Status and Trends of the Lake Huron Prey Fish Community, 1976-2021[1,2]

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Abstract

The U.S. Geological Survey Great Lakes Science Center has assessed annual changes in the offshore prey fish community of Lake Huron since 1973. Assessments are based on a bottom trawl survey conducted in October and an acoustic-midwater trawl survey conducted in September-October that began in 2004. Due to weather delays and continued travel restrictions during 2021, there were no bottom trawl samples collected off the port of Goderich, Ontario and two acoustic transects were cancelled in Georgian Bay. Prey fish biomass in Lake Huron in 2021 was dominated by two species, Bloater (*Coregonus hoyi*) and Rainbow Smelt (*Osmerus mordax*). In the main basin, prey fish biomass remained below levels observed prior to community-wide declines that began in the early to mid-1990s. Bloater was the most abundant prey fish species in the main basin. Rainbow Smelt was the most abundant prey species in the North Channel and in Georgian Bay. Both surveys suggested that Bloater biomass is increasing in the main basin. Low biomass of invasive species like Alewife (*Alosa pseudoharengus*) and Rainbow Smelt is consistent with fish community objectives focused on restoration of native fish communities. Abundance of invasive Round Goby (*Neogobius melanostomus*) increased in 2021 relative to 2019-2020. Biomass of native Cisco (*Coregonus artedi*) increased in the North Channel in 2021 but remained low in Georgian Bay, possibly as an artifact of reduced sampling. Biomass of Slimy Sculpin (*Cottus cognatus*) and Deepwater Sculpin (*Myoxocephalus*

thompsonii) in 2021 remained low but within the range observed over the past decade. Reduced lake productivity, predation by a recovering piscivore community, and shifts in food web dynamics that favor fish production in nearshore environments may prevent prey fish biomass in offshore areas from returning to levels observed prior to the early 1990s. However, increased biomass of Bloater and Cisco suggests that lake conditions may favor recovery of native coregonines.

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[1] The data associated with this report are currently under review and will be publicly available in 2022 at the following location: 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] Sampling and handling of fish during GLSC surveys are carried out in accordance with Guidelines for the Use of Fish in Research, a joint publication of the American Fisheries Society, the American Institute of Fishery Research Biologists, and the American Society of Ichthyologists and Herpetologists.

Introduction

Lake Huron historically supported a diverse and abundant prey fish community that provided food for native piscivores and commercial and recreational fishing opportunities (Berst and Spangler 1972). The endemic prey fish community in deep, offshore waters included several species of deepwater Cisco (*Coregonus hoyi*, *C. johannae*, *C. kiyi*, *C. nigripinnis*, *C. zenithicus*, *C. reighardi*, *C. alpenae*) and at least two species of sculpin (Cottidae). Deepwater ciscoes and sculpins were the primary prey of Lake Trout (*Salvelinus namaycush*), which sustained a large commercial fishery. Cisco (*C. artedi*) likely inhabited the entire lake but mainly occupied depths above the thermocline. Native prey fish in nearshore areas included Yellow Perch (*Perca flavescens*) and Emerald Shiner (*Notropis atherinoides*).

Overfishing, introduction of exotic species, and habitat degradation precipitated major shifts in the abundance and species composition of the Lake Huron prey fish community beginning in the late nineteenth century. Unsustainable harvest resulted in the extirpation of deepwater ciscoes except for Bloater (*C. hoyi*) and main basin populations of Cisco (*C. artedi*) by the early 1900s. Pollution and eutrophication of spawning habitats also may have contributed to Cisco declines (Berst and Spangler 1972). Losses of native prey species and commensurate declines in native piscivores such as Lake Trout and Burbot (*Lota lota*) created vacant niche space that was exploited by exotic Rainbow Smelt (*Osmerus mordax*) and Alewife (*Alosa pseudoharengus*), which were first detected in Lake Huron in 1925 and 1951, respectively. By the late 1950s or early 1960s, the Lake Huron prey fish community consisted primarily of Rainbow Smelt, Alewife, and Bloater (Berst and Spangler 1972). Starting in 1968, Pacific salmon (*Oncorhynchus* spp.) were stocked into Lake Huron to create a sport fishery and to control populations of Alewife and Rainbow Smelt (Johnson et al. 2010). Stocking of Lake

Trout commenced in 1970 in an effort to rehabilitate native predator populations (Eshenroder et al. 1995).

Quantitative assessment of the Lake Huron prey fish community was soon a critical need of fishery managers who were concerned that stocking rates of Pacific salmon and Lake Trout might exceed levels that could be supported by the available prey base. Assessment of the Lake Huron prey fish community also was considered necessary to evaluate potential negative impacts of exotic prey fish (e.g., Alewife) on native fish populations and food web dynamics (Crowder 1980, Evans and Loftus 1987, Madenjian et al. 2008, Smith 1970). To address the need for prey fish assessment, the U.S. Geological Survey Great Lakes Science Center (GLSC) began annual bottom trawl surveys on Lake Huron in 1973 and added an integrated acoustic-midwater trawl survey (hereafter "acoustic survey") in 2004. Addition of the acoustic survey was a response to concerns pelagic fish were underrepresented in the bottom trawl survey (Fabrizio et al. 1997). Both surveys are designed to assess prey fish communities in "offshore" waters (i.e., depth ≥ 9 m).

Numerous ecosystem changes have occurred during the time periods covered by the trawl and acoustic surveys that have the potential to influence the Lake Huron prey fish community. These include the initiation of nutrient controls mandated by the Great Lakes Water Quality Agreement of 1972; control of Sea Lamprey (*Petromyzon marinus*); introduction of dreissenid mussels and drastic declines in the abundance of the benthic amphipod *Diporeia* spp. (McNickle et al. 2006, Nalepa et al. 2005, Nalepa et al. 2007); significant changes in the abundance and species composition of phytoplankton and zooplankton (Barbiero et al. 2009, Barbiero et al. 2018, Burlakova et al. 2018); reduced Chinook Salmon (*O. tshawytscha*) abundance (Bence and He 2015, Dettmers et al. 2012); the invasion of the Round Goby (*Neogobius melanostomus*); and increased natural reproduction of Lake Trout and Walleye (*Sander vitreus*) (Fielder et al. 2007, Riley et al. 2007).

The goal of this report is to describe and explain changes in the Lake Huron prey fish community from 1976 (the first year of a complete bottom trawl survey) through 2021, the most recent year of data collection. Results from the 2021 bottom trawl and acoustic surveys are presented jointly in this report in order to provide a more cohesive picture of the status and trends in the Lake Huron prey fish community. Report objectives are to 1) describe temporal and spatial trends in species composition of the Lake Huron prey fish community; 2) describe temporal change in the abundance of dominant species (Alewife, Bloater, and Rainbow Smelt) and determine if trends are consistent between surveys; 3) describe the spatial distribution, size structure, and age structure of dominant species in 2021; and 4) describe abundance trends and population characteristics for other prey fish species of interest to fishery managers.

Methods

Bottom Trawl Survey—The GLSC has monitored prey fish abundance annually from 1973-2021 using 12-m headrope (1973-1991) and 21-m headrope (1992-2021) bottom trawls at fixed transects at up to eleven depths (9, 18, 27, 36, 46, 55, 64, 73, 82, 92, and 110 m) at five ports (De Tour, Hammond Bay, Alpena, Au Sable Point, and Harbor Beach) in the state of Michigan's waters of Lake Huron (Figure 1). Sampling has been conducted at Goderich (Ontario) since 1998 using the same trawling protocols that are used at U.S. ports. The bottom trawl survey was conducted between mid-October and early November most years. Single 10-min bottom trawl tows were conducted during daylight at each transect each year. Trawl catches were sorted by species and each species was counted and weighed in aggregate. For Alewife, Rainbow Smelt, and Bloater, length cut-offs (Table 1) were determined from length-frequency data (current year)

