Status and Trends of Pelagic and Benthic Prey Fish Populations in Lake Michigan, 2024^{1,2}

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Please direct questions to our Data Management Librarian, Sofia Silvis, at sasilvis@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). In recent years, wild juvenile (<400 mm) Lake Trout (Salvelinus namaycush) have also become more common in the fall bottom trawl. The AC survey has been conducted each late summer/early fall since 2004 (except 2020). The 2024 AC survey consisted of 24 transects [468] km total (291 miles)] covering bottom depths ranging from 16 to 173 m and 38 midwater trawl tows at 4 to 72 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. In spring of 2024, an additional spring bottom trawl survey (spring BT) was implemented across six of the transects sampled in the fall and sites ranged in depth from 9 to 237 m. The goal of the spring BT, conducted annually since 2021 with differing levels of effort, was to explore seasonal differences in biomass density and distributions of key prey species, most notably Alewife.

Total prey fish biomass density from the spring BT was 5.7 kg/ha. For the AC survey, total biomass density of prey fish equaled 10.8 kg/ha, more than double the long-term average (2004-2023) of 5.1 kg/ha but 4.0 kg/ha lower than the 2023 estimate. For the fall BT, total biomass density of prey fish equaled 2.1 kg/ha, the lowest value since 2020 and 69% lower than the average from 2004-2023 (6.8 kg/ha). The 2024 fall BT biomass density was only 6.3% of the average over the entirety of the time series (1973-2023; 33.1 kg/ha). Over the period both surveys have been conducted (2004-2024), total biomass density has trended downward in the fall BT (despite a high 2022 estimate) and remained relatively stable in the AC survey.

Deepwater Sculpin and Bloater were the most common species (by biomass) among prey fishes in the spring BT while the AC survey and fall BT reported co-dominance of Bloater and Alewife. Mean biomass of yearling and older (YAO) Alewife was 1.30 kg/ha in the spring BT, 4.7 kg/ha in the AC survey, and 0.68 kg/ha in the fall BT. Since 2014, annual survey results suggest that the catchability of YAO Alewives for the fall BT is substantially lower than the AC survey. Like previous spring surveys, Alewives were aggregated in deeper habitats, with 93% of biomass collected between 110 and 201 m. Results of the 2024 spring BT align with past spring surveys and do not suggest that spring bottom trawling provides a better index of age-2 and older Alewives than fall bottom trawling, even with adjustments for differences in habitat use. However, the spring BT does appear to index age-1 Alewives more effectively than the fall BT.

The 2024 AC survey YAO Alewife biomass density estimate was 77% higher than the average from 2004-2023. The Alewife population of Lake Michigan appears to be composed mostly of young fish and the proportion of age-4 and older Alewives was <1.8% in each of the three surveys. Age-0 Alewife numeric density from the AC survey was 510 fish/ha in 2024, slightly higher than the long-term mean (486 fish/ha). Biomass density of large (≥120 mm) Bloater was

5.2 kg/ha in the AC survey and 0.76 kg/ha in the fall BT, while total Bloater biomass in the spring BT was 1.8 kg/ha - all three estimates were much lower than what was estimated by the fall BT between 1981 and 1998. The density of small (<120 mm) Bloater was 456 fish/ha in the AC survey, the second highest value in the time series and potentially reflective of an above-average 2024 year-class. Meanwhile, small Bloater density estimated in the fall BT was only 16 fish/ha. Biomass density of large Rainbow Smelt (≥90 mm) was 0.21 kg/ha in the AC survey and 0.03 kg/ha in the fall BT survey, continuing the trend of low large Rainbow Smelt biomass observed since 2001. Numeric density of small (<90 mm) Rainbow Smelt was 31 fish/ha in the AC survey and 143 fish/ha in the fall BT.

All four prey fish species indexed only by the fall BT had below-average biomass densities regardless of trawling season. Deepwater Sculpin biomass density was 0.26 kg/ha, which makes 14 of the past 15 years with biomass <1 kg/ha. Spring BT Deepwater Sculpin biomass density (2.0 kg/ha) was higher than any fall BT estimate since 2006, likely reflective of including bottom trawls at greater depths in the spring than the fall. Slimy Sculpin was estimated to be < 0.04 kg/ha in the spring and fall BT, an order of magnitude lower than the long-term average from the fall BT. Round Goby biomass density estimates were low and similar across seasons (0.43 kg/ha in the spring and 0.10 kg/ha in the fall). Ninespine Stickleback density was 3.9 fish/ha in the fall BT and no fish were collected in the spring BT.

