Status and Trends of Pelagic and Benthic Prey Fish Populations in Lake Michigan, 2022[1,2]

Ralph W. Tingley III[3], David M. Warner[3], Charles P. Madenjian[3], Patricia M. Dieter[3], Ben Turschak[4], Dale Hanson[5], Kristy R. Phillips[3] and Caleb L. Geister[3]

[3]U.S. Geological Survey
Great Lakes Science Center
1451 Green Road
Ann Arbor, Michigan 48105

[4]Michigan Department of Natural Resources
Charlevoix Fisheries Research Station
96 Grant Street
Charlevoix, MI 49720

[5]U.S. Fish and Wildlife Service
Green Bay Fish and Wildlife Conservation Office
2661 Scott Tower Drive
New Franken,WI 54229

[1] The data associated with this report are currently under review and will be publicly available in 2023 (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 2022 survey consisted of 26 transects [570 km total (354 miles)] covering bottom depths ranging from 5 to 255 m and 37 midwater trawl tows above bottom depths ranging 5 to 232 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 2022, 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 236 m. The goal of the spring BT was to explore seasonal differences in biomass density and distributions of key prey species, mostly notably Alewife.

Total prey fish biomass density from the spring BT was 2.1 kg/ha. For the AC survey, total biomass density of prey fish equaled 6.2 kg/ha, 37% higher than the long-term average (2004-2021) of 4.5 kg/ha and 0.43 kg/ha higher than the 2021 estimate. For the fall BT, total biomass density of prey fish equaled 8.7 kg/ha, the highest value since 2013 and 21% higher than average value from 2004-2021 (6.8 kg/ha). The 2022 fall BT biomass density was still well below the average over the entirety of the time series (1973-2021; 34.3 kg/ha). Over the period both surveys have been conducted (2004-2021), total biomass density has trended downward in the fall BT (despite a high 2022 estimate) and remained relatively stable in the AC survey.

Bloater was the dominant species (by biomass) among prey fishes in both the spring and fall BT, while the AC survey reported co-dominance of Bloater and Alewife. Mean biomass of yearling and older (YAO) Alewife was 0.38 kg/ha in the spring BT, 3.0 kg/ha in the AC survey, and 0.10 in the fall BT. Alewife were aggregated in deepwater habitats in the spring of 2022 (> 110 m). Since 2014, catchability of YAO Alewives for the fall BT has been substantially lower than the AC survey. Results of the 2022 spring BT do not suggest that catchability is substantially higher in the spring than the fall.

Comparing the acoustic estimate to previous years, YAO Alewife biomass was 40% higher than the average from 2004-2021. An age-7 fish was recorded for the first time since 2009. Despite the rare catches of older fish, the Alewife age distribution still appears truncated, with age-1 fish as the most represented age class in all three surveys. Numeric density of age-0 Alewife from the AC survey was 7 fish/ha in 2022, which is the third lowest in the time series and well below the long-term mean of 452 fish/ha. Biomass density of large (≥120 mm) Bloater was 2.7 kg/ha in the AC survey and 4.4 kg/ha in the fall BT - each at least an order of magnitude lower than what was estimated by the fall BT between 1981 and 1998. Following a record high year in 2021 (1,037 fish/ha), the numeric density of small (<120 mm) Bloater was only 15 fish/ha in the AC survey.

Meanwhile, small Bloater density estimated in the fall BT was 261 fish/ha, the highest value since 1990 and likely partially reflective of a large 2021 year-class. Biomass density of large Rainbow Smelt (≥90 mm) was 0.29 kg/ha in the AC survey and 0.12 kg/ha in the fall BT survey, continuing the trend of low Rainbow Smelt biomass that has been observed since 2001. Numeric density of small (<90 mm) Rainbow Smelt was 21 fish/ha in the AC survey and 2.7 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 0.41 kg/ha, which makes 12 of the past 13 years when biomass was <1 kg/ha. Slimy Sculpin was estimated at 0.10 kg/ha, the highest estimate since 2016 but still only 25% of the long-term average. Round Goby was estimated at 1.3 kg/ha, above the average biomass of 0.82 kg/ha since 2008 but similar to intermittent high values observed throughout the dataset. Ninespine Stickleback density was 1.5 fish/ha. Burbot biomass remained near record low levels, and no age-0 Yellow Perch were caught, indicating a weak Yellow Perch year-class in 2022.

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 nonindigenous species, changing nutrient inputs, changing climate, and management activities including harvest regulation and fish stocking. Nonindigenous 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. Nonindigenous 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 densities in recent decades. Key native benthic species include Deepwater and Slimy Sculpin (*Myoxocephalus thompsonii* and *Cottus cognatus*, respectively). Since 2004, nonindigenous 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 nonindigenous dreissenid mussels (Bunnell et al. 2015). At the same time, Round Goby can negatively affect 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). 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. Given that Cisco (*Coregonus artedi*) is also resurging in Lake Michigan (Claramunt et al. 2019), it is also conceivable—based on Lake Superior sampling—that a spring

BT survey could index yearling Cisco (see Yule et al. 2008) and the AC survey could index adult Ciscoes (see Stockwell et al. 2006).

Since 2002, biomass indices for Alewife and other key prey fishes have declined in Lake Michigan to historically low levels (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). However, 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 to blame 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.

During winter months, Alewife overwinter in deepwater habitats in the Great Lakes, moving to more pelagic and inshore waters pre-spawn (Wells 1968, O'Gorman et al. 2000). Alewife historically dispersed into shallower waters as early as mid-March, but evidence from Lake Ontario indicates that Alewife now remain in deepwater habitats longer following changes in water clarity and the establishment of invasive mussels (O'Gorman et al. 2000). In 2022, following an exploratory field season in 2021, we implemented a spring bottom trawl survey (spring BT) on Lake Michigan in addition to our standard fall BT and AC survey to assess whether Alewife biomass density is better indexed via trawling in the spring than the fall. If YAO Alewife biomass indexed in the spring is notably higher than biomass in the fall, and Alewife appear to still be occupying overwintering habitats, it would indicate that establishing a spring survey on Lake Michigan could provide more useful information for managers and that a shift toward more pelagic habitat use in the fall may have occurred on Lake Michigan.

We have combined the results of the fall BT and AC survey in one report since 2019. We have added a summary of the 2022 spring BT with the goal of providing 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 published in 2019 and earlier (see Bunnell et al. 2019; Warner et al. 2019). 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. We also sampled three additional deepwater tows at 146 (Frankfort and Sturgeon Bay) and 165 m (Ludington), replicating efforts from 2021. 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.