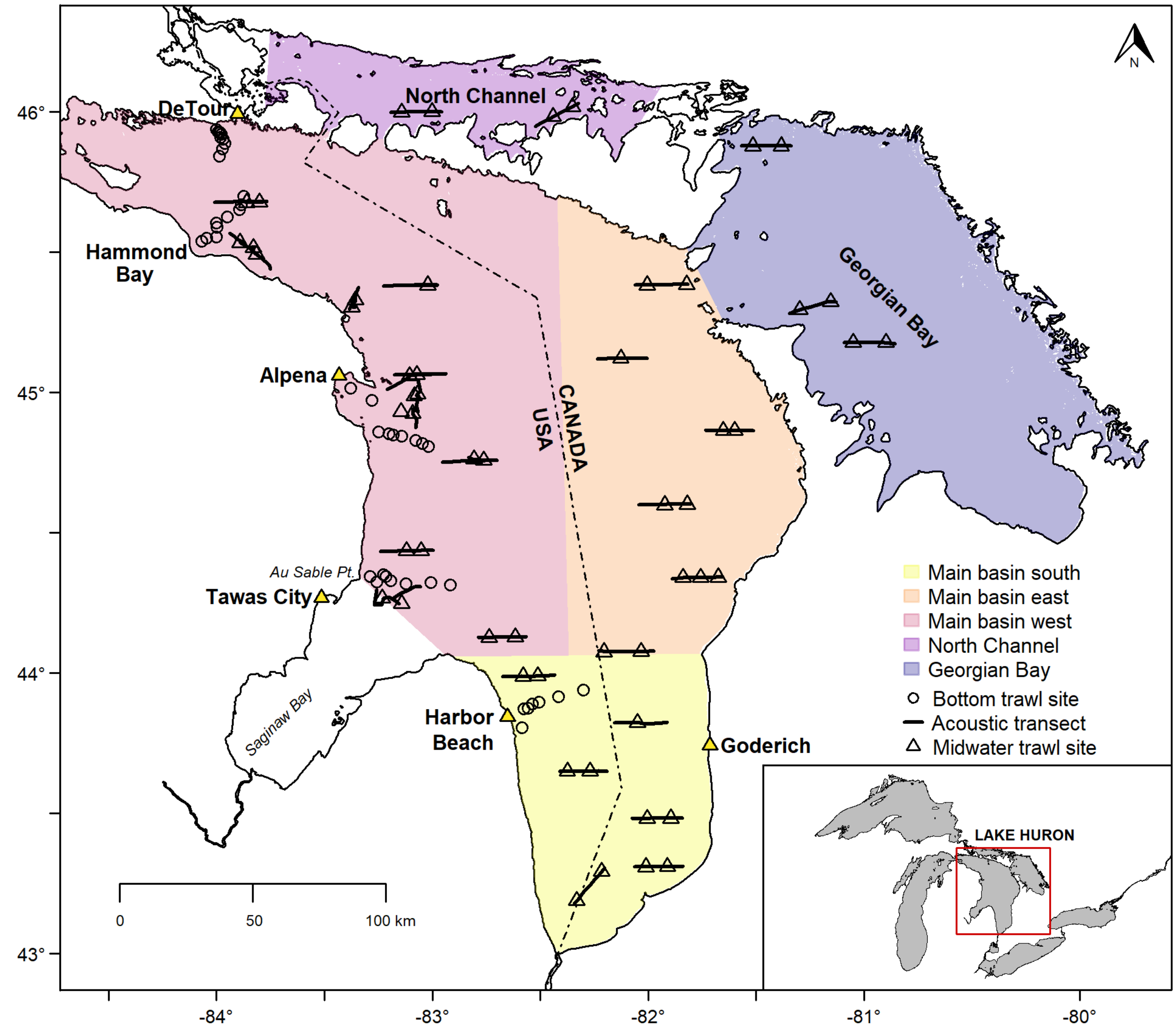

Figure 1. Location of bottom trawls, acoustic transects, and midwater trawls sampled in Lake Huron during 2021. Acoustic sampling strata (shaded areas) correspond to geographic regions: main-basin east, main-basin west, main-basin south, Georgian Bay, and North Channel. Saginaw Bay (unshaded) is not part of the standard acoustic survey area.

and used to apportion bottom trawl catches into age-0 fish (young-of-the-year, or YOY) and those age-1 or older (yearling and older, or YAO). Mean catch weighted by the area of the main basin occurring within 10-m depth strata was used to generate a main-basin estimate of prey fish abundance (for main west, east, and south regions) expressed in density (number/ha) or biomass (kg/ha). Data from surveys prior to 1976, and in 1992, 1993, 1998, 2000, and 2008 were excluded from analyses because surveys were conducted in a non-standard manner (1973-1975, 1992, 1993, 1998) or were not completed (2000, 2008). Additional details concerning survey design and data analysis are provided in the appendix.

Table 1. Length thresholds (total length, in mm) of major species (Bloater *Coregonus hoyi*, Alewife *Alosa pseudoharengus*, and Rainbow Smelt *Osmerus mordax*) sampled in U.S. Geological Survey, Great Lakes Science Center bottom trawl and acoustic surveys, 2021. Length thresholds are used to assign Bloater, Alewife, and Rainbow Smelt to age groups representing young-of-the-year (YOY) and yearling-and-older (YAO) individuals. Fish with total length < threshold length were classified as YOY.

	Survey	
Species	**Bottom Trawl**	**Acoustic**
Alewife	110	100
Rainbow Smelt	80	90
Bloater	110	100

Acoustic-midwater trawl survey— The GLSC has monitored pelagic prey fish abundance annually from 2004 using a scientific echosounder system deployed along randomly-selected transects within five geographic regions: main-basin east, main-basin west, main-basin south, Georgian Bay, and the North Channel (Figure 1). Each year, the first transect within each region was selected randomly based on latitude and longitude; subsequent transects were spaced equidistant (north to south, east to west for North Channel only) from the first within the constraints of region boundaries. Final transect location was selected by alternating deep and shallow depths to achieve a spatially balanced survey design within each region. Acoustic surveys are typically conducted in September through early October. In all years, daily sampling was initiated one hour after sunset and ended no later than one hour before sunrise. Fish catches from midwater trawl tows conducted along each acoustic transect were used to identify species composition of acoustic targets. Information from acoustic surveys was combined with trawl data to produce lake-wide fish abundances expressed as density (number/ha) or biomass (kg/ha) which were the weighted average of acoustic fish density, with region area as the weighting variable. Acoustic density of Alewife, Rainbow Smelt, and Bloater was apportioned by age group (YOY vs. YAO) using fixed length cut-offs determined from age-length relationships (see Table 1). Additional details concerning survey design and data analysis are provided in the appendix.

Data analysis—Data from both surveys were used to assess shifts in prey fish community biomass and species composition over time (Objective 1); describe trends in the abundance of individual species (Objectives 2, 4); determine if abundance trends for dominant species (Alewife, Bloater, and Rainbow Smelt) differed between surveys (Objective 2); and describe population length-frequency structure (Objective 3). Non-parametric correlation (Spearman Rank Sum Test) was used to test for temporal correlation between estimated mean fish abundance (biomass) estimated from the bottom trawl and acoustic surveys for each target species. Data from the acoustic survey alone were used to describe prey fish abundance and species composition by lake basin (Objective 1) and spatial distributions of dominant species in 2021 (Objective 3). Abundance was expressed in density (numbers/ha) for YOY Alewife, Rainbow Smelt, and Bloater, whereas abundance was expressed as biomass (kg/ha) for YAO Alewife, Rainbow Smelt, and Bloater and all species that were not subdivided by age group (Objective 4).

Results and Discussion

Survey overview—The Lake Huron acoustic and bottom trawl surveys were completed during 9 September - 8 October 2021 and 13-22 October 2021, respectively. The bottom trawl survey was conducted aboard the R/V *Arcticus*, and all standard ports and transects were sampled with the exception of Goderich, Ontario (42 total trawl tows). The acoustic survey was conducted jointly by the GLSC (R/V *Sturgeon*) and U.S. Fish and Wildlife Service (M/V *Spencer F. Baird*). Twenty-eight acoustic survey transects were sampled, and 55 midwater trawl tows were conducted in conjunction with acoustic data collection (Figure 1).

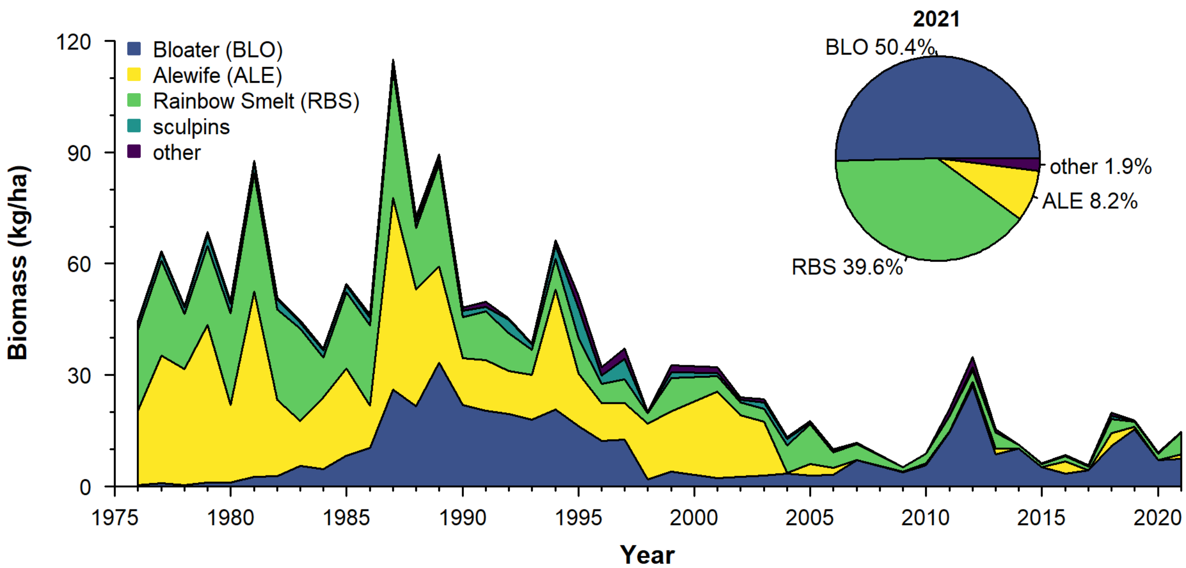

Figure 2. Prey fish biomass and species composition in the region sampled by the bottom trawl (i.e., 9-110 m depth) in Lake Huron, 1976-2021, and in 2021 (pie chart). Data shown are for major species (Bloater *Coregonus hoyi*, Alewife *Alosa pseudoharengus*, Rainbow Smelt *Osmerus mordax*, and sculpins). Other species are listed in Table 2.