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

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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. The non-native species Alewife (Alosa pseudoharengus) is a key prey fish in the Lake Michigan food web because it serves as the primary prey for Lake Michigan salmonines (Elliott 1993; Rybicki and Clapp 1996; Warner et al. 2008; Jacobs et al. 2013). Alewife also influence food web structure 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 that 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 component of the food web given their importance as prey for Lake Trout and other fishes (Happel et al. 2018, Leonhardt et al. 2020), Brown Trout (Salmo trutta, Leonhardt et al. 2020), Cisco (Coregonus artedi; Breaker 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 acoustic (AC) 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 and has consistently collected wild juvenile Lake Trout since the early 2000s. In turn, the AC survey provides an abundance index for age-0 Alewife, which is an early indicator of Alewife year-class strength (Warner et al. 2008), as well as Cisco. Both surveys provide relative indices of Bloater,

Rainbow 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 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 a long-term shift in the depth distribution of Deepwater Sculpins (Madenjian et al. 2015; Bunnell et al. 2018). The decline in YAO Alewife biomass as indexed by the fall BT has been accompanied by a divergence from the AC survey index, which has been an order of magnitude higher in recent years (Warner et al. 2024). 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 (refer to 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 (refer to Bunnell et al. 2019; Warner et al. 2019; Tingley et al. 2023). Below, we provide a high-level overview of all methods.

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 2024, we sampled 11 deepwater sites between 128 and 164 m in depth. 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 lake bottom for each tow with a head-rope depth sensor that provides a more accurate estimate of area (ha) swept.

We designed the 2024 spring BT survey so that the prey fish indices generated from the survey would be directly comparable with those from the 2024 fall and 2022 spring BT surveys. We conducted 60 tows in 18 m increments between 9 and 237 m depth across six extended fall transects (excluding Manistique; Fig. 1). We chose to allocate the number of tows per 18 m depth-bin by optimizing sampling effort based on depth-bin area and the standard deviation of Alewife biomass density from recent spring daytime trawls conducted on Lake Michigan (Adams et al. 2006; Tingley et al. 2023). We ensured that at least three tows were conducted in each depth bin

and that the two shallowest standard fall BT sites (9 m) were sampled, given the potential for Alewife to have already moved towards shallow spawning grounds. A total of 33 tows were conducted at standard fall BT sites (9 - 110 m) and 27 tows at depths between 128 m and 236 m.

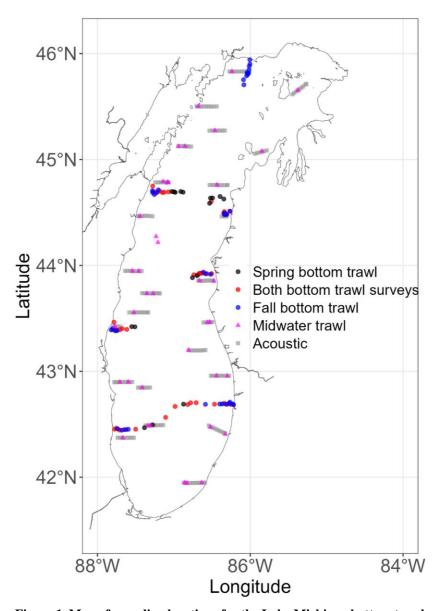


Figure 1. Map of sampling locations for the Lake Michigan bottom trawl and acoustic surveys in 2024. Gray squares represent acoustic transects and magenta triangles represent midwater trawl locations. Bottom trawl sites are color-coded by season in which they were sampled: spring (black), fall (blue), and both seasons (red).

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, spring BT) and a stratified cluster design (AC). For the AC survey, split beam transducers with a nominal frequency of 120 kHz (range 120-129) were used to estimate numeric fish density along each of the 24 transects sampled in 2024 (Fig. 1). While sampling those transects, midwater deployed to trawls are 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 fish density estimates were generated with consideration of the six geographic strata (north nearshore north east. nearshore west, north offshore, south nearshore, south offshore, west nearshore: refer to Warner et al. 2019) and vertical depth layer. Numeric fish density estimates for the upper part of the water column (<40 m)

were derived using the NearD method whereby catch from the nearest midwater trawl (Euclidean distance) in the same depth layer was used to apportion acoustic data to fish categories (age or size groups within species; Yule et al. 2013). 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 refer to Warner et al. (2019). Lakewide average numeric and biomass density are estimated by calculating the population mean for a stratified cluster with known areas.

Given the importance of the Alewife age distribution for the stock assessment model, sagittal otoliths were removed from a subset of 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 deemed unknown. In 2024, ages from 603 and 212 otoliths were successfully obtained from Alewife sampled in the spring and fall BT surveys, respectively, and ages from 227 otoliths were successfully estimated from Alewife sampled in the AC survey. Aging was unsuccessful for nineteen Alewife across all surveys. 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 2024 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 used for the fall BT and acoustic surveys (e.g., YAO Alewife, large Bloater).