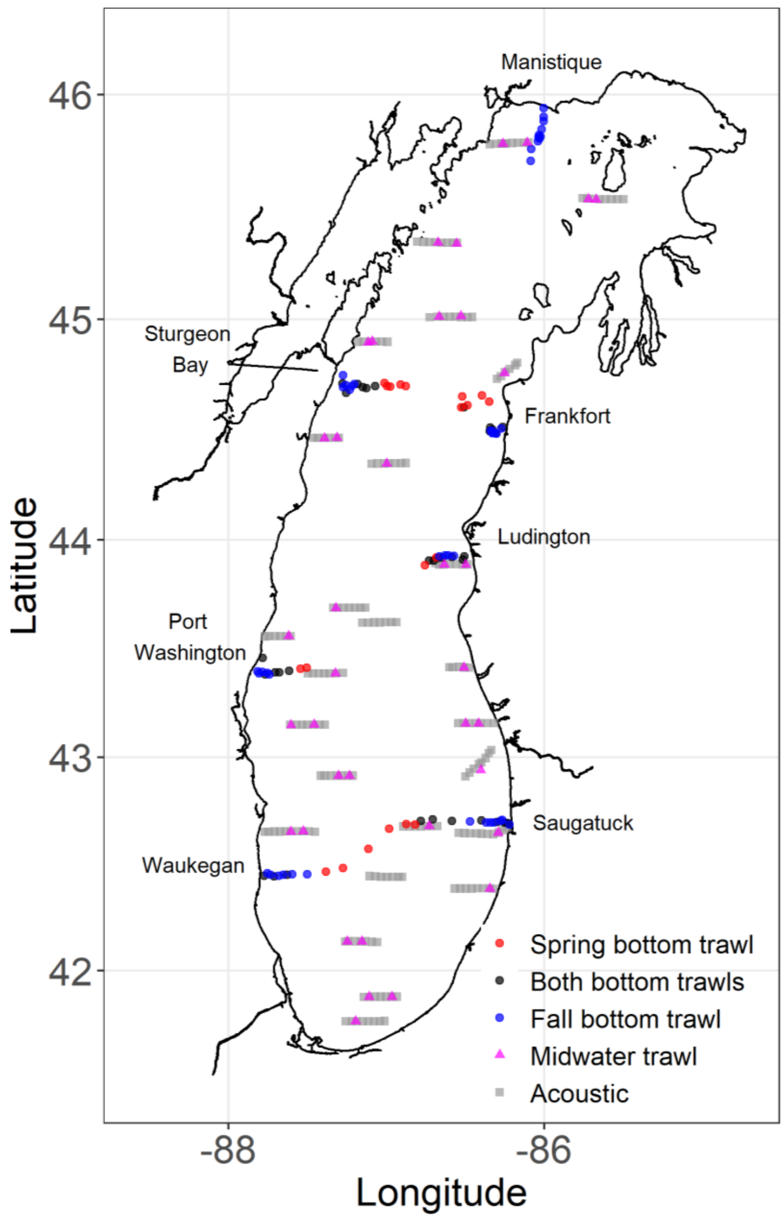

Figure 1. Map of sampling locations for the Lake Michigan bottom trawl and acoustic surveys in 2022. Gray squares represent acoustic transects, magenta triangles represent midwater trawl locations and red, black and blue circles represent bottom trawl surveys conducted in the spring, both seasons, and fall, respectively.

We designed the 2022 spring BT to mirror the protocols established for the fall BT while expanding the spatial extent to depths encompassing suspected Alewife overwintering habitat. We conducted 55 tows in 18 m increments between 9 and 236 m in depth across six extended fall transects (excluding Manistique; Fig. 1). Given we were limited on the time available to conduct the spring survey over such a large spatial extent, 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 (following Adams et al. 2006). However, we ensured that at least 3 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 spawning grounds. A total of 28 tows were conducted at standard fall BT sites (9 – 110 m) and 27 tows at depths between 128 m and 236 m.

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 and spring BT) and a stratified cluster design (AC). While we compare weighted mean biomass densities between the spring and fall BT, comparisons should be taken with caution as expanding the spatial extent may encompass more or less of a species' range. In 2022, we also used generalized additive models (GAMs) to examine differences in Alewife depth distributions across seasons. We implemented GAMs in statistical software ("gam" function, mgcv package in R; Wood 2019) with a tweedie error distribution (log link function) because density estimates were highly variable with several very high estimates, but most values were zero. Bottom depth (approximated using the headrope sensor) was modeled as a smoothed relationship with biomass density, which allows for the examination of nonlinear depth distributions. We ran separate models for each season to examine general trends instead of testing across seasons within a single model because of the large difference in depth ranges sampled. Results are reported as the partial effect of bottom depth on biomass density.

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 26 transects sampled in 2022 (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. 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 (estimateLake function, EchoNet2Fish package in R; Adams 2018), with consideration of the five geographic strata (north nearshore, north offshore, south nearshore, south offshore, west nearshore; see Warner et al. 2019) and vertical depth layer. This function calculates numeric fish density estimates and apportions them to user-defined fish groups using the midwater catch data. 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 (Adams et al. 2006; 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 is estimated (stratClust function; Adams 2018) which calculates the population mean for a single stage stratified cluster estimator with known stratum sizes.

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 2022, ages from 451 and 209 otoliths were successfully estimated from Alewife sampled in the spring and fall BT surveys, respectively, and ages from 302 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, while no recent Rainbow Smelt and Yellow Perch aging data are available. Therefore, we reserve the term YAO for Alewife. 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 2022 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 2022 was 0.38 kg/ha in the spring BT, 3.0 kg/ha in the AC survey and 0.10 kg/ha in the fall BT (Fig. 2, Fig. 3a). During the spring BT, Alewife densities were highest in the southern Lake Michigan and 110 m throughout the lake (Fig. 4a; Fig. 5a). YAO Alewife were most common in northwestern Lake Michigan in the fall BT and the AC survey (Fig. 4b,4c), but were also found in higher densities throughout the lake during the AC survey.

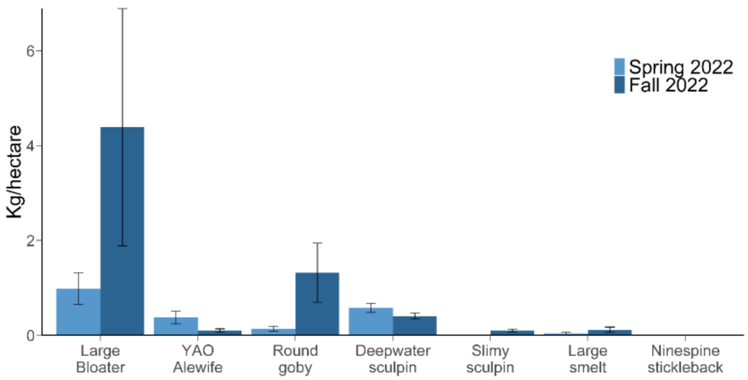

Figure 2. Density of prey species collected in the spring and fall trawl surveys. Yearling and older (YAO) Alewife as well as "large" Bloater and Rainbow Smelt include all individuals from the spring survey but excludes likely age-0 fish in the fall. Refer to Table 1 for scientific names.

Between 2004 and 2013, the standard error (SE) of the means for the fall BT and AC survey overlapped each year except 2005 (BT higher) and 2008 (AC higher; Fig. 3a). However, from 2014-2021, the SE of the means never overlapped. Standard errors did not overlap between the two surveys in 2022 and the AC survey estimate was an order of magnitude higher than the fall BT. Assuming the AC survey more accurately indexes YAO Alewife biomass, estimates from the AC survey during the last five years sampled (averaging 2.4 kg/ha) are still markedly lower than 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). When compared to the AC time series, the 2022 AC estimate is 1.3 kg/ha higher than what was measured in 2021 and is 0.79 kg/ha higher than the mean biomass from 2004-2021.

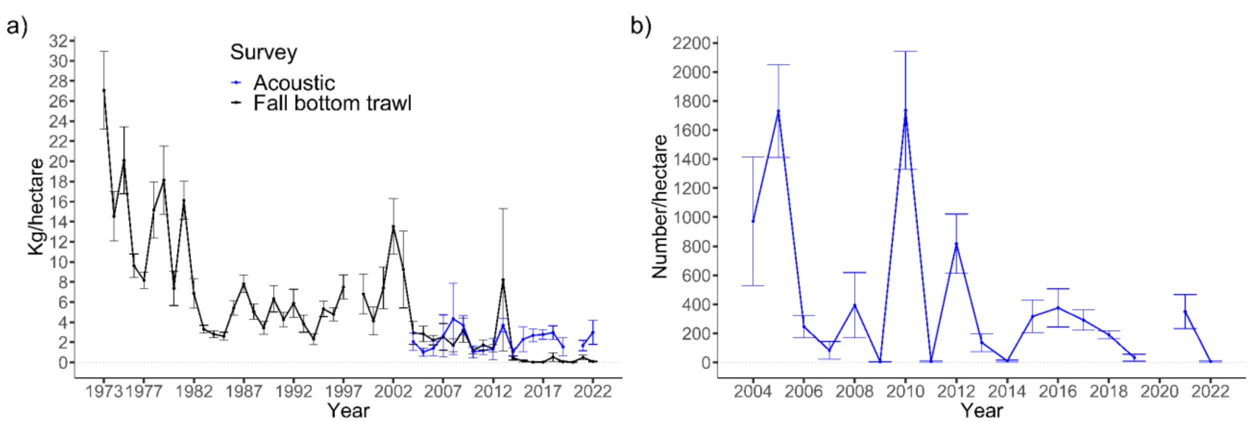

Figure 3. Yearling and older (YAO) Alewives, *Alosa pseudoharengus*, (≥100 mm) as biomass density for the fall bottom trawl and acoustic survey from 1973-2022 (a) and age-0 Alewife density directly estimated from the acoustic survey from 2004-2022 (b) in Lake Michigan. Error bars in both panels are +/- standard error.