Community biomass and species composition— Mean benthic prey fish biomass in main basin (9-110 m) in 2021 averaged 14.7 kg/ha, which was below levels observed prior to basin-wide declines in prey fish biomass that occurred during the early 2000s (Figure 2). Prey fish biomass estimated from the acoustic survey in 2021 varied by region (Figure 3), with the highest biomass occurring in the North Channel (17.05 kg/ha) and lower biomass in the main basin (12.5 kg/ha) and Georgian Bay (8.6 kg/ha). The prey fish community in 2021 was dominated by Bloater and Rainbow Smelt, which together accounted for 92 % of the estimated total prey fish biomass for acoustic and 90%

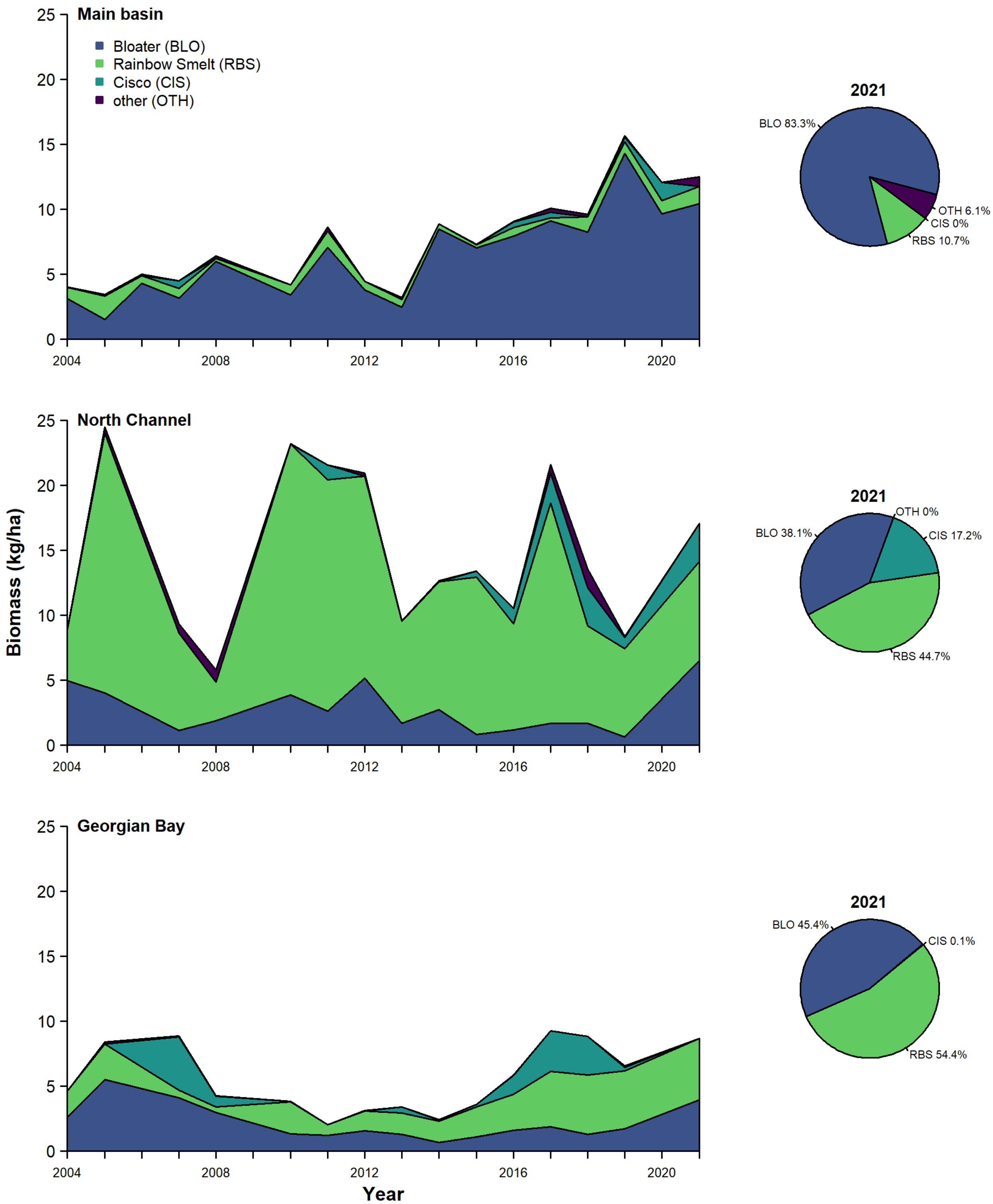

Figure 3. Acoustic survey prey fish biomass and species composition by year and region. Pie charts to the right of each area plot denote species composition (% biomass) in 2021. Data shown are for major species (Bloater *Coregonus hoyi*, Cisco *Coregonus artedi*, and Rainbow Smelt *Osmerus mordax*. Other species are listed in Table 2. No sampling occurred in Georgian Bay or the North Channel in 2006 and 2020.

of the bottom trawl estimates (Figures 2, 3). Bloater and Rainbow Smelt have been the most abundant species in USGS bottom trawl surveys since the collapse of Alewife in 2004 (Figure 2). Alewife has remained the third-most abundant species in bottom trawl catches despite the scarcity of YAO individuals. Results of the acoustic survey suggested that Bloater were the dominant prey fish species in the main basin while Rainbow Smelt were dominant in the North Channel and Georgian Bay (Figure 3). In the North Channel and Georgian Bay, non-Rainbow Smelt biomass was mainly comprised of Cisco and Bloater (Figure 3). All other prey fish species combined accounted for less than 1 % of prey species (by weight) sampled in both surveys across all lake regions.

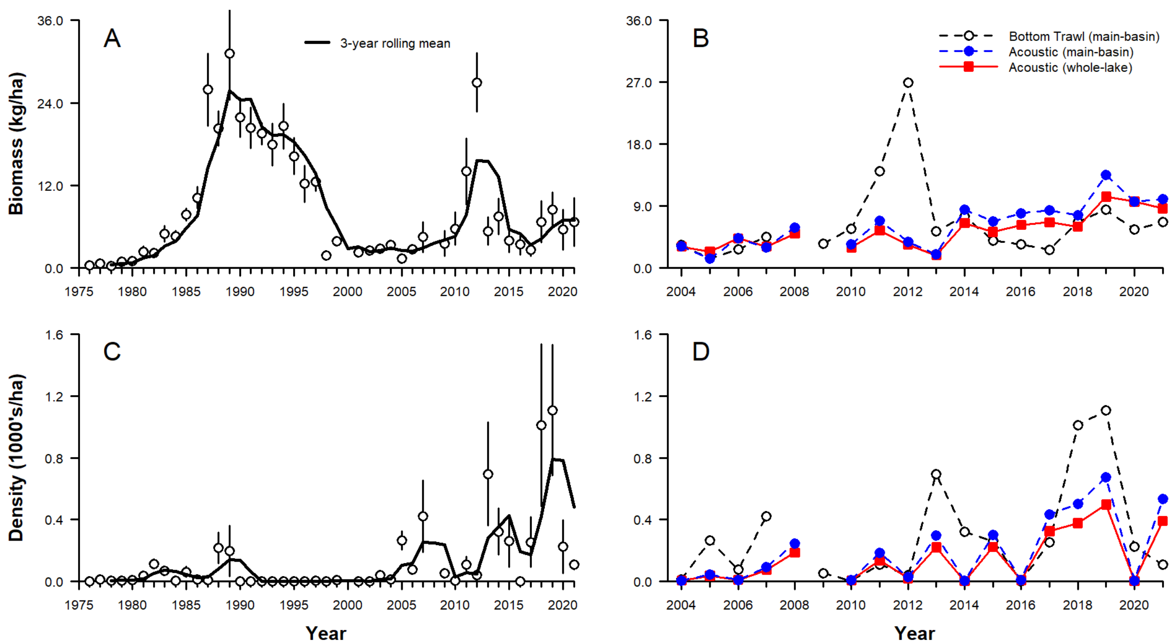

Figure 4. Bloater *Coregonus hoyi* abundance in Lake Huron by age group (yearling-and-older, young-of-year), period (1976-2021, 2004-2021), and survey (bottom trawl, acoustic). A-B: Estimated biomass of yearling-and-older Bloater from bottom trawl and acoustic surveys during 1976-2021 (A) and 2004-2021 (B). C-D: Estimated density of young-of-year bloater from bottom trawl and acoustic surveys during 1976-2021 (C) and 2004-2021 (D). Points in panels A and C represent annual means for the bottom trawl only. Lines in panels A and C represent the 3-year running mean. Error bars in panels A and C represent ±1 standard error. Colored lines in panels B and D represent mean acoustic survey biomass (B) or density (D) for all three basins combined (red) and for the main basin only (blue).

Bloater—Bloater have been the most abundant prey fish in the main basin of Lake Huron over the past decade and accounted for roughly 50% of total prey fish biomass in bottom trawl catches during 2021. Biomass of YAO Bloater estimated from bottom trawls increased from historical lows in the late 1970s to peak levels from 1987-1994 (Figure 4A). Biomass declined rapidly from 1995 to 2001 and remained relatively low through the 2000s before peaking again in 2011-12. Both surveys indicated an increasing trend in YAO biomass from 2017 to 2019 which leveled off between 2020-2021. Biomass of YAO Bloater estimated from the 2021 bottom trawl survey (6.6 kg/ha) and acoustic survey (8.6 kg/ha) were consistent with increased biomass observed since 2017 (Figure 4B). Trends in YAO Bloater biomass since 2004 were poorly correlated between the bottom trawl and acoustics time series (Spearman Rank-sum test; ρ = 0.38, P = 0.14) mainly due to the spike in bottom trawl biomass that occurred in 2012 that was not observed in the acoustics time series (Figure 4B). Despite their prevalence across Lake Huron, Bloater remain a minor component of piscivore diets (Happel et al. 2018, Roseman et al. 2014), so predation is not likely driving temporal variability in YAO abundance.