Results

Alewife

Yearling and older Alewife biomass density estimates in 2024 were 1.3 kg/ha in the spring BT, 4.7 kg/ha in the AC survey, and 0.68 kg/ha in the fall BT (Fig. 2). The AC survey YAO Alewife biomass density estimate was the second highest in the time series and marks the second consecutive year of an above average biomass density estimate. Like past surveys in April and May (Tingley et al. 2023, Warner et al. 2024), spring BT Alewife densities were highest in deepwater habitats (≥110 m) throughout the lake, with biomass >5 kg/ha in six tows between 110 and 201 m (Fig. 3a). By contrast, YAO Alewives were only collected sporadically in deepwater tows (128-164 m) during the fall BT, with almost 88% of total biomass coming in a single 18 m tow along the Sturgeon Bay transect in northwestern Lake Michigan (Fig 3b). YAO Alewives were relatively well-distributed throughout the lake during the AC survey, with the highest catches occurring in northwestern Lake Michigan (79.5 kg/ha, Fig. 3c).

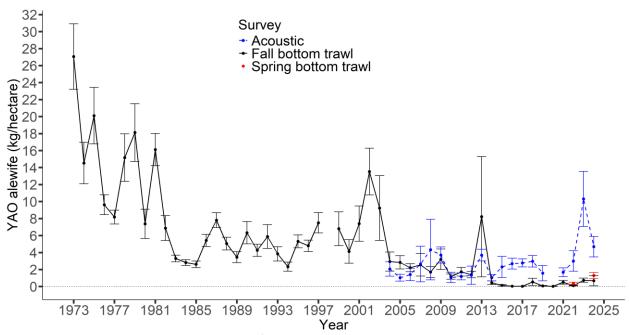


Figure 2. Yearling and older (YAO) Alewife (*Alosa pseudoharengus*; ≥100 mm) biomass density for the spring bottom trawl, fall bottom trawl, and acoustic surveys in Lake Michigan, United States. Error bars are +/-standard error.

Fall BT and AC survey YAO Alewife biomass densities did not have overlapping standard error (SE) bars for the ninth consecutive year, a departure from general agreement through the first ten years of the AC survey (2004-2013). Results of the annual surveys over the past decade indicate that fall BT catchability has declined resulting in a notable reduction in annual index values that have remained below 0.75 kg/ha since 2014. However, assuming the AC survey more accurately indexes YAO Alewife biomass, estimates from the AC survey during the last five years sampled (averaging 4.7 kg/ha) are 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).

The spring BT YAO Alewife biomass density index was double the value observed in the fall BT but SE bars were overlapping between the two surveys; by contrast, the Spring BT index was 73% lower than the AC survey index, and error bars did not overlap (Fig. 2). The relative differences in biomass density indices across the three surveys were similar to 2022, the last time a full spring BT was completed. However, we note that the YAO Alewife numeric density was far lower in the fall BT than the spring BT in 2024 (42 ± 39 vs. 236 ± 62 ha) and 2022 (4 ± 1 vs. 43 ± 15 /ha). The difference between numeric density but not biomass density across seasons is due to higher yearling Alewife catchability during the spring than fall. YAO Alewife catch in the 2024 spring BT was 95% yearlings while the fall BT was 54% yearling fish, similar to differences observed in 2022 (85% in the spring, 29% in the fall) and reflective of observed underrepresentation of age-1 fish in the fall BT on Lake Michigan (Fig. 4a; Eck and Brown 1985; Krause 1999). Greater catchability of yearlings during the spring than the fall aligns with differences observed in Lake Ontario, where yearling Alewife catch is consistently higher in the spring (B. Weidel, USGS, oral comm, 2022).

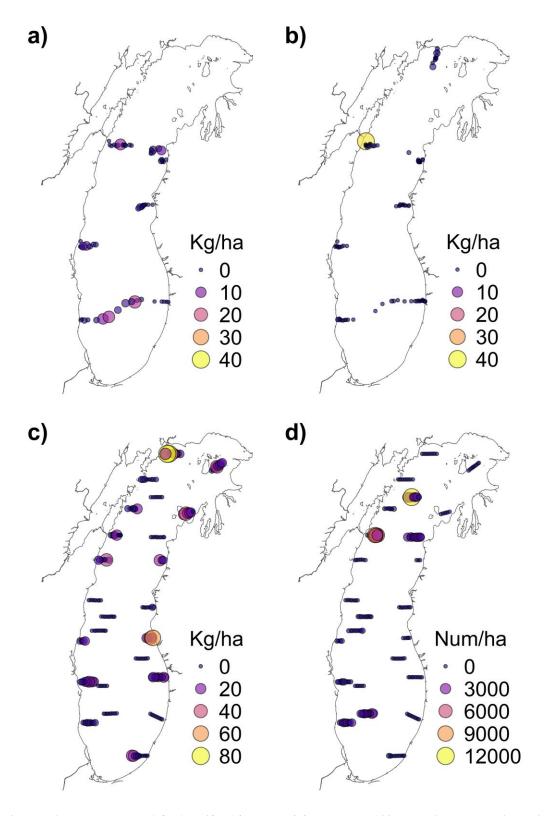


Figure 3. Yearling and older (YAO) Alewife (Alosa pseudoharengus; ≥ 100 mm) biomass density as indexed by the spring bottom trawl survey (a), by the fall bottom trawl survey (b), and by the acoustic survey (c), and the numeric density of age-0 Alewife from the acoustic survey (d) Lake Michigan, United States in 2024. Note the scale difference between maps.