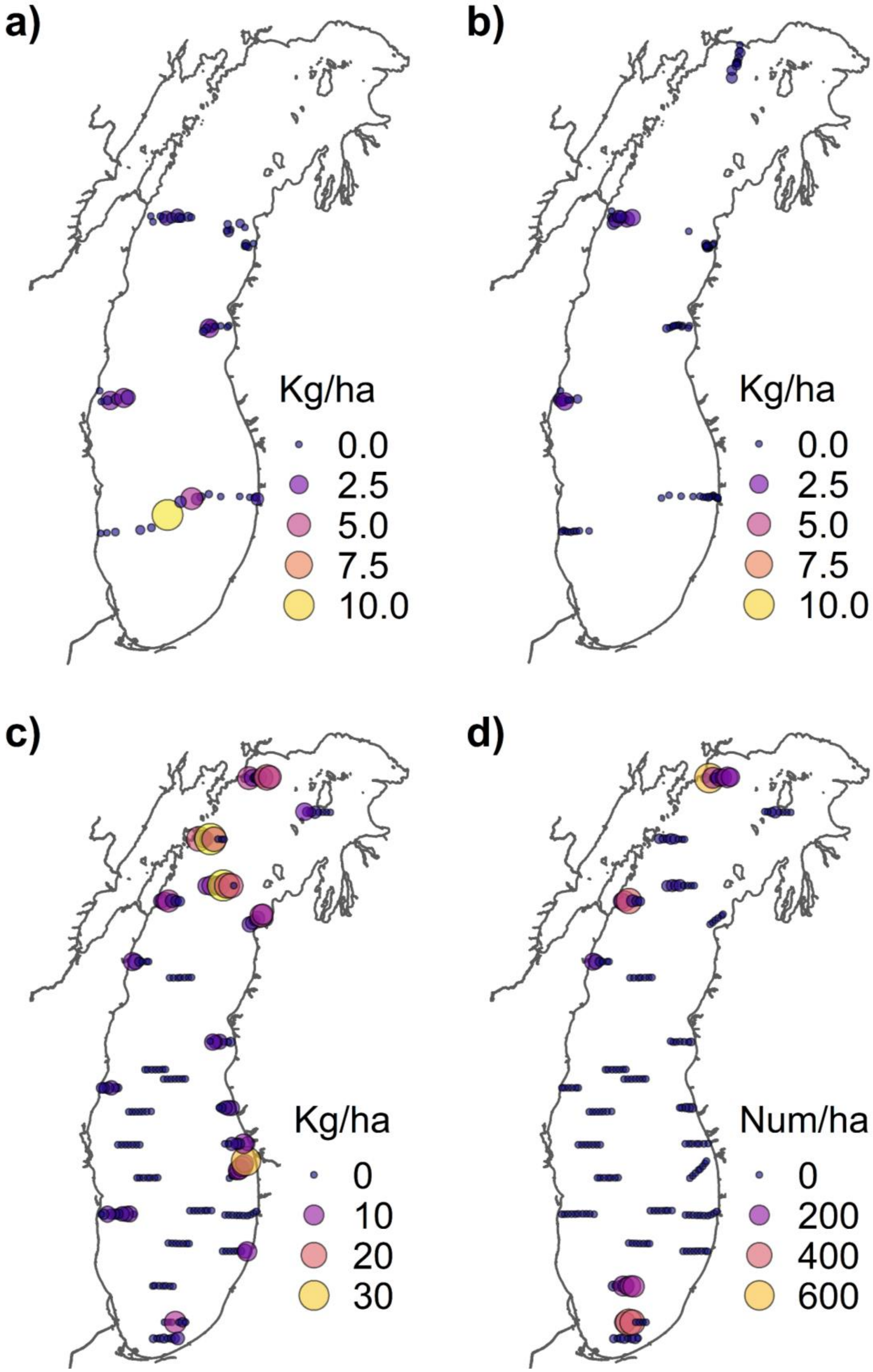

Figure 4. Alewife (*Alosa pseudoharengus)* biomass density (kg/ha) collected during the spring bottom trawl (a), YAO Alewife (≥ 100 mm) collected in the fall bottom trawl (b) and acoustic survey (c), and the numeric density of age-0 Alewife collected in both the acoustic survey (d). Note the scale difference between maps.

The spring BT index of YAO Alewife biomass density was more than three times the estimate from the fall BT, but the value was still < 1 kg/ha; an order of magnitude below the 2022 AC survey index and far below the average from the 1970's, 1980's and 1990's. Depth was a significant predictor of biomass density in both seasons, explaining 57% (p<0.001) and 17% (p=0.006) of deviance in the spring and fall GAMs, respectively. Through early May, Alewife largely remained in deep overwintering habitat with peak densities near 150 m (Fig. 5a) and were distributed over a wider range of depths in fall but were less common in shallow waters (Fig 5b). While the primary depth effect in the spring was negative in waters < 75 m, at very shallow sites the effect of depth is negligible. This is the result of a single tow at Saugatuck (9 m) where Alewife biomass density was 0.67 kg/ha. While low compared to deepwater tows (Fig. 4a), the presence of Alewife at 9 m could indicate that a portion of the population had moved into shallow habitats by the time of the spring BT in southern Lake Michigan. However, the 9 m tow crossed into the plume of the Kalamazoo River. If Alewife are present in Kalamazoo Lake (42°39'6.0", -86°12'14.8"), in winter months or if some alewife move into turbid river outflows earlier than the majority of the population, it is possible trawling into the plume affected total catch. We conducted an additional exploratory tow for 27-minutes cross-contour from 5 - 14 m outside of the river plume following the high catch at 9 m, capturing only a single Alewife.

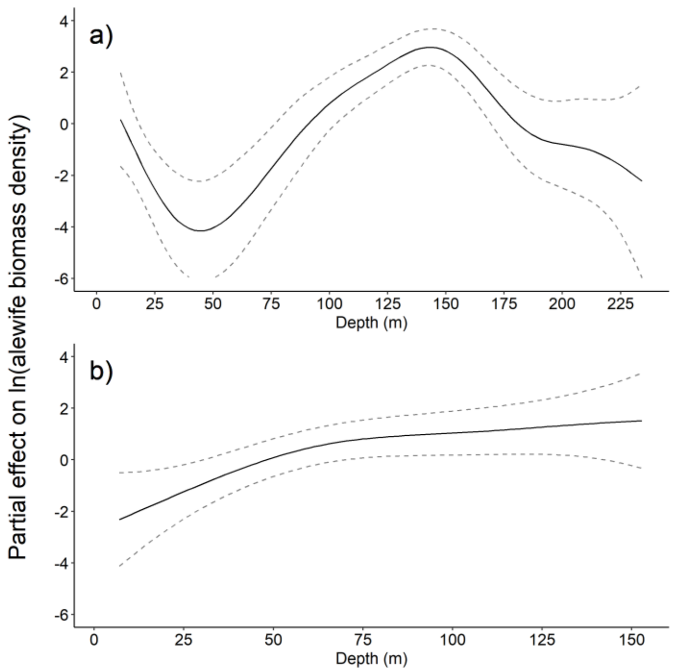

Figure 5. Partial effect of depth distribution on Alewife (*Alosa pseudoharengus)* biomass density in Lake Michigan, 2022 during the spring (a) and fall (b) bottom trawl.

Despite sampling habitats where Alewife appear to be concentrated during the winter and early spring, we did not find any evidence that would indicate substantial numbers of Alewife are no longer being sampled effectively in the fall BT. The low catchability apparent in the fall also appears to be present during spring, suggesting that a more pelagic orientation may now occur for Alewife during spring and fall. We do note that the slightly higher biomass density estimate in the spring BT survey aligns with both historic trends observed on Lake Michigan and an exploratory spring BT conducted in 2021 (Ralph Tingley, U.S. Geological Survey, unpublished data, 2022). It would also be consistent with mortality that would be expected to occur between spring and fall.