Densities of YOY Bloater estimated by the bottom trawl in 2021 declined for the second year in a row following record high abundance in 2019 (Figures 4C, 4D). Densities of YOY Bloater in the acoustic survey increased in 2021 (Figure 4D) in contrast to the bottom trawl results. YOY Bloater abundance trends from the bottom trawl and acoustic surveys have tracked each other well over the 15-year time series, however 2021 marked a departure from this concordance (Spearman Rank-sum test; ρ = 0.51, P = 0.04). Regardless, both time series suggest that YOY Bloater density has increased since 2016 (Figures 4C, 4D).

Large Bloater year classes (e.g., in 2007, 2013, 2018, and 2019) have occurred more frequently since the crash of Alewife in 2004, which is consistent with the hypothesized negative effect of Alewife on YOY Bloater survival (Collingsworth et al. 2014). Persistent strong year classes since 2007 have bolstered Bloater stocks and resulted in a population composed of multiple age classes (Figure 5). The age structure of the Bloater population in 2020 was over 60% age-1 and age-2 fish from the 2018 and 2019 year classes and the maximum age was estimated at 13. These older age classes that remain in the population underscore the importance of strong recruitment events (e.g., 2007) to the long-term health of Bloater stocks in Lake Huron (Figure 5). Age data from the 2021 surveys was being processed at the time of this writing.

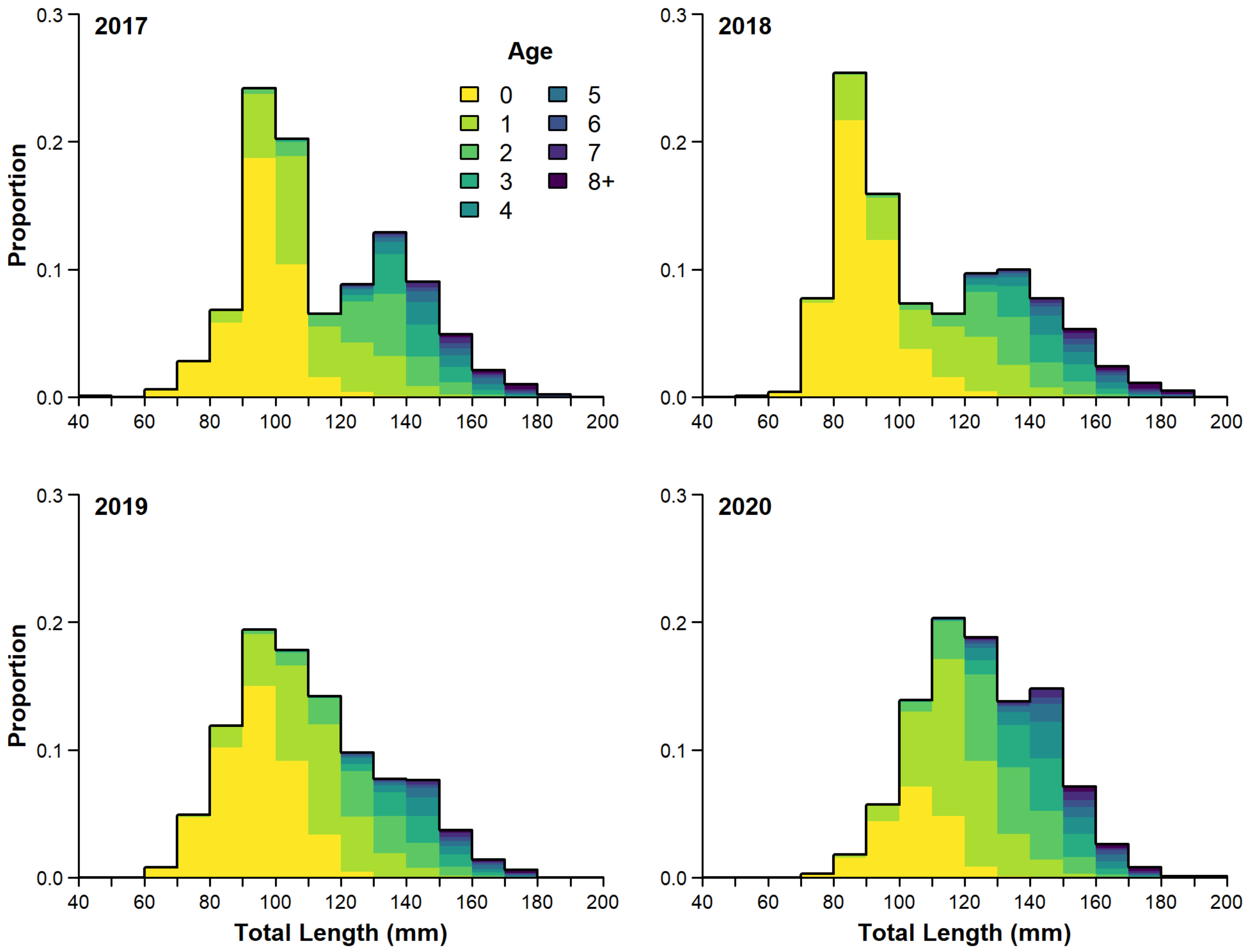

Figure 5. Estimated proportions-at-age for Bloater *Coregonus hoyi* by 10 mm length bin in Lake Huron during 2017-2020. Otolith ages were estimated from bottom-trawl collected fish in the main basin of Lake Huron during October of each year. Ages are estimated from a subsample of 10 fish/10 mm length bin for each port where Bloater are sampled and expanded to the total length frequency: 2017 n=1741, 2018 n=1330, 2019 n=2221, 2020 n=1432.

Bloater in 2021 were most abundant in the southeast portion of the lake (Figure 6). Size distribution of Bloater from midwater trawl catches in September 2021 was bi-modal with the peak at 70-90 mm total length representing YOY-sized individuals (Figure 6). Bottom trawl catches in October 2021 consisted mainly of individuals with total length between 90 and 150 mm (Figure 6).

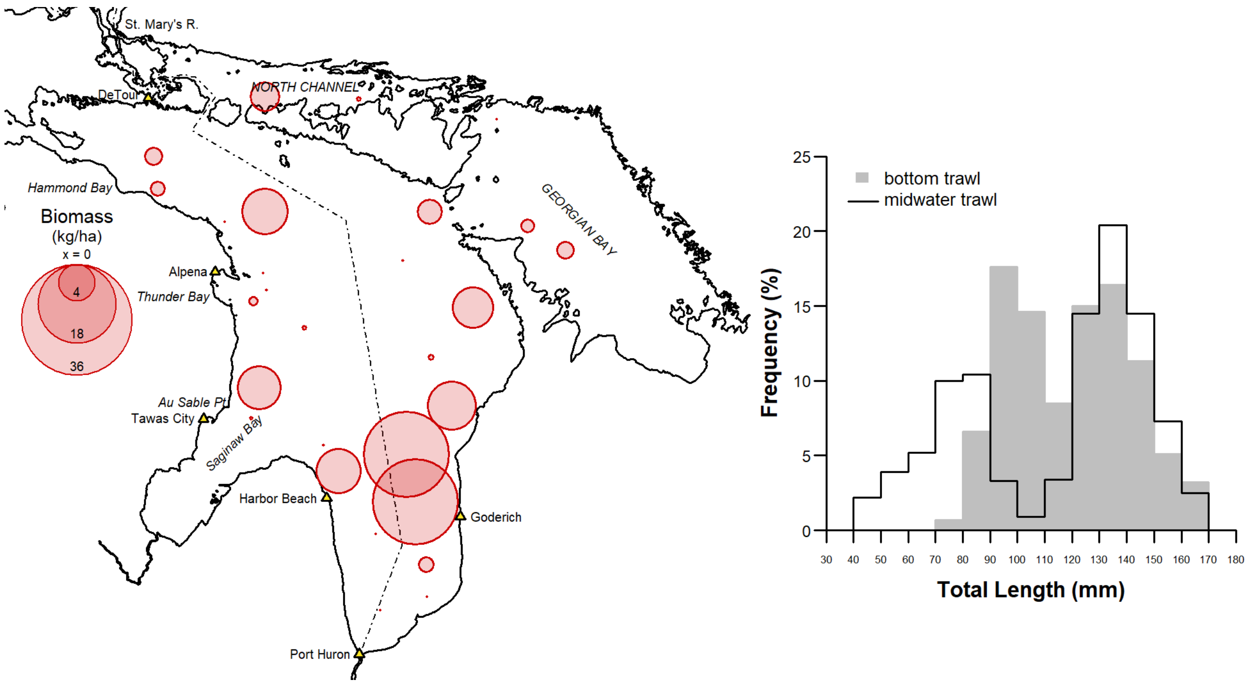

Figure 6. Bloater *Coregonus hoyi* biomass distribution (left) and size structure (right) in Lake Huron in 2021. Biomass distribution was estimated from the acoustic survey and includes all age groups.