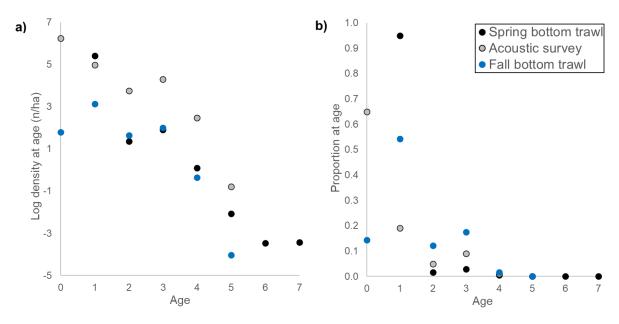


Figure 4: Natural log-transformed density at age (n/ha; a) and proportion at age (b) for Alewives (*Alosa pseudoharengus*) collected in the 2024 spring bottom trawl, acoustic survey, and fall bottom trawl in Lake Michigan, United States.

The AC survey was predominately age-0 (65%) and age-1 fish (19%; Fig. 4b). The 2021 year-class (age-3 fish) made up 9% of the total AC survey estimate, while other ages made up the remaining 6%. Age-1 fish were 54% of the fall BT catch, with age-3 Alewife being the next most abundant year-class (Fig. 4b). No survey recorded age-4 and older fish accounting for more than 1.8% of catch. Evidence from the two annual surveys and the spring BT still indicate age truncation in the Alewife population, likely due to high predation pressure (refer to Warner et al. 2022 and prior reports for a complete summary).

Similar to 2023, age-0 Alewives sampled in the AC survey were at the highest densities in the northwest and northcentral portion of the lake (Warner et al. 2024; Fig. 3d). Numeric density of age-0 Alewives estimated from the AC survey was 510 fish/ha in 2024 (Fig. 5). The 2024 estimate is just above the mean over the entire time series (486 fish/ha) and follows the 3rd strongest year class on record; however, it is less than one-third of the numeric densities reported during the high recruitment events observed in 2005 and 2010.

Bloater

Biomass density of large Bloater in 2024 was 1.8 kg/ha in the spring BT, 5.2 kg/ha in the AC survey, and 0.76 kg/ha in the fall BT (Fig. 6). Large Bloater densities in BT survey tows were highest in northern Lake Michigan and were more dispersed in the AC survey (Fig. 7a-c). Large Bloater biomass indices remain an order of magnitude lower than the maximum biomass density measured during 1981-1997. However, the AC survey has shown an increasing trend beginning in 2011 and the current large Bloater biomass estimate is the highest recorded in the AC survey dataset (2004-2024).

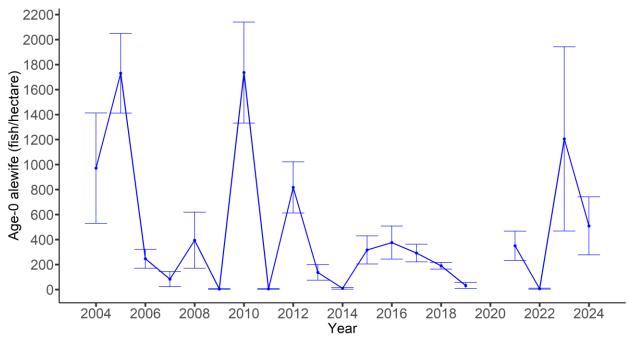


Figure 5. Age-0 Alewife (*Alosa pseudoharengus*) numeric density as indexed by the acoustic survey from 2004-2024 in Lake Michigan, United States. Error bars are +/- standard error.

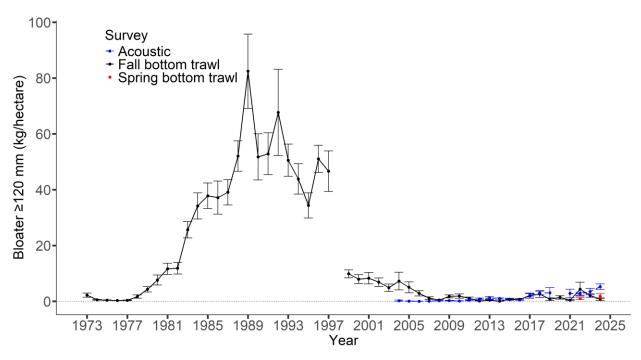


Figure 6. Biomass density of large Bloater (*Coregonus hoyi*; ≥120 mm) in Lake Michigan, United States as indexed by the spring bottom trawl, fall bottom trawl, and acoustic survey. Error bars are +/- standard error.