Numeric density of age-0 Alewives estimated by the AC survey was 7 fish/ha in 2022, a weak year-class and the third lowest in the acoustic time series (Fig. 3b). This estimate is well below the mean over the entire time series (452 fish/ha) and follows an average year-class in 2021. Age-0 Alewife collected during the AC survey were most common at the southernmost transects and in northwest region of Lake Michigan, with few individuals captured in the central portions of the lake (Fig. 4d).

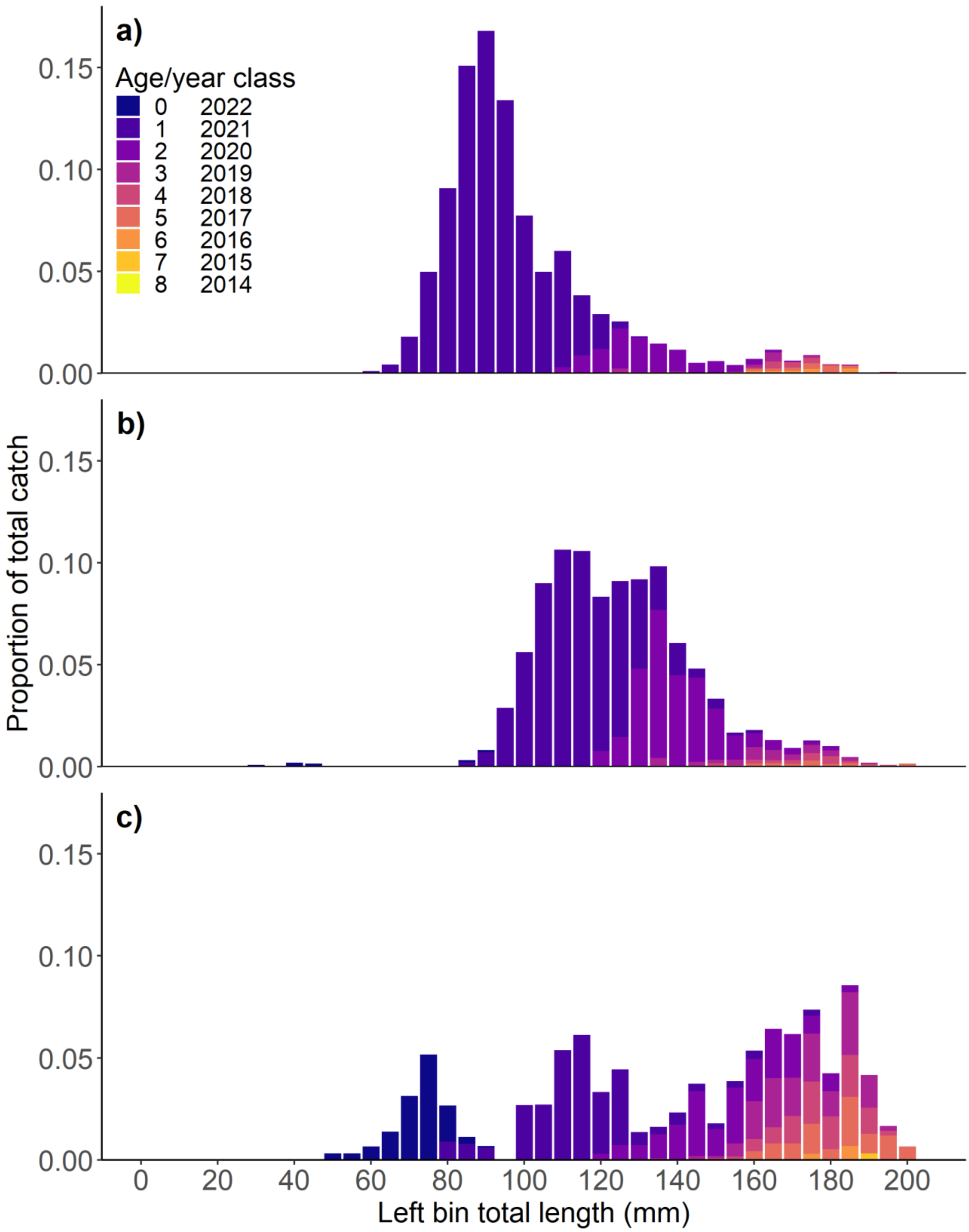

Figure 6. Age-at-length composition of Lake Michigan Alewife (*Alosa pseudoharengus*), as indexed by the spring bottom trawl (a), midwater trawl (b) and fall bottom trawl (c) surveys in 2022.

Spring BT Alewife catch was 85.2% yearlings and 10.4% age-2, with all other ages accounting for <1.4% each (Fig. 6a). The AC survey was also predominately yearling (64.2%) and age-2 fish (28.5%; Fig. 6b). All other ages accounted for <3.5% each. Age-6 (n=3) and age-7 (n=1) fish were collected in the annual surveys for the first time since 2009. Yearlings also accounted for the largest proportion of catch in the fall BT, but ages 2-5 and age-0 were 10-21% of total catch each (Fig. 6c). Only 1% of the alewife catch was attributable to age-6 and 7 fish. Age-3+ Alewife represented the highest proportion of the fall BT survey since 2015 (excluding the Covid-19 shortened 2020 field season), but biomass densities are close to all-time lows (0.10 kg/ha). 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).

Bloater

Biomass density of large Bloater in 2022 was estimated as 0.98 kg/ha in the spring BT, 2.7 kg/ha in the AC survey and 4.4 kg/ha in the fall BT (Fig. 2, Fig. 7a). Standard error of the means for large Bloater from the AC survey and fall BT overlapped for the first time since 2018, and for only the third time between 2004 and 2021. From 2004-2011 and 2017, the mean from the fall BT was higher. The mean from the AC survey has tended to be higher in more recent years: 2012-2014, 2016, 2019, and 2021. Regardless, the maximum biomass density measured from any survey from the 2004-2021 period was 7.3 kg/ha, which is an order of magnitude lower than the biomass measured in every year between 1981 and 1998.

Higher densities of large Bloater in the fall (4.4 kg/ha) versus the spring (0.98 kg/ha) BT could be related to age-specific or seasonal differences in foraging and habitat use. Crowder and Crawford (1984) found that Bloater in Lake Michigan shift from pelagic to benthic resources by the end of the second summer of life. It is possible that following a strong 2021 year-class a large proportion of yearling bloater had yet to move into benthic habitats by the spring BT but had by the late summer.

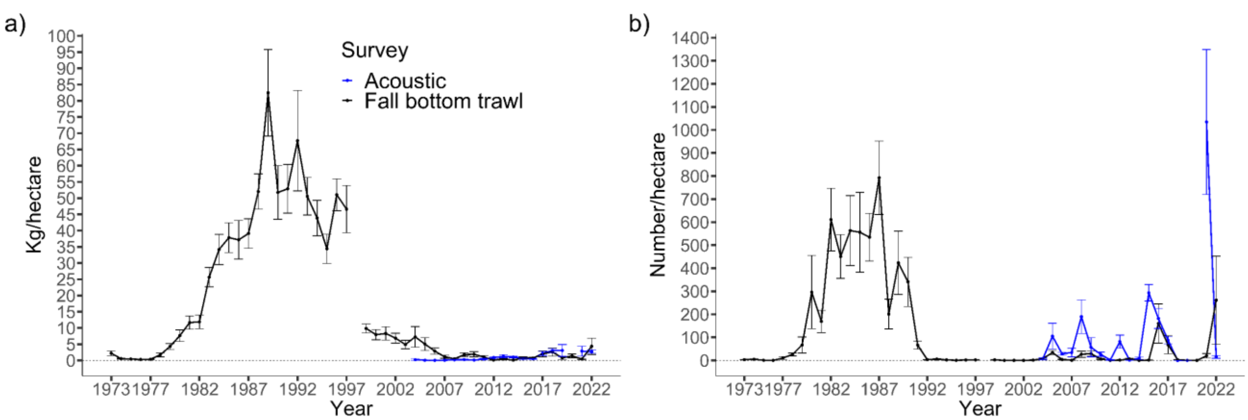

Figure 7. Density of large Bloater, *Coregonus hoyi,* (≥120 mm) as biomass density (a) and of small Bloater (<120 mm) as numeric density (b) in Lake Michigan as indexed by the fall bottom trawl and acoustic survey. Error bars in both panels are +/- standard error.