Rainbow Smelt—Rainbow Smelt have been important prey for Chinook Salmon, Lake Trout, and Walleye since their introduction into Lake Huron (Diana 1990, Roseman et al. 2014), but current biomass of YAO Rainbow Smelt is low relative to historical levels (Figure 7A). Biomass of YAO Rainbow Smelt decreased steadily between 1990 and 2003 and has remained at all-time lows since (Figure 7A). Biomass since 2004 has fluctuated with no distinct trend at both the main-basin and lake-wide scales (Figure 7B). Main-basin biomass of YAO rainbow smelt was significantly correlated between surveys (Spearman Rank-sum test; $\rho = 0.70$, $P < 0.01$). Acoustic biomass for YAO Rainbow Smelt is often higher at lake-wide than main-basin scales due to large concentrations of Rainbow Smelt in the North Channel and Georgian Bay. Declines in YAO Rainbow Smelt abundance in Lake Huron preceded the crash of adult Alewife in 2004, so predators switching from Alewife to Rainbow Smelt cannot entirely explain declines in YAO abundance.

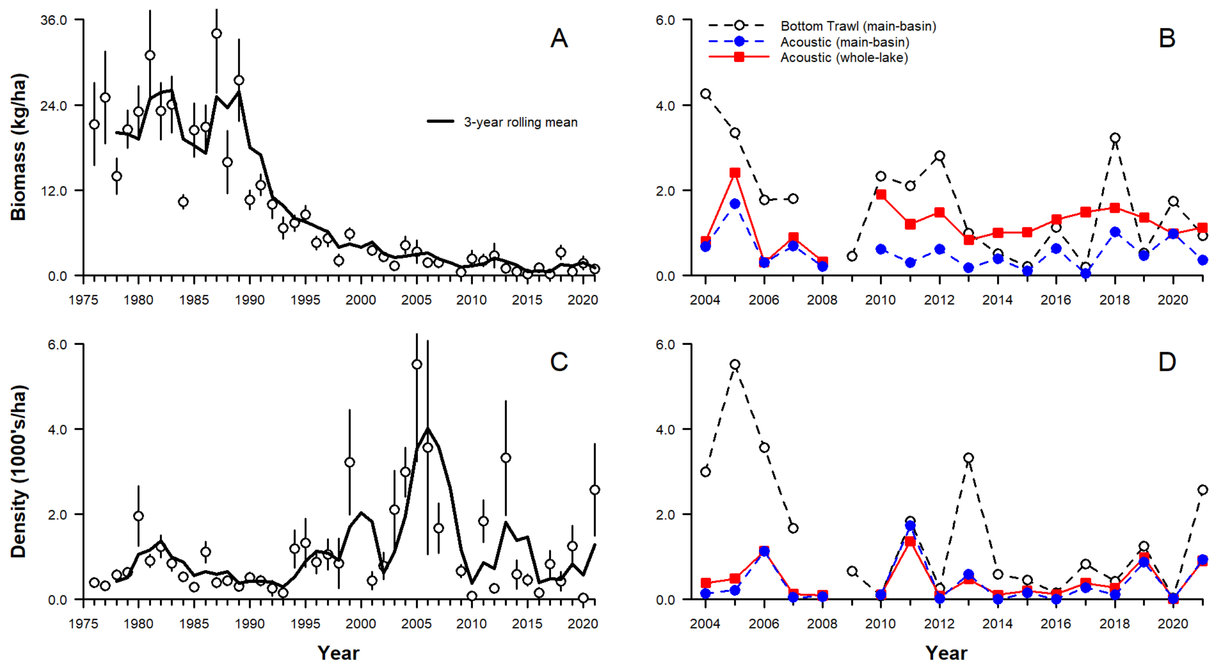

Figure 7. Rainbow Smelt *Osmerus mordax* abundance in Lake Huron by age group (yearling-and-older, young-of-year), period (1976-2021, 2004-2021), and survey (bottom trawl, acoustic). A-B: Estimated biomass of yearling-and-older Rainbow Smelt from bottom trawl and acoustic surveys during 1976-2021 (A) and 2004-2021 (B). C-D: Estimated density of young-of-year Rainbow Smelt from bottom trawl and acoustic surveys during 1976-2021 (C) and 2004-2021 (D). Points in panels A and C represent annual means for the bottom trawl only. Lines in panels A and C represent the 3-year running mean. Error bars in panels A and C represent ±1 standard error. Colored lines in panels B and D represent mean acoustic survey biomass (B) or density (D) for all three basins combined (red) and for the main basin only (blue).

Abundance of YOY Rainbow Smelt has fluctuated with few distinct trends throughout the time series (Figures 7C, 7D). Large spikes in YOY density since 1999 may have been the result of declines in YAO Rainbow Smelt, which are known to cannibalize smaller individuals (Henderson and Nepszy 1989). However, these strong reproductive events did not kindle a recovery in the YAO population, which suggests the existence of a recruitment bottleneck. Additionally, sustained predation by Lake Trout on age-1 and older Rainbow Smelt was likely a factor that limited recovery of YAO populations following strong recruitment events in the early 2000s (O'Brien et al. 2014). Estimated density of YOY Rainbow Smelt from bottom trawls and acoustics exhibited similar trends (Spearman Rank-sum test; $r = 0.70$, $P < 0.01$) and both indicated that abundance of YOY Rainbow Smelt increased from 2020 to 2021 (Figures 7C, 7D).

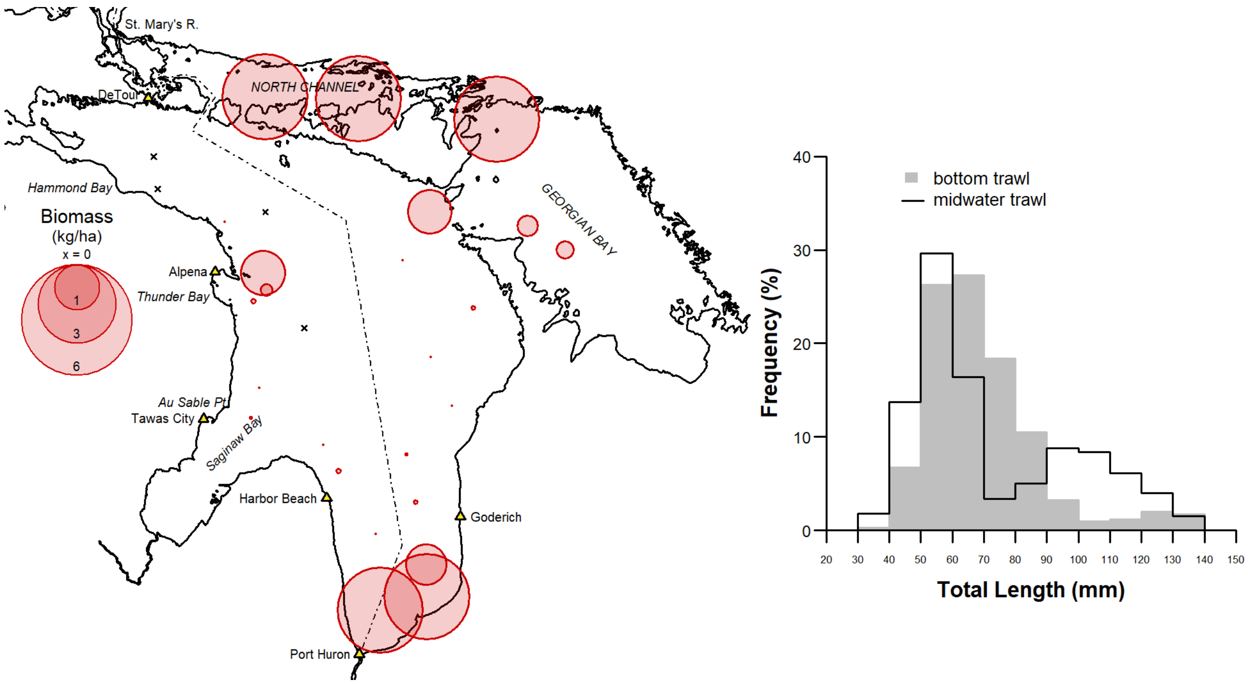

Figure 8. Rainbow Smelt *Osmerus mordax* biomass distribution (left) and size structure (right) in Lake Huron in 2021. Biomass distribution was estimated from the acoustic survey and includes all age groups.

Rainbow Smelt were widely distributed in Lake Huron in 2021 but were most abundant in the North Channel, northern Georgian Bay, and main basin south regions (Figure 8). Rainbow Smelt were collected in all but one of 41 bottom trawl tows and in roughly 70% of midwater trawls in 2021. Size distributions of Rainbow Smelt in 2021 were bimodal with the peaks at 50-60 mm (midwater trawl) and 50-70 mm (bottom trawl) representing the 2021-year class (Figure 8). The shift towards larger Rainbow Smelt in the bottom trawl survey in 2021 suggests that juvenile Rainbow Smelt grew rapidly during the period between surveys (Figure 8).

Alewife—Alewives were once the dominant prey item consumed by salmonines in Lake Huron (Diana 1990, Madenjian et al. 2006) and were the first- or second-most abundant prey species in Lake Huron until 2004 when YAO individuals disappeared from trawl catches (Figures 9A, 9B). Alewife abundance in Lake Huron has been driven by sporadic catches of YOY fish since the collapse of the adult population. Time series of YOY Alewife density from the two surveys have agreed since 2004 ($\rho = 0.63$, $P < 0.01$) with similar estimates in 2021 and both suggesting that YOY Alewife density increased relative to 2020 (Figures 9C, 9D).

