (Fig. 15b) and the 2009 and 2010 year-classes also were higher than average. In the 2023 fall BT survey, a numeric density of 2.2 small Yellow Perch/ha was recorded, indicating a weak year-class. By comparison, a numeric density of over 150 small Yellow Perch/ha was estimated for 2005.

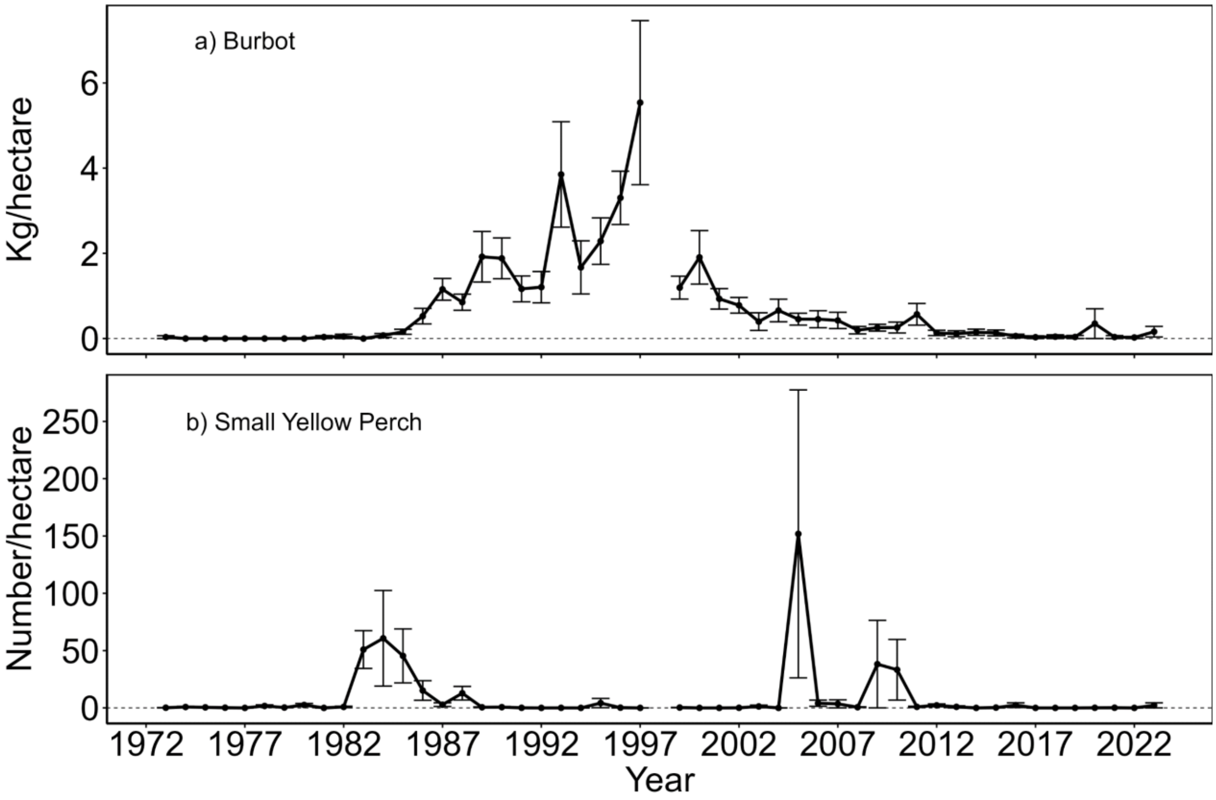

Figure 15. Biomass density of a) Burbot and b) numeric density of small Yellow Perch (<100 mm) in Lake Michigan, 1973-2023, as measured by the fall bottom trawl survey. Error bars in both panels are +/- standard error. Refer to Table 1 for scientific names of fish species.