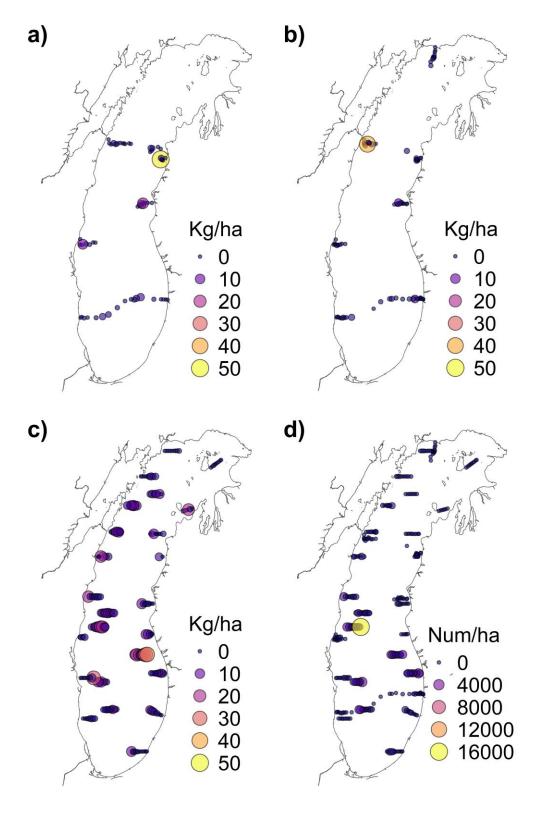


Figure 7. Large Bloater (Coregonus hoyi; \geq 120 mm) biomass density as indexed by the spring bottom trawl survey (a), by the fall bottom trawl survey (b), and by the acoustic survey (c), and the numeric density of small Bloater (< 120 mm) from the acoustic and fall bottom trawl survey (d) in 2024 in Lake Michigan, United States. Note the scale difference between maps.

The small Bloater (<120 mm) numeric density estimate from the AC survey was 456 fish/ha in 2024, the second highest value in the time series (Fig. 8). However, only 16 fish/ha were recorded in the fall BT, well below the long-term mean but consistent with low recruitment years. Small bloater densities in the AC survey were highest in the central and southern basin (Fig. 7d).

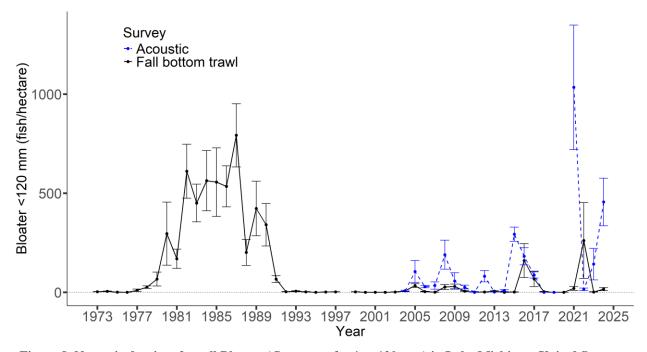


Figure 8. Numeric density of small Bloater ($Coregonus\ hoyi; < 120\ mm$) in Lake Michigan, United States as indexed by the fall bottom trawl and acoustic surveys. Error bars are +/- standard error.

Rainbow Smelt

The 2024 index of large Rainbow Smelt biomass density was <0.20 kg/ha in all three surveys (Fig. 9). 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 2024 AC survey was 31 fish/ha compared and 143 fish/ha by the fall BT, nearly opposite the values observed in 2023 (Fig. 10). The value indexed by the fall BT was the highest in seven years, but most fish (84%) were collected in a single 18 m tow outside of Manistique. The 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. Current evidence suggests 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, yet those age-0 fish do not appear to be surviving to adulthood (Feiner et al. 2015). In recent years, age-0 indices similar to what was observed in the 2024 fall BT have not translated into notably higher adult biomass in Lake Michigan.

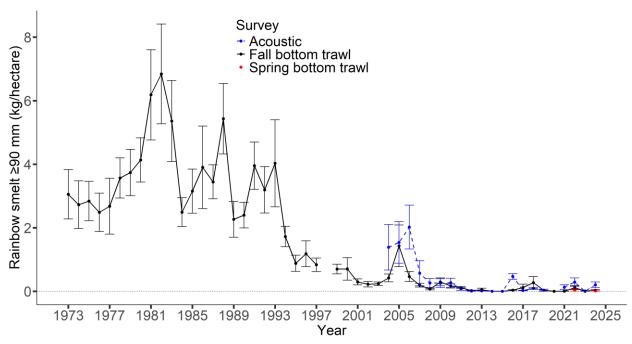


Figure 9. Biomass density of large Rainbow Smelt (Osmerus mordax; \geq 90 mm) in Lake Michigan, United States as indexed by the fall bottom trawl and acoustic surveys. Error bars are +/- standard error.