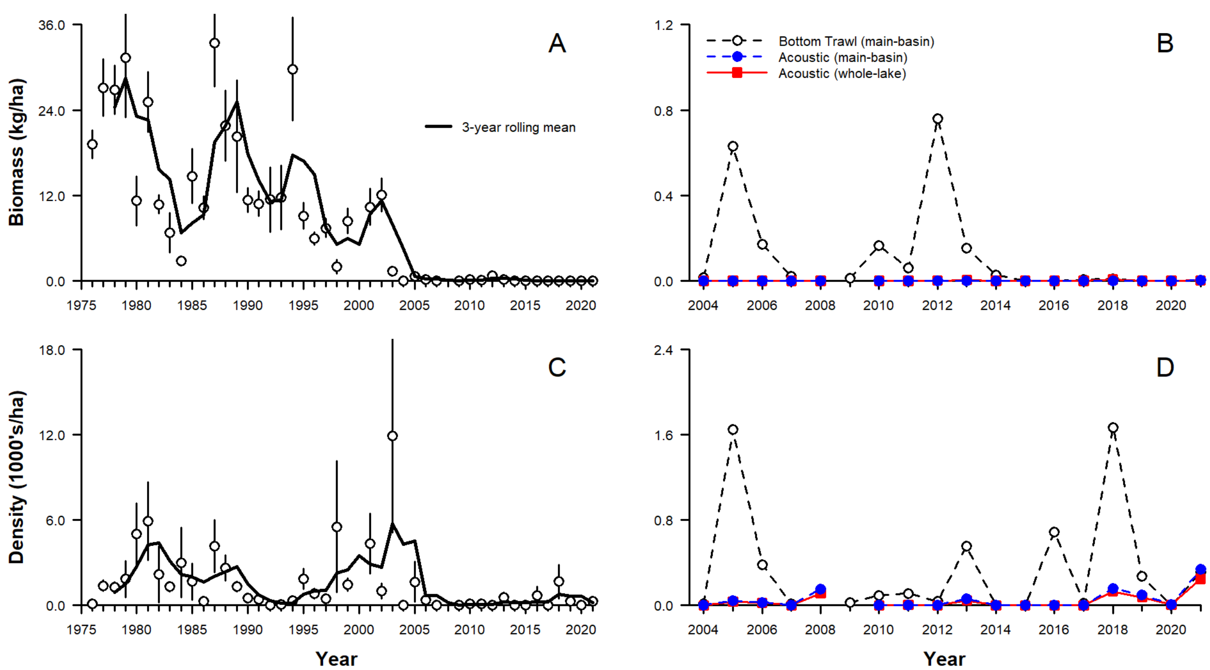

Figure 9. Alewife *Alosa pseudoharengus* abundance in Lake Huron by age group (yearling-and-older, young-of-year), period (1976-2021, 2004-2021), and survey (bottom trawl, acoustic). A-B: Estimated biomass of yearling-and-older Alewife from bottom trawl and acoustic surveys during 1976-2021 (A) and 2004-2021 (B). C-D: Estimated density of young-of-year Alewife from bottom trawl and acoustic surveys during 1976-2021 (C) and 2004-2021 (D). Points in panels A and C represent annual means for the bottom trawl only. Lines in panels A and C represent the 3-year running mean. Error bars in panels A and C represent ±1 standard error. Colored lines in panels B and D represent mean acoustic survey biomass (B) or density (D) for all three basins combined (red) and for the main basin only (blue).

Size-at-age and spatial distribution of Alewives in Lake Huron during 2021 indicate that the population was composed of few age classes in limited areas of the lake. Age estimates for Lake Huron Alewife since 2017 confirm the paucity of YAO individuals across the survey area (Figure 10). All but one individual collected in both 2020 and 2021 (not shown) surveys was age-0, which suggests that few individuals from the 2018 and 2019 year-classes survived to the end of 2021. The largest concentrations of YOY Alewife occurred in the western main basin from Hammond Bay south to Thunder Bay (Figure 11). Alewife sampled in bottom trawls in October were larger than conspecifics sampled in midwater trawls during September-October (Figure 11). Age data from the 2021 surveys was being processed at the time of this writing.

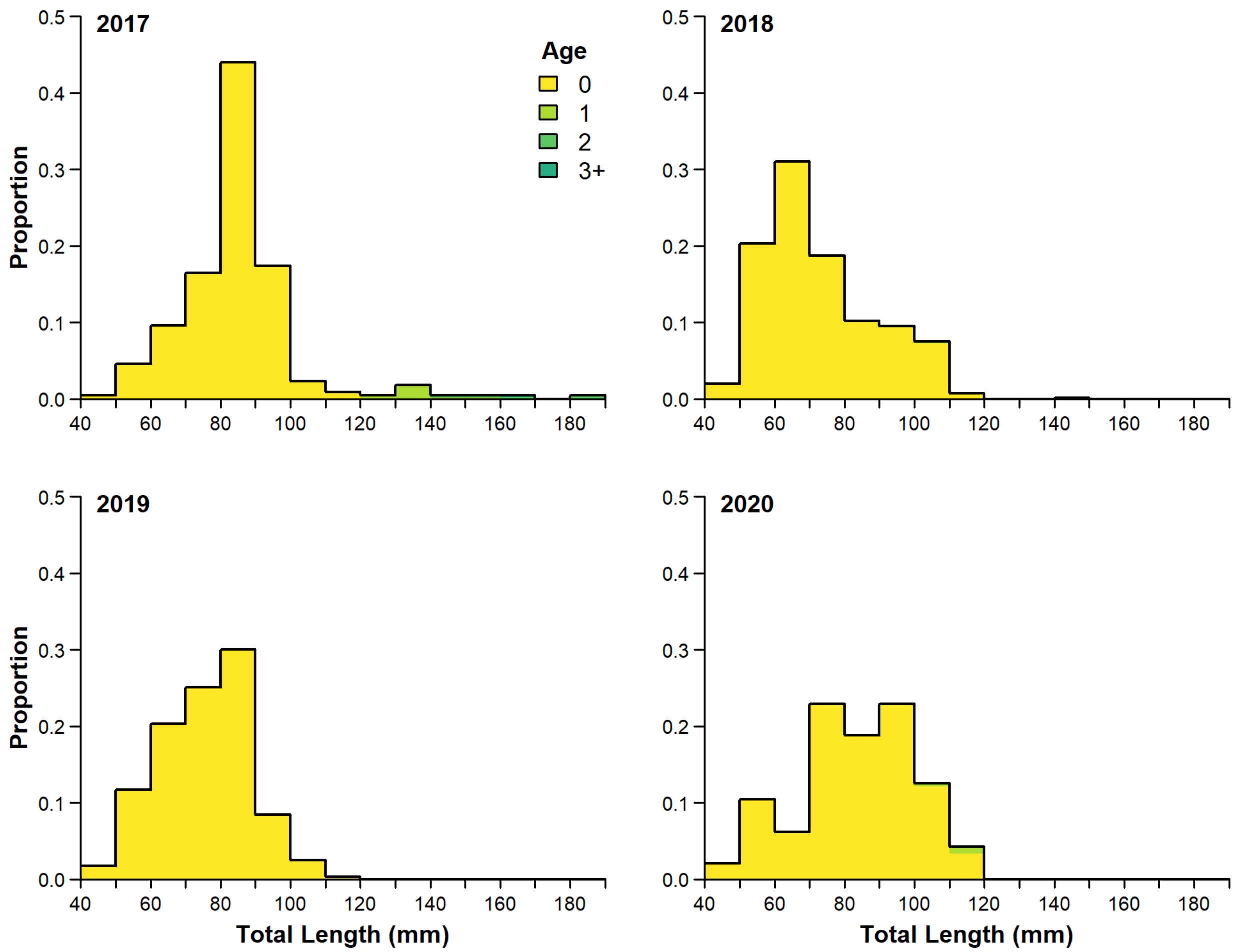

Figure 10. Estimated proportions-at-age for Alewife *Alosa pseudoharengus* by 10 mm length bin in Lake Huron during 2017-2020. Otolith ages were estimated from bottom-trawl collected fish in the main basin of Lake Huron during October each year. Ages are estimated from a subsample of 7 fish/5 mm length bin for each port where Alewife are sampled and expanded to the total length frequency: 2017 n=218, 2018 n=1342, 2019 n=634, 2020 n=48.