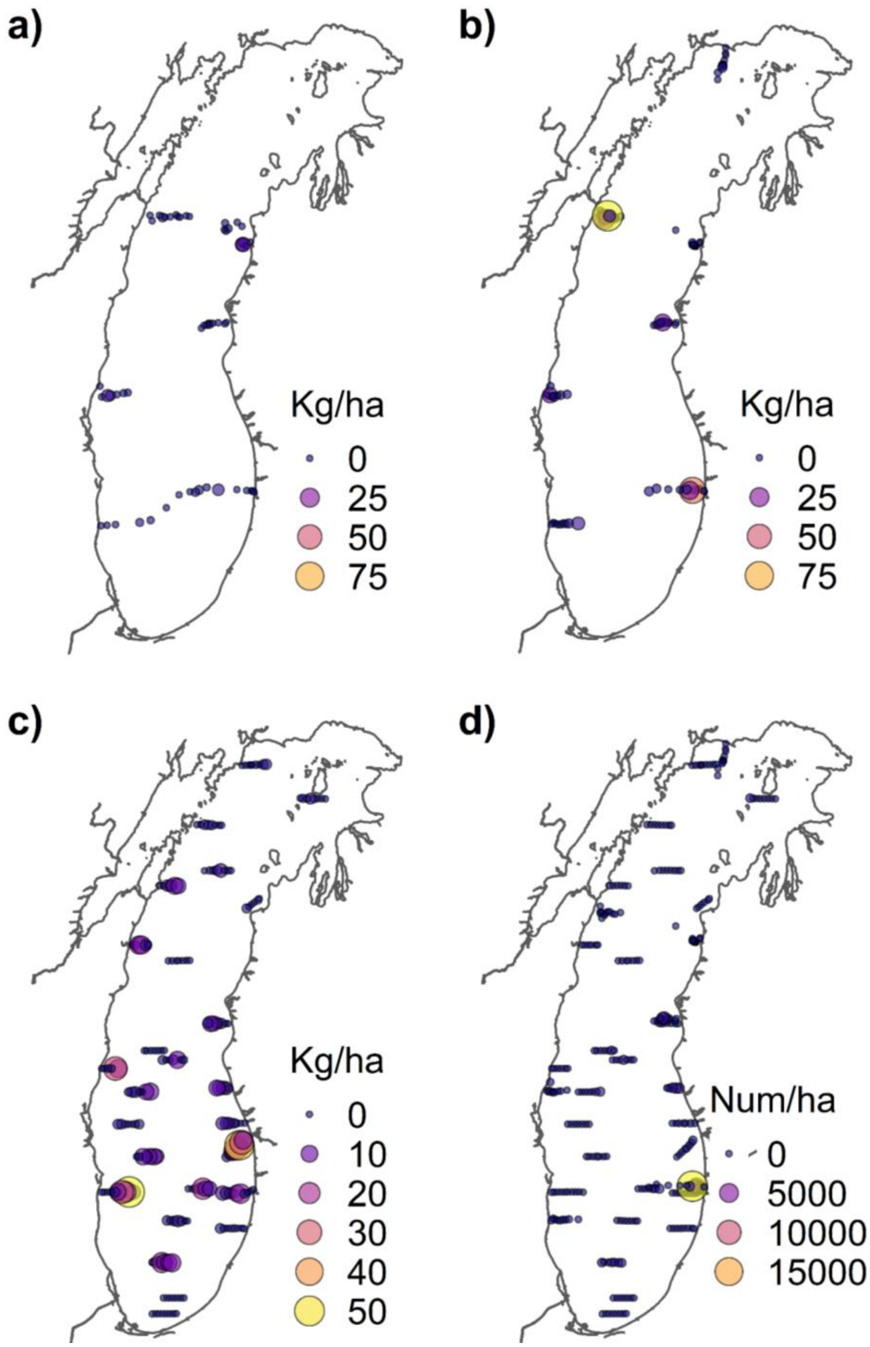

Figure 8. Bloater (*Coregonus hoyi*) biomass density (kg/ha) during the spring bottom trawl (a), large Bloater (≥ 120 mm) collected in the fall bottom trawl (b) and acoustic survey (c), and the numeric density of small Bloater (<120 mm collected in both the acoustic and fall bottom trawl surveys (d). Note the scale difference between maps.

Following a historically high estimate in 2021 (1,037 fish/ha), the small Bloater (<120 mm) numeric density estimate from the AC survey was only 15 fish/ha in 2022, well below the average over the time series (126 fish/ha; Fig. 7b). Conversely, the fall BT numeric density estimate of small Bloater was 261 fish/ha, the highest value since 1990. It is likely that the high numeric density of small Bloater in the fall BT is reflective of the strong 2021 year-class, as many yearlings may be below the 120 mm cutoff used to delineate "large" versus "small" fish. A similar pattern of a strong small Bloater index in the AC survey followed by a peak in the fall BT can be observed in 2015 and 2016 and preliminary investigation of available age data from 2016-2018 appears to indicate many small Bloater in 2016 and 2017 were not age-0 fish (GLSC 2019). Further analysis of Bloater otoliths collected in 2022 may provide additional insight into 2021 and 2022 year-class strengths.

Catches of large Bloater in the spring BT were relatively sporadic (Fig. 8a), while the highest densities in the fall BT occurred between 46 and 82 m in depth, primarily along the Sturgeon Bay and Saugatuck transects (Fig. 8b). Densities of large Bloater in the AC survey were high throughout the southern and central portion of Lake Michigan (Fig. 8c). Small Bloater from both the fall BT and AC survey were primarily observed in the southern basin with a single catch of over 18,000 fish/ha in the fall BT at the Saugatuck 55 m site (Fig. 8d).

The exact mechanisms underlying the apparently poor Bloater recruitment from 1992-2004 period, and the resultant low large Bloater biomass, 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. 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 consecutive 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 ± 0.03 vs. 2017-2022: 2.76 kg/ha ± 0.07) and the 2022 fall BT survey density is the highest since 2004, indicating increasing biomass in Lake Michigan.

Rainbow Smelt

The index of large Rainbow Smelt biomass density was 0.04 kg/ha in the 2022 spring BT, 0.29 in the AC survey and 0.12 kg/ha in the fall BT (Fig. 2, Fig. 9a). Fall BT and AC survey estimates have been similar in 13 of the previous 17 years as the SE of the means for the two surveys overlapped; in 2022, both density estimates increased from 2021. Still, 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.

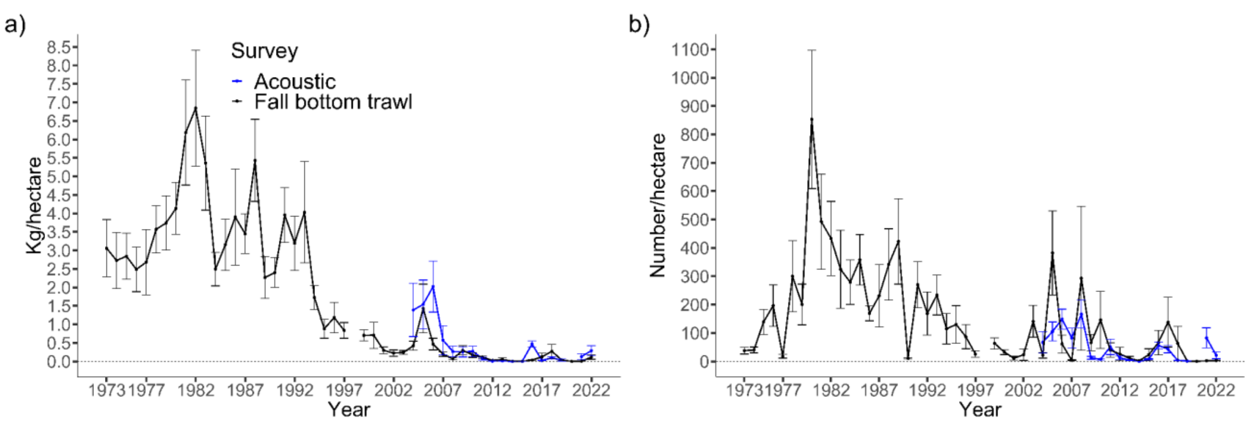

Figure 9. Density of large Rainbow Smelt, *Osmerus mordax,* (≥90 mm) as biomass density (a) and of small Rainbow Smelt (<90 mm) as numeric density (b) in Lake Michigan as indexed by the fall bottom trawl and acoustic survey. Error bars in both panels are +/- standard error.