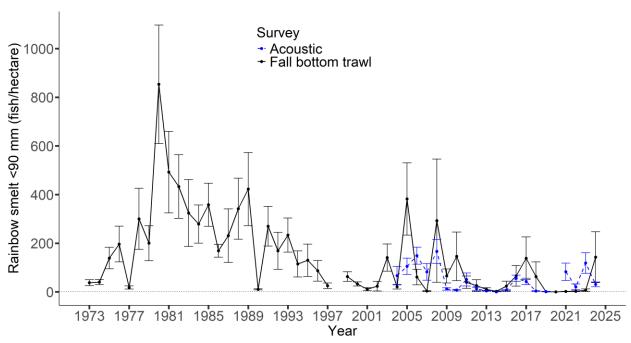
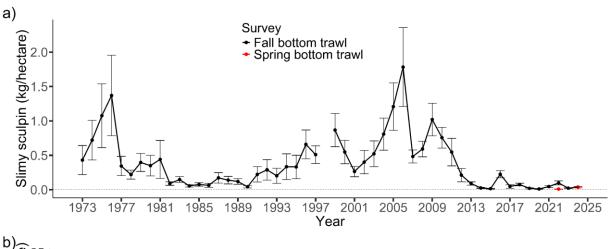


Figure 10. Numeric Density of small Rainbow Smelt (*Osmerus mordax*; <90 mm) in Lake Michigan, United States as indexed by the fall bottom trawl and acoustic surveys. Error bars are +/- standard error.



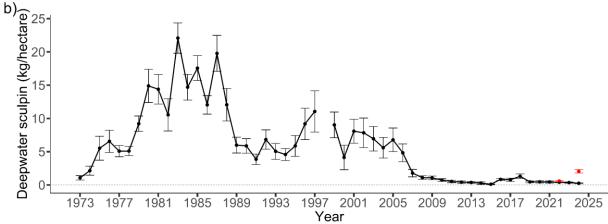


Figure 11. Biomass density of Slimy Sculpin (*Cottus cognatus*; a) and Deepwater Sculpin (*Myoxocephalus thompsonii*; b) in Lake Michigan, United States as measured by the bottom trawl surveys. Error bars in both panels are +/- standard error.

Slimy Sculpin

Slimy Sculpin biomass was < 0.04 kg/ha in the spring and fall BT surveys in 2024. Biomass density estimates from the fall BT have remained below 1 kg/ha for 15 consecutive years and Spring BT values in 2024 were similar to those observed in 2022 (Fig. 11a). While declines in total biomass have been observed in recent years across multiple prey species, Slimy Sculpin abundance is at least partially regulated by juvenile Lake Trout predation (Madenjian et al. 2005). In fact, Slimy Sculpin biomass began declining in 2010, which coincides with a substantial increase in juvenile Lake Trout stocking and natural recruitment (FWS/GLFC 2017; Lake Michigan LTWG 2019). The decline in Slimy Sculpin biomass does not appear to be an artifact of only sampling to 110 m during our standard survey. Comparisons of mean depth at capture and changes in biomass density with and without 128 m sites 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).

Deepwater Sculpin

The biomass density of Deepwater Sculpin in 2024 was 2.0 kg/ha in the spring and 0.26 kg/ha in the fall bottom trawl surveys (Fig. 11b). Previous analysis of the fall BT 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 has increased since 2007, these mechanisms likely do not underlie the long-term downward trend in the fall BT dataset. A likely explanation is that some portion 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. Mean depth at capture and biomass density estimates are substantially higher when 128 m sites are included (Madenjian et al. 2022). Further, 95% of Deepwater Sculpin biomass was collected at depths greater than 110 m in the spring of 2024, with the highest average tow density in the 237 m depth strata, highlighting the contemporary importance of habitats outside the historical range of the fall BT.

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. Ninespine Stickleback biomass density has also been low (i.e., <0.01 kg/ha) since 2010 and was only 0.008 kg/ha in the fall BT (Fig 12a). No Ninespine Sticklebacks were collected in the spring

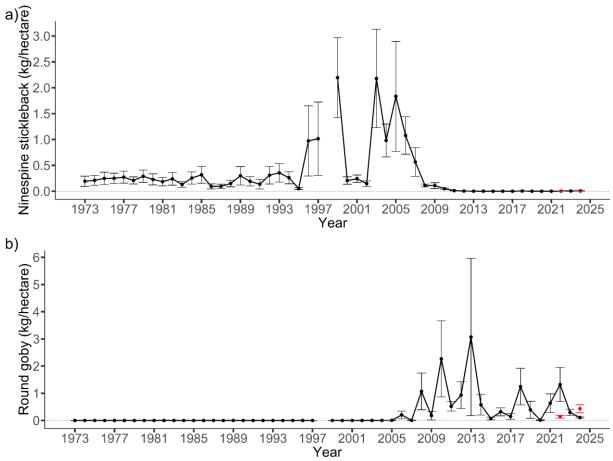


Figure 12. Biomass density of Ninespine Stickleback (*Pungitius pungitius*; a) and Round Goby (*Neogobius melanostomus*; b) in Lake Michigan, United States as measured by the fall bottom trawl survey. Error bars in both panels are +/- standard error.