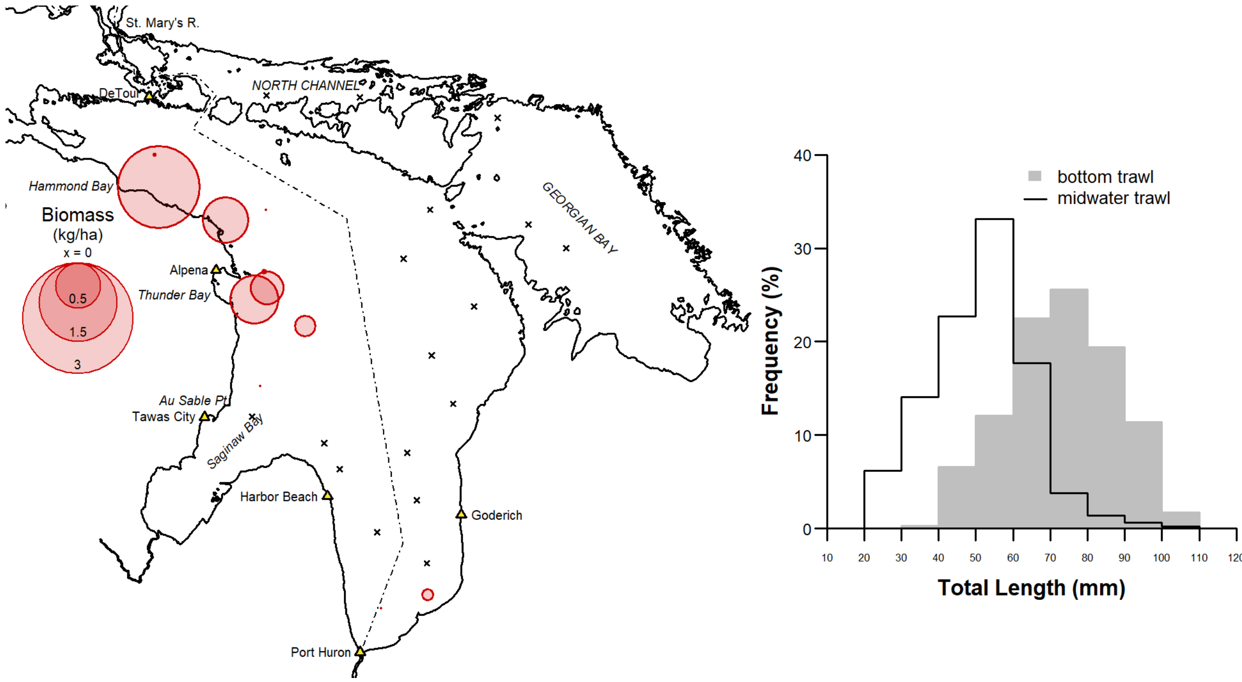

Figure 11. Alewife *Alosa pseudoharengus* biomass distribution (left) and size structure (right) in Lake Huron in 2021. Biomass distribution was estimated from the acoustic survey and includes all age groups.

Causes of the Alewife decline in Lake Huron have been debated and include unsustainable levels of predation by Pacific salmon and Lake Trout (He et al. 2015), a severe winter mortality event in 2003 (Dunlop and Riley 2013), bottom-up forces related to nutrient reduction (Kao et al. 2016), dreisennid mussel-induced disruption of inshore-offshore energy exchange (Barbiero et al. 2018), and declines in the abundance of the benthic amphipod *Diporeia* spp., an important Alewife prey (Nalepa et al. 2007). We hypothesize that the severe winter of 2002-03 reduced the adult Alewife population to historically low levels, but that recovery of the adult population currently is restricted both by bottom-up and top-down forces. Alewife abundance and population dynamics are more influenced by nutrients and primary production in Lake Huron than in Lake Michigan (Bunnell et al. 2014, Collingsworth et al. 2014), so we concur with Kao et al. (2016) that reductions in phosphorous inputs to Lake Huron and the sequestration of nutrients in mussel biomass has likely reduced Alewife carrying capacity below historical levels. Predation by a recovering Lake Trout population may keep Alewife biomass below current carrying capacity if they and other predators are able to use alternate prey (e.g., Round Goby) when Alewife are unavailable (He et al. 2015, Madenjian et al. 2013).

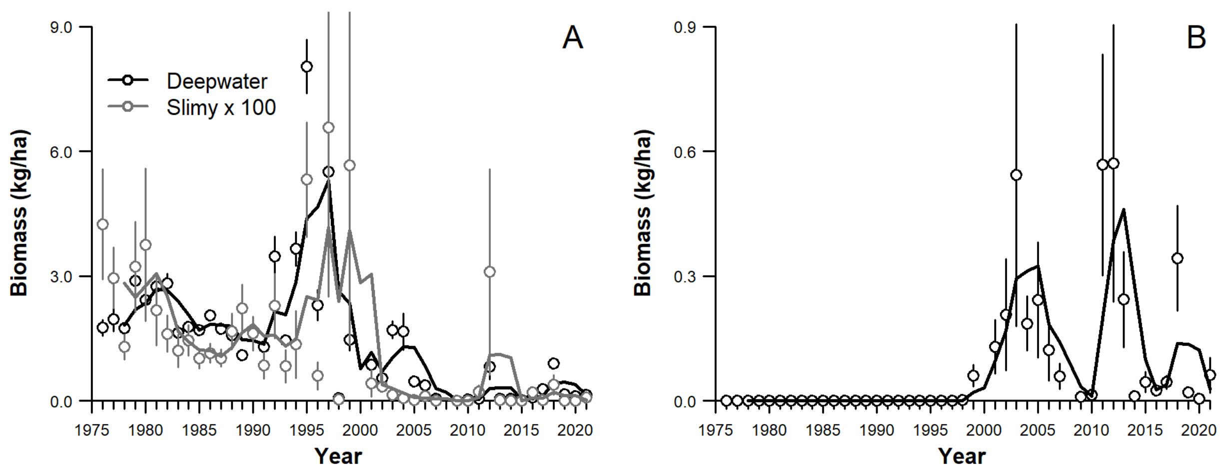

Figure 12. Estimated biomass of sculpins (A) and Round Goby *Neogobius melanostomus* (B) from bottom trawls during 1976-2021. Lines represent the 3-year running mean. Error bars represent ±1 standard error. Slimy Sculpin abundance was multiplied by 100 to facilitate comparison of abundance trends between sculpin species.

Sculpin—Historically, Slimy Sculpin *Cottus Cognatus* and Deepwater Sculpin *Myoxocephalus thompsonii* were important prey of the native piscivore community in offshore waters of Lake Huron (Van Oosten and Deason 1938). Juvenile and adult sculpins are confined to the lake bottom, so they are sampled only during the bottom trawl survey. Sculpin populations in Lake Huron declined gradually between 1976 and 1992, experienced a brief resurgence in the middle to late 1990s, and then declined rapidly in the early to mid-2000s (Figure 12A). Slimy Sculpin have become rare since 2010, with surveys failing to collect a single individual in 2010, 2014, 2015, and 2019, and 2020. The current low abundance of sculpin in Lake Huron coincides with the expansion and proliferation of a potential competitor, Round Goby, as well as the decline of an important prey, *Diporeia* spp.

Round Goby—Round Goby have become a significant part of Lake Trout diets in some areas of the Great Lakes (Dietrich et al. 2006, Leonhardt et al. 2020), including Lake Huron (Roseman et al. 2014). Round Goby were first captured in the Lake Huron bottom trawl survey in 1997, reached a peak in abundance in 2003, and declined in abundance until increasing again in 2011-2012 and 2018 (Figure 12B). Our results suggest that Round Goby increased from 2020 to 2021 but remained at relatively low abundance in the offshore waters of Lake Huron (Figure 12B). However, the bottom trawl may not provide a robust estimate of Round Goby abundance because the species is thought to be concentrated in nearshore (depth < 9 -m) and/or rocky (i.e., untrawlable) habitat(s) not sampled in GLSC bottom trawl surveys. Round Goby also may seasonally migrate offshore (Pennuto et al. 2021, Walsh et al. 2007), which explains why they are sometimes caught in high numbers in the bottom trawl survey.

Cisco—Cisco is a native planktivore that was once common in offshore areas throughout Lake Huron. They were overfished to historically low abundance and most spawning populations in the main basin were extirpated by the early 1900s (Berst and Spangler 1972). Cisco, which exhibit diel, vertical feeding migrations and spawning migrations into nearshore, shallow waters (Hrabik et al. 2006, Stockwell et al. 2009), are important to the transfer of energy and nutrients between benthic and pelagic habitats and between nearshore and offshore areas. Cisco are only sampled in the acoustics survey and have only been collected in the North Channel, Georgian Bay, and adjacent waters of the main basin since 2007. Catches of Cisco in midwater trawls in 2021 were low. Six adult Cisco were captured in 2021, two in Georgian Bay and four in the North Channel ranging in total length from 177- 453 mm. Cisco numbers in Georgian Bay and the North Channel have increased since 2015 (Figure 13), which suggests current lake conditions in these basins may favor Cisco recovery.

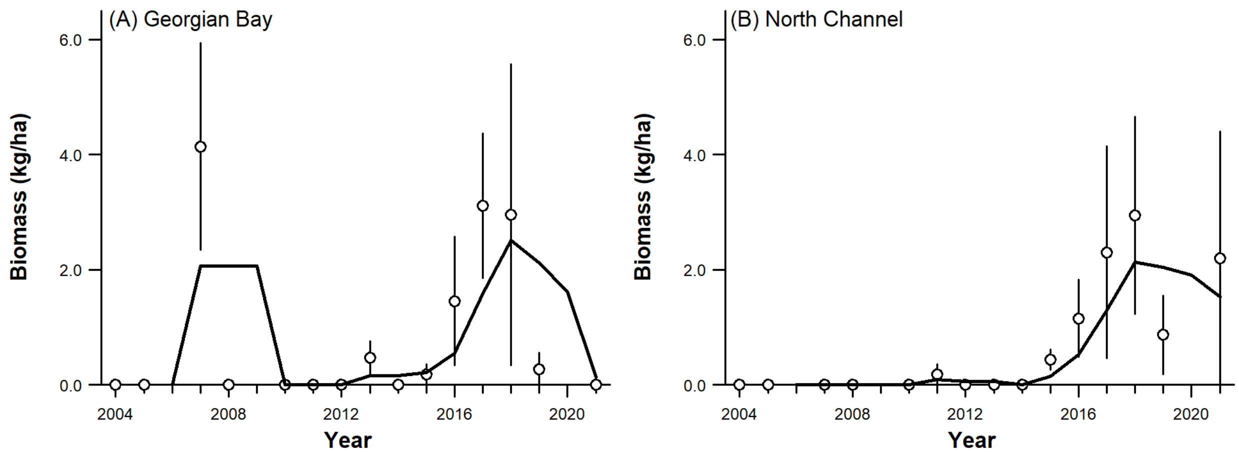

Figure 13. Estimated biomass of Cisco from acoustic surveys in Georgian Bay (left) and the North Channel (right), Lake Huron, during 2004-2021. Lines represent 3-year running means. Error bars represent ±1 standard error.