Numeric density of small Rainbow Smelt estimated by the 2022 AC survey was 21 fish/ha and 2.7 fish/ha by the fall BT (Fig. 9b). The low value indexed by the AC survey in 2022 follows a year that recorded the highest estimate of small Smelt since 2009, while the fall BT has now indexed <3 fish/ha for small Rainbow Smelt each year since 2019.

The highest biomass densities of large Rainbow Smelt in both BT surveys occurred in the southern basin (Fig. 10a,b), while densities were highest in the northern half of the lake during the AC

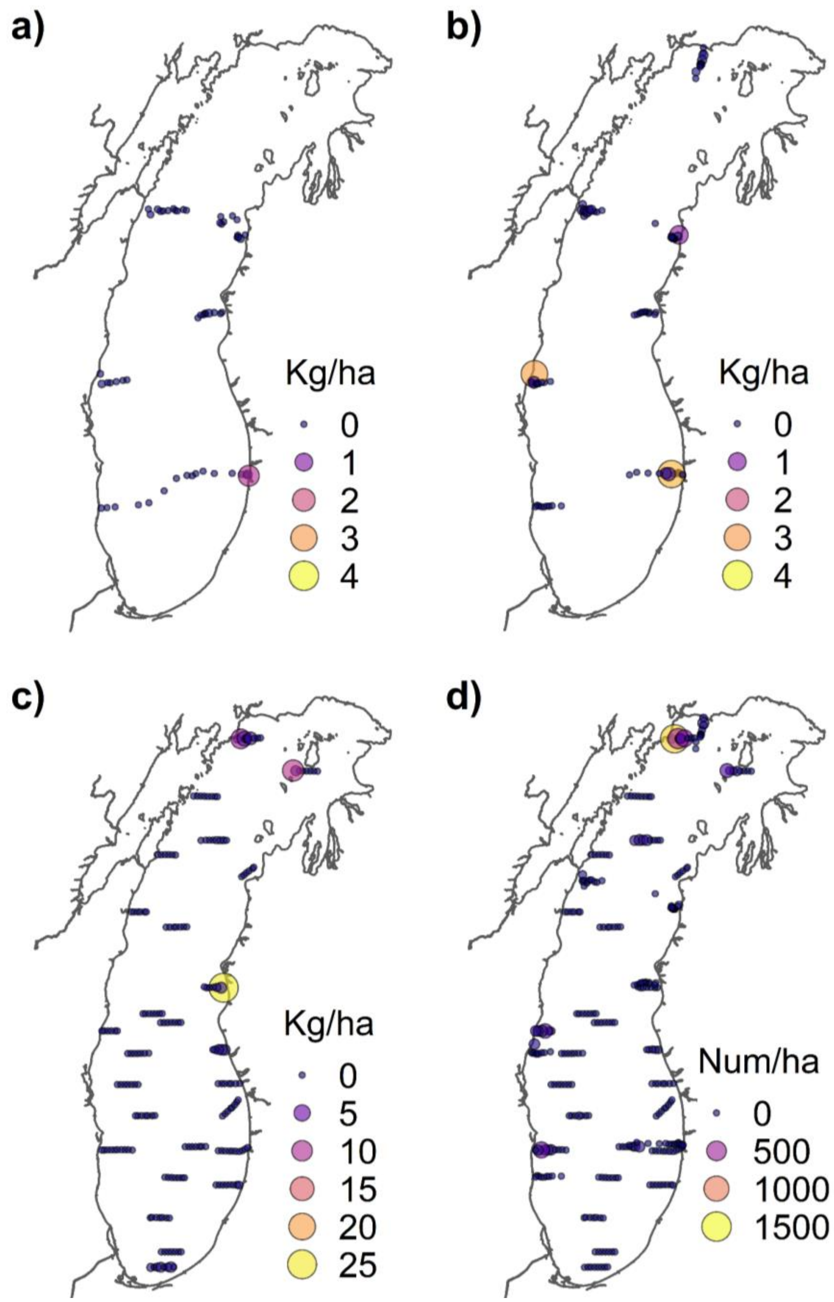

Figure 10. Rainbow Smelt (*Osmerus mordax*) biomass density (kg/ha) collected during the spring bottom trawl (a), large smelt (≥ 90 mm) collected in the fall bottom trawl (b) and acoustic survey (c), and the numeric density of small smelt (<90 mm collected in both the acoustic and fall bottom trawl surveys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

survey (Fig. 10c). High numeric densities of small Rainbow Smelt were most common in shallow waters (≤ 37 m) in the fall BT and AC survey but were relatively sporadic across the lake, with the highest density observed in the northwest region of Lake Michigan during the AC survey (1,359 fish/ha; Fig. 10d)

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).

Slimy sculpin

Slimy Sculpin biomass indexed by the BT surveys was 0.01 kg/ha in the spring and 0.1 kg/ha in the fall (Fig. 2). In 2013, Slimy Sculpin biomass density declined below 0.25 kg/ha and has not rebounded (Fig. 11a). Slimy Sculpin abundance is regulated, at least in part, by predation from juvenile Lake Trout (Madenjian et al. 2005b). 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 in Slimy Sculpin distributions outside our spatial extent have impacted density estimates (Madenjian et al. 2022).

Deepwater Sculpin
Biomass density of Deepwater Sculpin in 2022 indexed by the spring BT was 0.58 kg/ha and 0.41 kg/ha by the fall BT (Fig. 2). Deepwater Sculpin have remained at relatively low levels in the fall BT since 2007 (mean = 0.64 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 recent downward trend. A more 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 capture and biomass density are higher when 128 m sites are included in recent biomass density estimates (Madenjian et al. 2022).

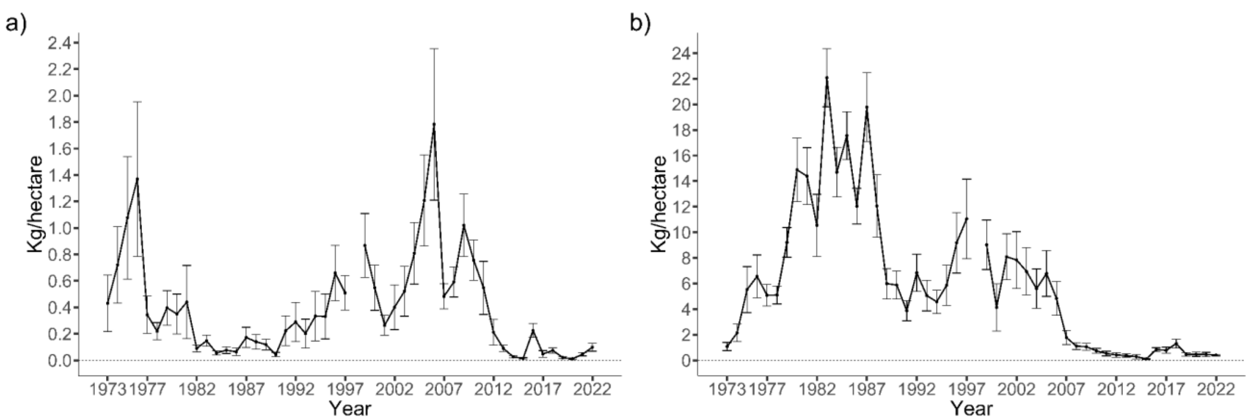

Figure 11. Biomass density of a) Slimy Sculpin and b) Deepwater Sculpin in Lake Michigan, 1973-2022, as measured by the fall bottom trawl survey. Error bars in both panels are +/- standard error. Refer to Table 1 for scientific names of fish species.