Conclusions

The 2023 Alewife year-class appears to be strong, but uncertainty in this numeric density estimate exists due to unusually high abundance at a single transect (outside Sturgeon Bay). Removal of this transect from the analysis reduced mean age-0 density to 488 fish/ha, which is near the time series average. Our results indicate that the 2021 Alewife year-class is also a strong one. Yellow Perch and Rainbow Smelt appear to have had poor recruitment events in 2023. An average year-class for Bloater in 2023 is likely, but otolith aging will help confirm that small Bloater captured in the AC survey were largely age-0 fish. Comparing the 2023 AC estimate of YAO Alewife biomass to the previous estimates shows a >350% increase over the average value for the 2004-2022 period, and the 2023 estimate is the highest since the 1990s. YAO Alewife biomass from the 2023 fall bottom trawl survey was slightly higher than that in previous years and >5 kg/ha of Alewife were captured in a relatively high proportion of bottom trawl tows (6%) during 2023. Results from both surveys indicate an increase in biomass density of YAO Alewife from 2022 to 2023. Overall biomass as indexed by the fall bottom trawl still suggests that prey fish biomass is very low relative to that in previous decades, and while the biomass density estimated from the AC survey is the highest on record since 2004, it is still well below historic estimates in the late 1980s and mid-1990s. Age structure of the Alewife population still appears to be truncated.

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References

Argyle, R.L. 1992. Acoustics as a tool for the assessment of Great Lakes forage fishes. Fish. Res. 14:179-196.

Argyle, R. L., G. W. Fleischer, G. L. Curtis, J. V. Adams, and R. G. Stickel. 1998. An Integrated Acoustic and Trawl Based Prey Fish Assessment Strategy for Lake Michigan. A report to the Illinois Department of Natural Resources, Indiana Department of Natural Resources, Michigan Department of Natural Resources, and Wisconsin Department of Natural Resources. U. S. Geological Survey, Biological Resources Division, Great Lakes Science Center, 1451 Green Road, Ann Arbor, MI USA.

Brandt, S. B., 1980. Spatial segregation of adult and young-of-the-year alewives across a thermocline in Lake Michigan. Trans. Am. Fish. Soc. 109:469-478.

Breaker, B. S., K. L. Pangle, K. C. Donner, J. B. Smith, B. A. Turschak, R. M. Claramunt, D. B. Bunnell, and J. L. Jonas. 2020. Piscivory in recovering Lake Michigan cisco (*Coregonus artedi*): The role of invasive species. J. Great Lakes Res. 46:1402-1411.

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

Bunnell, D. B., J. G. Mychek-Londer, and C. P. Madenjian. 2014. Population-level effects of egg predation on a native planktivore in a large freshwater lake. Ecol. Freshw. Fish 23: 604-614.

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

Bunnell, D. B., H. J. Carrick, C. P. Madenjian, E. S. Rutherford, H. A. Vanderploeg, R. P. Barbiero, E. Hinchey-Malloy, S. A. Pothoven, C. M. Riseng, R. M. Claramunt, H. A. Bootsma, A. K. Elgin, M. D. Rowe, S. M. Thomas, B. A. Turschak, S. Czesny, K. L. Pangle, and D. M. Warner. 2018. Are changes in lower trophic levels limiting the capacity of prey fish biomass in Lake Michigan? Great Lakes Fish. Comm. Spec. Pub. 2018-01.

Bunnell, D. B., C. P. Madenjian, T. J. Desorcie, P. Armenio, and J. V. Adams. 2019. Status and trends of prey fish populations in Lake Michigan, 2018. A report to the Great Lakes Fishery Commission, Lake Michigan Committee, Ypsilanti, MI, March 25, 2019.

Chotkowski, M. A., and J. E. Marsden. 1999. Round goby and mottled sculpin predation on lake trout eggs and fry: field predictions from laboratory experiments. J. Great Lakes Res. 25: 26-35.

Clapp, D. F., P. J. Schneeberger, D. J. Jude, G. Madison, and C. Pistis. 2001. Monitoring round goby (*Neogobius melanostomus*) population expansion in eastern and northern Lake Michigan. J. Great Lakes Res. 27:335-341.

Crane, D. P., and D. W. Einhouse. 2016. Changes in growth and diet of smallmouth bass following invasion of Lake Erie by the round goby. J. Great Lakes Res. 42:405-412.

Elliott, R. F. 1993. Feeding habits of Chinook salmon in eastern Lake Michigan. M.S. Thesis. Michigan State University, East Lansing, MI.

Eshenroder, R. L. and M. K. Burnham-Curtis. 1999. Species succession and sustainability of the Great Lakes fish community. Pages 145-184 in W. W. Taylor and C. P. Ferreri (ed) Great Lakes Fisheries Policy and Management: A Binational Perspective. Michigan State University Press, East Lansing, MI.