BT, likely because the primary transect where they are collected, Manistique, was not sampled in the spring. Ninespine Stickleback biomass density 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 Sticklebacks 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.

Round goby

Invasive 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 by the fall BT until 2003. By 2008, Round Gobies 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 0.43 in the spring BT and 0.11 kg/ha in the fall 2024 BT survey, continuing the pattern of large yearly fluctuations in density estimates (Fig. 12b). Densities were highest in the spring BT between 90 and 150 m (Fig. 13a). By contrast, densities in the fall BT were highest in shallow habitats (Fig. 13b), reflective of seasonal migrations from rocky nearshore habitats to offshore waters during winter months (Janssen et al. 2005; Robinson et al. 2021).

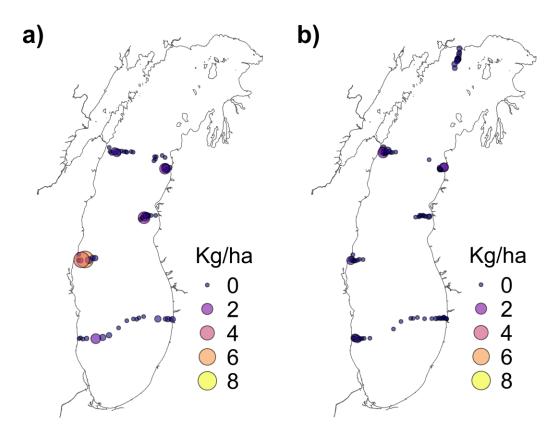


Figure 13. Round Goby (*Neogobius melanostomus*) biomass estimates in Lake Michigan, United States as measured by the 2024 spring bottom trawl survey (a) and fall bottom trawl survey (b).

Round Gobies 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).

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 was 5.7 kg/ha in the spring and 2.1 kg/ha in the fall. Differences between the two BT surveys were partially due to sample design (i.e., Deepwater Sculpin habitat is sampled to a greater extent in the spring) and higher catchability of yearling Alewife in the spring than in the fall. Total fall BT biomass is still well below the long-term average of 33.1 kg/ha (Fig. 14a). Total biomass density first dropped below 10 kg/ha in 2007 and has since remained below that level

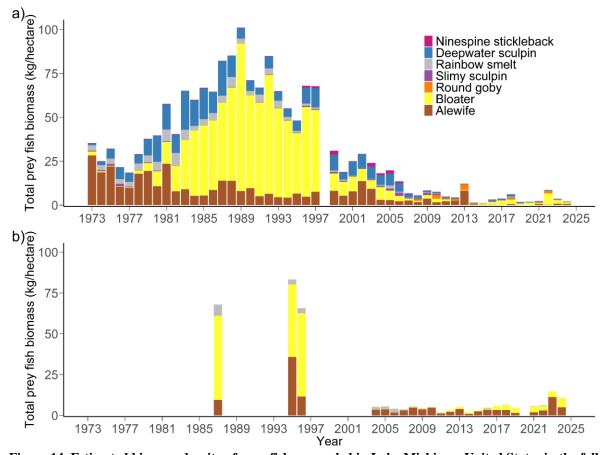


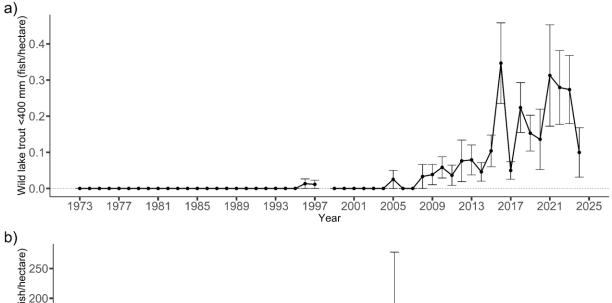
Figure 14. Estimated biomass density of prey fishes sampled in Lake Michigan, United States in the fall bottom trawl survey, 1973-2024 (a) and the estimated biomass density of prey fishes sampled by the current acoustic survey, 2004-2024, with historic estimates included (b). Refer to Table 1 for scientific names of fish species.

except in 2013, when the biomass estimates for Alewife and Round Goby were uncertain due to high catches at single tow locations.