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., <0.5 kg/ha) since 2007. The densities in 2022 were <0.01 kg/ha in both BT surveys (Fig. 2). 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 2011, 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.

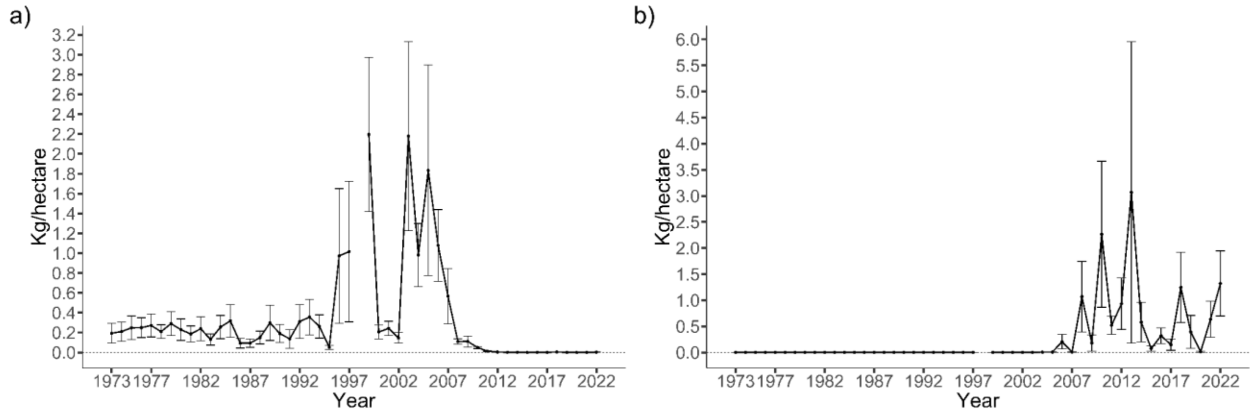

Figure 12. Biomass density of a) Ninespine Stickleback and b) Round Goby in Lake Michigan, 1973-2022, as measured by the fall bottom trawl survey. Error bars in both panels are +/- standard error. Refer to Table 1 for scientific names of fish species.

Round goby

Nonindigenous 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. As our survey samples only soft substrates deeper than 9 m, 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 0.14 kg/ha in the spring and 1.3 kg/ha in the fall (Fig. 2). The fall BT biomass estimate was more than double that of 2021 (Fig. 12b). Biomass density was surprisingly low in the spring BT relative to the fall; we anticipated goby may be more susceptible to the bottom trawl during the overwintering period and prior to movement inshore from deepwater habitats (Robinson et al. 2020).

While Round Goby density estimates were low in the spring BT, the highest catches did occur deepwater habitats along the Frankfort transect (110 and 128 m; Fig. 13a). In the fall BT, catches were highest in shallow tows (<37 m) along the western shoreline (Fig. 13b). One potential explanation for higher fall densities on the

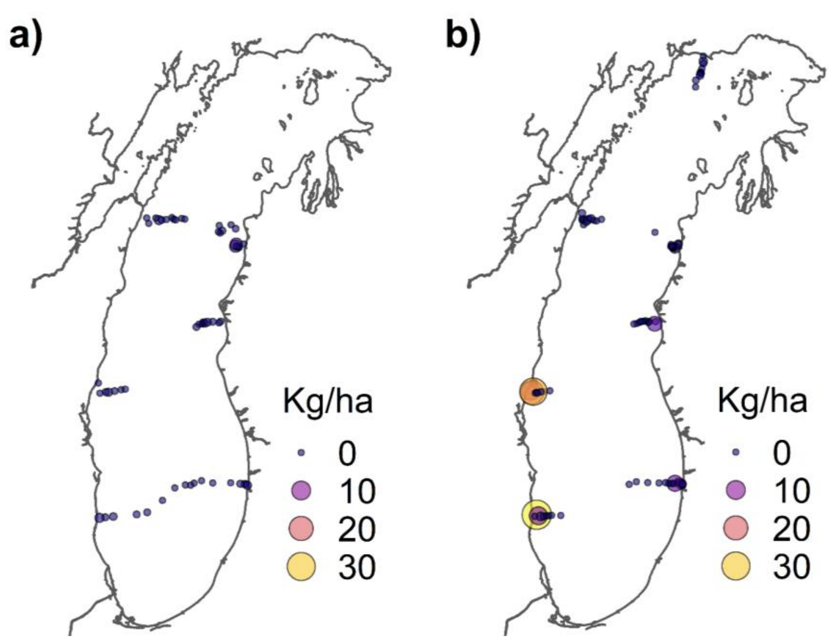

Figure 13. Map of Round Goby (*Neogobius melanostomus*) biomass estimates in Lake Michigan as measured by spring (a) and fall (b) bottom trawl surveys in 2022.

western side of the lake is rockier habitat relative to the eastern side of the lake (Janssen et al. 2005). Round Goby are consumed by diverse fish 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), 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 rates 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 estimated by the spring BT was 2.1 kg/ha and was predominately Bloater (46%), Deepwater Sculpin (27%), Alewife (18%) and goby (6%; Fig. 2). All other species were below 2% of total biomass. Total prey fish biomass density from the fall BT was equal to 8.7 kg/ha, 76% of which was comprised of Bloater (Fig. 14a). Total fall BT biomass was highest since 2013, largely a result of an increase in Bloater biomass, but was still well below the long-term average of 34.2 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.

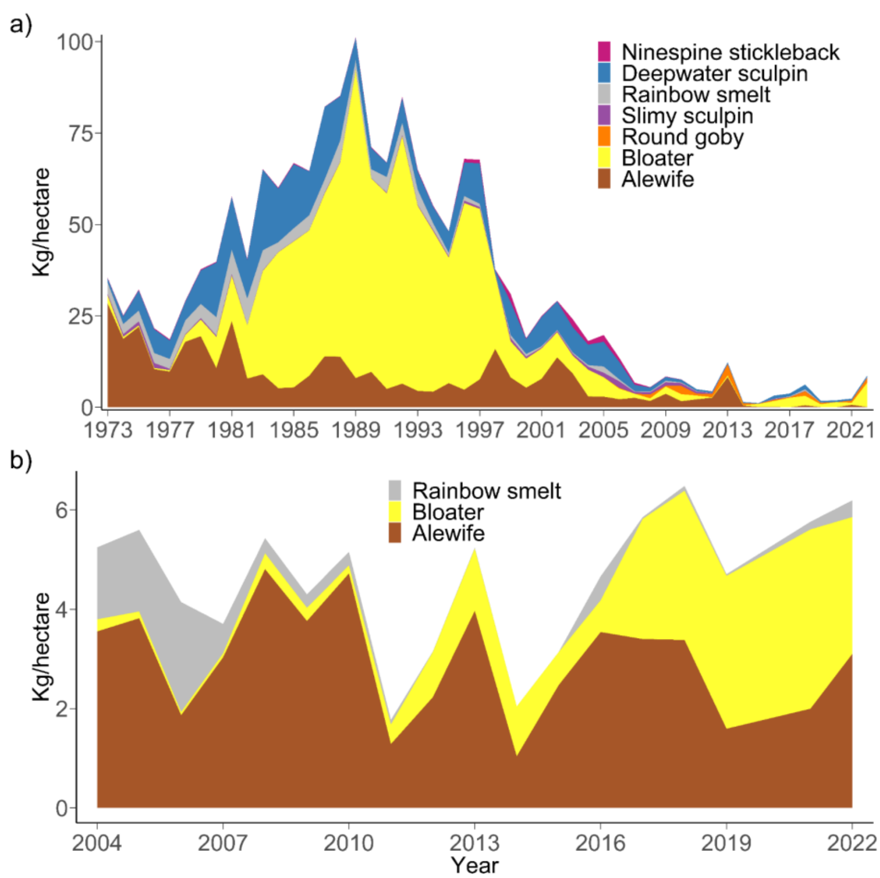

Figure 14. Estimated biomass of prey fishes sampled in the fall bottom trawl survey, 1973-2022 (a) and the estimated biomass of prey fishes sampled by the acoustic survey, 2004-2022 (b). Refer to Table 1 for scientific names of fish species.