Feiner, Z. S., D. B. Bunnell, T. O. Höök, C. P. Madenjian, D. M. Warner, and P. D. Collingsworth. 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.

FWS/GLFC. 2017. Great Lakes Fish Stocking database. U. S. Fish and Wildlife Service, Region 3 Fisheries Program, and Great Lakes Fishery Commission.

USGS, 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.

Happel, A., J. L. Jonas, P. R. McKenna, J. Rinchard, J. X. He, and S. J. Czesny. 2018. Spatial variability of lake trout diets in Lakes Huron and Michigan revealed by stomach content and fatty acid profiles. Can. J. Fish. Aquat. Sci. 7:95–106.

Huo, B., C. P. Madenjian, C. X.. Xie, Y. Zhao, T. P. O'Brien, and S. J. Czesny. 2014. Age and growth of round gobies in Lake Michigan, with preliminary mortality estimation. J. Great Lakes Res. 40:712-720.

Jacobs, G. R., C. P. Madenjian, D. B. Bunnell, D. M. Warner, and R. M. Claramunt. 2013. Chinook salmon foraging patterns in a changing Lake Michigan. Trans. Am. Fish. Soc. 142:362-372.

Jacobs, G. R., C. P. Madenjian, D. B. Bunnell, and J. D. Holuszko. 2010. Diet of lake trout and burbot in Northern Lake Michigan during spring: Evidence of ecological interaction. J. Great Lakes Res. 36:312-317.

Janssen, J., M. B. Berg, and S. J. Lozano. 2005. Submerged terra incognita: Lake Michigan's abundant but unknown rocky zones. Pages 113-139 in T. Edsall and M. Munawar (ed) State of Lake Michigan: Ecology, Health, and Management. Ecovision World Monograph Series, Aquatic Ecosystem Health and Management Society.

Lake Michigan LTWG. 2019. 2018 Lake Michigan Lake Trout Working Group Report. A report to the Great Lakes Fishery Commission, Lake Michigan Committee. Ypsilanti, MI. March 25, 2019.

Leonhardt, B.S., A. Happel, H. Bootsma, C. R. Bronte, S. Czesny, Z. Feiner, M. S. Kornis, J. Rinchard, B. Turschak, T. Höök. 2020. Diet complexity of Lake Michigan Salmonines: 2015-2016. J. Great Lakes Res. 46: 1044-1057.

Luo, M. K., C. P. Madenjian, J. S. Diana, M. S. Kornis, and C. R. Bronte. 2019. Shifting diets of lake trout in northeastern Lake Michigan. N. Am. J. Fish. Manage. 39:793-806.

Madenjian, C. P., and D. B. Bunnell. 2008. Depth distribution dynamics of the sculpin community in Lake Michigan. Trans. Am. Fish. Soc. 137:1346-1357.

Madenjian, C. P., G. L. Fahnenstiel, T. H. Johengen, T. F. Nalepa, H. A. Vanderploeg, G. W. Fleischer, P. J. Schneeberger, D. M. Benjamin, E. B. Smith, J. R. Bence, E. S. Rutherford, D. S. Lavis, D. M. Robertson, D. J. Jude, and M. P. Ebener. 2002. Dynamics of the Lake Michigan food web, 1970-2000. Can. J. Fish. Aquat. Sci. 59:736-753.

Madenjian, C. P., D. W. Hondorp, T. J. Desorcie, and J. D. Holuszko. 2005. Sculpin community dynamics in Lake Michigan. J. Great Lakes Res. 31:267-276.

Madenjian, C. P., R. O'Gorman, D. B. Bunnell, R. L. Argyle, E. F. Roseman, D. M. Warner, J. D. Stockwell, and M. A. Stapanian. 2008. Adverse effects of alewives on Laurentian Great Lakes fish communities. N. Am. J. Fish. Manage. 28:263-282.

Madenjian, C. P., D. B. Bunnell, and O. T. Gorman. 2010. Ninespine stickleback abundance in Lake Michigan increases after invasion of dreissenid mussels. Trans. Am. Fish. Soc. 139:11-20.

Madenjian, C. P., D. B. Bunnell, D. M. Warner, S. A. Pothoven, G. L. Fahnenstiel, T. F. Nalepa, H. A. Vanderploeg, I. Tsehaye, R. M. Claramunt, and R. D. Clark, Jr. 2015. Changes in the Lake Michigan food web following dreissenid mussel invasions: a synthesis. J. Great Lakes Res. 41(Suppl. 3):217-231.