The prey fish community sampled by the AC survey includes Alewife, Bloater, Rainbow Smelt, and Cisco. In 2024, this survey estimated a total biomass density of 10.8 kg/ha (Fig. 14b), the second highest since the modern AC survey began in 2004 but only 15% of the mean of the 1987, 1995, and 1996 surveys [72.4 kg/ha, Argyle 1992; Argyle et al. 1998)].

Other species of interest

Burbot and Lake Trout - Lake Trout and Burbot represent the native top predators in Lake Michigan. Burbot biomass density in the fall BT survey was 0.04 kg/ha, in line with recent low estimates observed since 2012 (Warner et al. 2024). 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. Conversely, wild juvenile Lake Trout (<400 mm) have been collected by the bottom trawl each year since 2008 (Leonhardt et al. 2024). In 2024, wild juvenile Lake Trout abundance was 0.10 fish/ha, higher than any value observed prior to 2015 but lower than the past three years



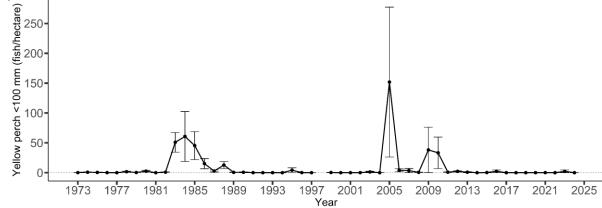


Figure 15. Biomass density of wild juvenile Lake Trout (*Salvelinus namaycush*; <400 mm; a) and numeric density of small Yellow Perch (*Perca flavescens*; <100 mm; b) in Lake Michigan, United States as indexed by the fall bottom trawl survey. Error bars in both panels are +/- standard error.

(average = 0.29 kg/ha; Fig. 15a). While catches are sporadic, the fall BT does appear to track the increase in Lake Trout natural recruitment in Lake Michigan.

Small Yellow Perch - The Yellow Perch population in Lake Michigan has supported valuable recreational and commercial fisheries (Wells 1977). The fall BT 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 were also higher than average. In the 2024 fall BT survey, no age-0 Yellow Perch were collected, continuing a 14-year trend of poor recruitment index values.

Conclusions

Alewife year-class strength in 2024 appears to be at least average, and densities of age-0 Alewife were highest in the northwestern portion of Lake Michigan for the second consecutive year. Our results indicate that three of the last four years produced relatively strong Alewife year-classes, but older fish (age-4 and older) are still uncommon across our surveys. Results of all three surveys still suggest high predation on Alewives and an age-truncated population. Rainbow Smelt and small Yellow Perch remain in low abundance. While there is some support for a moderate recruitment event for Rainbow Smelt in 2024, we do not anticipate the adult population to increase substantially in the coming years. Estimates of small Bloater from the AC survey indicate a strong recruitment event for Bloater in 2024, but further otolith aging will provide additional insight. The AC estimate of YAO Alewife biomass remains well above the 2004-2022 mean, providing evidence of an increase in biomass since 2022. This year's fall BT survey did not indicate an increase in Alewife biomass density from 2023, but we note the high uncertainty associated with the estimate. Overall, prey fish biomass remains low relative to previous decades.

Differences in Alewife habitat use, biomass density, and life-stage specific catchability between the 2024 spring and fall BT align with results from past years (2021-2023; Tingley et al. 2023, Warner et al. 2024). For the fourth consecutive spring season, Alewives were largely absent from shallow habitats and mean densities were highest in the 146 m strata, outside the historical range of the fall BT. The 2024 survey results support the hypothesis that Alewives in the Great Lakes overwinter in deepwater habitats, perhaps to take advantage of slightly warmer conditions (Wells 1968; O'Gorman et al. 2000; Weidel et al. 2023). Alewives were still aggregated in deepwater habitats in late April 2024, providing more evidence of a later migration to the nearshore environment than historically observed in lakes Michigan and Ontario (Wells 1968, O' Gorman et al. 2000). Bottom trawling in the spring provides a better index of age-1 Alewife than the fall on Lake Michigan, as values in 2022 and 2024 are comparable to AC survey estimates while the fall BT likely underestimated yearling fish in both years (Tingley et al. 2023). However, as we observed in 2022, the YAO Alewife spring BT biomass density index is only slightly higher than the index generated from the 2024 fall BT. Further, few age-3 and older Alewives were captured in the 2024 spring BT, and age-specific density estimates of ages 2-5 from both the spring and fall BT surveys were an order of magnitude lower than those from the AC survey. Together, our results suggest that a spring survey does not more effectively sample older Alewives than the fall BT, but an annual spring BT would provide an additional early indicator of year-class strength. The mechanism for the apparently reduced catchability of YAO Alewives, especially age-2 and older fish, in the Lake Michigan bottom trawl surveys since 2014 remains unclear.

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