The prey fish community sampled by the AC survey includes Alewife, Bloater, Rainbow Smelt, and Cisco. In 2022, this survey estimated a total biomass density of 6.19 kg/ha (Fig. 14b), 37% higher than the long-term average total biomass of 4.5 kg/ha and only 0.43 kg/ha higher than the 2021 estimate. Total biomass density has exhibited no strong trend since 2004. Unlike the fall BT survey, Alewife (50%) and Bloater (44%) were equally well represented in the AC survey.

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 reduction in Sea Lamprey (*Petromyzon marinus*; Wells and McLain 1973) and perhaps Alewife, which 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 spring BT was 0.63 kg/ha and 0.02 kg/ha by the fall BT. The fall BT index is consistent with low estimates since 2012 (Fig. 15a), while the spring BT estimate is higher than any value over this same time period. 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). Our 2022 spring BT survey supports this hypothesis; 85% of Burbot biomass in the spring was caught at sites that are beyond the depth range of the fall BT (≥128 m), with the highest density recorded at 146 m (18.1 kg/ha). Madenjian et al. (2022) determined that a major expansion of the fall BT survey would be required to conclude whether Burbot populations have moved deeper during the fall.

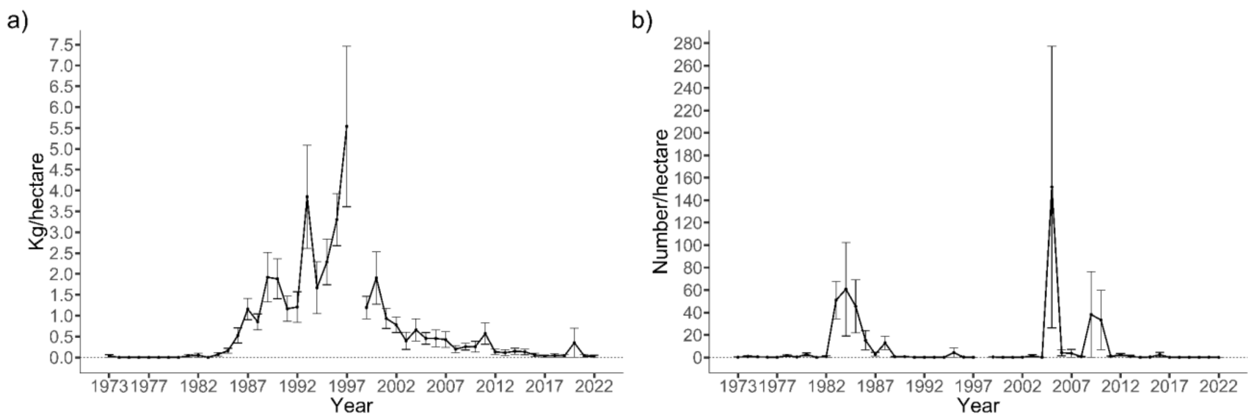

Figure 15. Biomass density of a) Burbot and b) numeric density of small Yellow Perch (<100 mm) in Lake Michigan, 1973-2022, as measured by the fall bottom trawl survey. Error bars in both panels are +/- standard error. Refer to Table 1 for scientific names of fish species.

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 also were higher than average. In the 2022 fall BT, no age-0 perch were caught, indicating a weak year-class. By comparison, nearly 1,700 age-0 Yellow Perch were captured in 2005.

Conclusions

The year 2022 appears to have poor recruitment for at least three species in Lake Michigan: Alewife, Rainbow Smelt, and Yellow Perch. Otolith aging of Bloater could help determine if small Bloater captured in the fall BT are evidence of a strong year-class in 2022 or an artifact of slow growth in yearling fish. Comparing 2022 estimates of prey fish biomass to previous years depends on the temporal perspective. Focusing on the AC survey results that date back to 2004, total prey fish biomass was higher than the long-term average and the 2022 YAO Alewife biomass estimate is 40% higher. Hence the AC survey indicates relative stability and a modest increase in Alewife biomass in 2022, relative to surveys since 2004. However, longer-term comparisons to the results from the fall BT survey reveal considerable declines during the 1990s or early 2000s for these three key species and the forage fish community in general.

When compared to historic spring bottom trawl records (Wells 1968; Ralph Tingley, U. S. Geological Survey, unpublished data), results of the spring BT suggest that Alewife in Lake Michigan now occupy deep overwintering habitats longer. Therefore, sampling Alewife while they are aggregated in deep areas of the lake during the early spring could be an effective strategy for indexing the population. However, the spring BT biomass density index is only slightly higher than the YAO index generated from the 2022 fall BT (0.38 kg/ha vs. 0.10 kg/ha) and few age-3+ Alewife were captured, suggesting that a spring survey does not provide a more robust index of adult Alewife biomass. Implementation of a spring BT survey in 2023 could offer validation of the findings from the 2022 surveys and provide insight into other seasonal differences in habitat use of forage (i.e., Deepwater Sculpin, Bloater) and predator (i.e., Burbot) species.

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References

Adams, J. V., R. L. Argyle, G. W. Fleischer, G. L. Curtis, and R. G. Stickel. 2006. Improving the design of acoustic and midwater trawl surveys through stratification, with an application to Lake Michigan prey fishes. N. Amer. J. Fish. Manage. 26:612-621.

Adams, J.V. 2018. EchoNet2Fish: estimate fish abundance from acoustic echoes and net catch. R package 0.3.1.9000. https://github.com/JVAdams/EchoNet2Fish.

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 panktivorous 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.

Claramunt, R. M., J. Smith, K. Donner, A. Povolo, M. E. Herbert, T. Galarowicz, T. L. Claramunt, S. DeBoe, W. Stott, and J. L. Jonas. 2019. Resurgence of Cisco (*Coregonus artedi*) in Lake Michigan. J. Great Lakes Res. 45:821-829.

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.

Crowder, L. B., and H. L. Crawford. 1984. Ecological shifts in resource use by bloaters in Lake Michigan. Trans. Am. Fish. Soc. 113(6): 694-700.

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.

O'Gorman, R., J. H. Elrod, R.W. Owens, C. P. Schneider, T. H. Eckert, and B. F. Lantry. 2000. Shifts in depth distributions of alewives, rainbow smelt, and age-2 lake trout in southern Lake Ontario following establishment of dreissenids. Trans. Am. Fish. Soc.129:1096-1106.

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

Robinson, K. F., C. R. Bronte, D. B. Bunnell, P. T. Euclide, D. W. Hondorp, J. A. Janssen, M. S. Kornis, D. H. Ogle, W. Otte, S. C. Riley, M. R. Vinson, S. L. Volkel, and B. C. Weidel. 2020. A synthesis of the biology and ecology of sculpin species in the Laurentian Great Lakes and the implications for the adaptive capacity of the benthic ecosystem. Rev Fish Sci Aquac. 29: 96-121.

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.

Stockwell, J. D., D. L. Yule, O. T. Gorman, E. J. Isaac, and S. A. Moore. 2006. Evaluation of bottom trawls as compared to acoustics to assess adult lake herring (*Coregonus artedi*) abundance in Lake Superior. J. Great Lakes Res. 32:280–292.

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., 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. 1968. Seasonal depth distribution of fish in southeastern Lake Michigan. U.S. Fish and Wildlife Service Fishery Bulletin 67:1–15.

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.

Wood, S. N. 2019. Package 'mgcv': Mixed GAM computation vehicle with automatic smoothness estimation version 1.8–28. 2019. Available from: https://cran.r-project.org/web/packages/mgcv/index.html.

Yule, D. L., J. D. Stockwell, J. A. Black, K. I. Cullis, G. A. Cholwek, and J. T. Myers. 2008. How systematic age underestimation can impede understanding of fish population dynamics: lessons learned from a Lake Superior cisco stock. Trans. Am. Fish. Soc. 137:481–495.

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.