Madenjian, C. P., D. B. Bunnell, R. W. Tingley, and P. M. Dieter. 2022. Additional deepwater sampling of prey fish in Lake Michigan annual bottom trawl survey reveals new insights for depth distribution dynamics. J. Great Lakes Res. 48:1288-1297.

Pothoven, S. A., and C. P. Madenjian. 2013. Increased piscivory by lake whitefish in Lake Huron. N. Am. J. Fish. Manage. 33:1194-1202.

Rybicki, R. W., and D. F. Clapp. 1996. Diet of chinook salmon in eastern Lake Michigan, 1991-93. MDNR Fisheries Research Report No 2027.

Stedman, R. M., and Bowen II, C. A. 1985. Introduction and spread of the threespine stickleback (*Gasterosteus aculeatus*) in lakes Huron and Michigan. J. Great Lakes Res. 11:508-511.

Steinhart, G. B., R. A. Stein, E. A. Marschall. 2004a. High growth rate of young-of-the-year smallmouth bass in Lake Erie: a result of round goby invasion? J. Great Lakes Res. 30, 381-389.

Steinhart, G. B., E. A. Marschall, and R. A. Stein. 2004b. Round goby predation on smallmouth bass offspring in nests during simulated catch-and-release angling. Trans. Amer. Fish. Soc. 133: 121-131.

Tingley III, R. W., D. M. Warner, C. P. Madenjian, P. D. Dieter, B. Turschak, D. Hanson, K. R. Phillips, and C. L. Geister. 2023. Status and trends of pelagic and benthic prey fish populations in Lake Michigan, 2022. Great Lakes Fishery Commission, Ypsilanti, MI.

Truemper, H. A., T.E. Lauer, T.S. McComish, and R.A. Edgell. 2006. Response of yellow perch diet to a changing forage base in southern Lake Michigan, 1984-2002. J. Great Lakes Res. 32:806-816.

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

Turschak, B. A., C. R. Bronte, C. Czesny, B. Gerig, A. Happel, T. O. Höök, M. S. Kornis, B. S. Leonhardt, B. G. Matthias, J. Rinchard, and H. Bootsma. 2022. Temporal variation in the niche partitioning of Lake Michigan salmonines as it relates to alewife abundance and size structure. Can. J. Fish. Aquat. Sci. 79:487-502.

Warner, D.M., L.G. Rudstam, and R.A. Klumb. 2002. In situ target strength of alewives in freshwater. Trans. Am. Fish. Soc. 131:212-223.

Warner, D. M., C. S. Kiley, R. M. Claramunt, and D. F. Clapp. 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., R. M. Claramunt, J. S. Schaeffer, D. L. Yule, T. R. Hrabik, B. Pientka, L. G. Rudstam, J. D. Holuszko, and T. P. O'Brien. 2012. Relationship between mid-water trawling effort and catch composition uncertainty in two large lakes (Huron and Michigan) dominated by alosines, osmerids, and coregonines. Fisheries Research 123/124:62-69.

Warner, D. M., K. Phillips, B. Turschak, D. Hanson, and J. Smith. 2019. Status of pelagic prey fishes in Lake Michigan, 2018. A report to the Great Lakes Fishery Commission, Lake Michigan Committee, Ypsilanti, MI.

Warner, D. M., R. W. Tingley, III, C. P. Madenjian, B. Turschak, D. Hanson. 2022. Status and trends of pelagic and benthic prey fish populations in Lake Michigan, 2021. Great Lakes Fishery Commission, Ypsilanti, MI.

Wells, L., and A. L. McLain. 1973. Lake Michigan: man's effects on native fish stocks and other biota. Great Lakes Fish. Comm. Tech. Rep. 20. 56 p.

Wells, L. 1977. Changes in yellow perch (*Perca flavescens*) populations of Lake Michigan, 1954-75. J. Fish. Res. Board Can. 34:1821-1829.

Yule, D. L., J. V. Adams, D. M. Warner, T.R. Hrabik, P.M. Kocovsky, B. C. Weidel, L. G. Rudstam, and P. J. Sullivan. 2013. Evaluating analytical approaches for estimating pelagic fish biomass using simulated fish communities. Can. J. Fish. Aquat. Sci. 70:1845-1857.