Minor species—Gizzard Shad *Dorosoma cepedianum*, Threespine Stickleback *Gasterosteus aculeatus*, Ninespine Stickleback *Pungitius pungitius*, Trout-perch *Percopsis omiscomaycus*, Emerald Shiner *Notropis hudsonius*, and Yellow Perch *Perca flavescens* were the only other prey fish species sampled in bottom trawl and acoustic surveys in Lake Huron in 2021. Collectively, these species comprised less than 2 % of prey fish community biomass in 2021 (Table 2). Ninespine Stickleback and Yellow Perch were the most abundant minor species in bottom trawls, while Emerald Shiner was the most abundant minor species sampled in the acoustic survey (Table 3).

Table 2. Mean (±SE) prey fish biomass (g/ha) by species and survey in 2021. Biomass estimates for Alewife, Rainbow Smelt, Bloater, and Cisco are stratified by age class (YOY = young-of-year; YAO = yearling and older, dash denotes no stratification by age class). Estimates are main-basin means for the bottom trawl survey and whole lake-means for the acoustic survey.

			Survey	
Common Name	**Scientific Name**	**Age Class**	*Bottom Trawl*	*Acoustics*
Alewife	*Alosa Pseudoharengus*	YOY	1.2014 ± 1.0273	0.3553 ± 0.1372
Alewife	*Alosa Pseudoharengus*	YAO	0.0018 ± 0.0018	0.0023 ± 0.0023
Bloater	*Coregonus hoyi*	YOY	0.7624 ± 0.2307	0.6937 ± 0.6937
Bloater	*Coregonus hoyi*	YAO	6.6493 ± 3.5332	8.6427 ± 2.5134
Cisco	*Coregonus artedi*	YOY	0.0 ± 0.0	0.0121 ± 0.0102
Cisco	*Coregonus artedi*	YAO	0.0 ± 0.0	0.1134 ± 0.1134
Deepwater Sculpin	*Myoxocephalus thomsonii*	—	0.1447 ± 0.0156	0.0 ± 0.0
Emerald Shiner	*Notropis atherinoides*	—	0.0 ± 0.0	0.1518 ± 0.1169
Gizzard Shad	*Dorosoma cepedianum*	—	0.0012 ± 0.0011	0.0 ± 0.0
Johnny Darter	*Etheostoma nigrum*	—	0.0 ± 0.0	0.0 ± 0.0
Logperch	*Percina caprodes*	—	0.0 ± 0.0	0.0 ± 0.0
Ninespine Stickleback	*Pungitius pungitius*	—	0.0251 ± 0.0166	0.0002 ± 0.0002
Rainbow Smelt	*Osmerus mordax*	YOY	4.8924 ± 2.3593	0.9575 ± 0.3575
Rainbow Smelt	*Osmerus mordax*	YAO	0.9283 ± 0.4315	1.1120 ± 0.3825
Round Goby	*Neogobius melanostomus*	—	0.0613 ± 0.0425	0.0 ± 0.0
Slimy Sculpin	*Cottus cognatus*	—	0.0007 ± 0.0005	0.0 ± 0.0
Spottail Shiner	*Notropis hudsonius*	—	0.0 ± 0.0	0.0 ± 0.0
Threespine Stickleback	*Gasterosteus aculeatus*	—	0.0007 ± 0.0006	0.0068 ± 0.0042
Trout-perch	*Percopsis omiscomaycus*	—	0.0 ± 0.0	0.0 ± 0.0
White Bass	*Morone chrysops*	—	0.0 ± 0.0	0.0 ± 0.0
White Perch	*Morone americanus*	—	0.0 ± 0.0	0.0 ± 0.0
Yellow Perch	*Perca flavescens*	—	0.045 ± 0.0371	0.0 ± 0.0

Table 3. Mean (±SE) prey fish density (number/ha) by species and survey in 2021. Density estimates for Alewife, Rainbow Smelt, Bloater, and Cisco are stratified by age class (YOY = young-of-year; YAO = yearling and older, dash denotes no stratification by age class). Estimates are main-basin means for the bottom trawl survey and whole lake-means for the acoustic survey.

			Survey	
Common Name	**Scientific Name**	**Age Class**	*Bottom Trawl*	*Acoustics*
Alewife	*Alosa Pseudoharengus*	YOY	307 ± 256	248 ± 87
Alewife	*Alosa Pseudoharengus*	YAO	0 ± 0	0 ± 0
Bloater	*Coregonus hoyi*	YOY	108 ± 31	393 ± 211
Bloater	*Coregonus hoyi*	YAO	404 ± 227	170 ± 40
Cisco	*Coregonus artedi*	YOY	0 ± 0	0 ± 0
Cisco	*Coregonus artedi*	YAO	0 ± 0	0 ± 0
Deepwater Sculpin	*Myoxocephalus thomsonii*	—	29 ± 3	0 ± 0
Emerald Shiner	*Notropis atherinoides*	—	0 ± 0	114 ± 79
Gizzard Shad	*Dorosoma cepedianum*	—	0 ± 0	0 ± 0
Johnny Darter	*Etheostoma nigrum*	—	0 ± 0	0 ± 0
Logperch	*Percina caprodes*	—	0 ± 0	0 ± 0
Ninespine Stickleback	*Pungitius pungitius*	—	16 ± 10	0 ± 0
Rainbow Smelt	*Osmerus mordax*	YOY	2570 ± 1079	907 ± 323
Rainbow Smelt	*Osmerus mordax*	YAO	115 ± 51	155 ± 66
Round Goby	*Neogobius melanostomus*	—	16 ± 12	0 ± 0
Slimy Sculpin	*Cottus cognatus*	—	0 ± 0	0 ± 0
Spottail Shiner	*Notropis hudsonius*	—	0 ± 0	0 ± 0
Threespine Stickleback	*Gasterosteus aculeatus*	—	0 ± 0	10 ± 6
Trout-perch	*Percopsis omiscomaycus*	—	0 ± 0	0 ± 0
White Bass	*Morone chrysops*	—	0 ± 0	0 ± 0
White Perch	*Morone americanus*	—	0 ± 0	0 ± 0
Yellow Perch	*Perca flavescens*	—	9 ± 8	0 ± 0

Summary and Conclusions

1. Prey fish biomass in the main basin of Lake Huron remains low relative to levels observed prior to 1995. Return to historical levels of prey fish biomass as was seen between 1976-1995 in offshore waters is unlikely due to reduced nutrient inputs, high predation levels by recovering piscivore populations (e.g., Lake Trout, Walleye), and changes in food web dynamics that potentially favor nearshore benthic species such as Round Goby. We note, however, that the current trophic state of Lake Huron – characterized by ongoing oligotrophication – appears favorable to the native coregonines Bloater and Cisco whose abundance has increased in recent years.

2. Persistent low abundance of Alewife and reduced abundance of Rainbow Smelt in the main basin of Lake Huron means an uncertain future for recreational fisheries focused on Pacific salmon, but is consistent with fish community objectives focused on restoration of native fish communities (Dettmers et al. 2012). Current efforts to reestablish Cisco into the main basin also may benefit from low abundance of YAO Alewife and Rainbow Smelt.

3. Offshore prey fish communities in Lake Huron, particularly in the main basin, are characterized by extremely low species diversity relative to the historic prey fish community. At present, a single species, Bloater, accounts for ~90% of prey fish biomass in the main basin's offshore waters. Theory suggests that community resiliency is positively related to species diversity (Mellin et al. 2014), so offshore prey fish abundance and species composition in Lake Huron could change quickly in response to climate change and other ecosystem-scale disturbances (e.g., invasive species).

4. Trends in main-basin abundance of major species were similar between surveys, so inferences about prey fish population dynamics in areas sampled by both surveys are robust to the use of different sampling gears and survey designs. However, use of complementary surveys (bottom trawl, acoustics) remains important for characterizing change in offshore prey fish communities in Lake Huron. This is particularly true for species that show strong benthic or pelagic preferences and for non-major species that are less common trawl catches.

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Appendix[1, 2]

Bottom trawl survey design and methods

The GLSC has monitored fish abundance annually from 1973-2021 using 12-m headrope (1973-1991) and 21-m headrope (1992-2021) bottom trawls (4.76 mm square mesh cod end) at fixed transects at up to eleven depths (9, 18, 27, 36, 46, 55, 64, 73, 82, 92, and 110 m) at five ports (Detour, Hammond Bay, Alpena, Au Sable Point, and Harbor Beach) in the Michigan waters of Lake Huron. These transects were sampled by the USGS R/V *Kaho* during 1973-1977, the USGS R/V *Grayling* during 1978-2014, and the USGS R/V *Arcticus* in 2015-2021; in addition, some transects were fished from the USGS R/V *Cisco* in 1990. Sampling began at Goderich (Ontario) in 1998 using the same trawling protocols used at U.S. ports.

A single 10-min bottom trawl tow was conducted during daylight at each transect each year. Tow duration was occasionally less than 10 min due to large catches or obstacles in the tow path; catches for these tows were corrected to be equivalent to 10-min tows (see below). Occasionally, presence of trap nets over trawl stations necessitated skipping entire transects, but these instances have been infrequent, and every effort is made to tow part of, or adjacent to, the transect. Trawl catches were sorted by species and each species was counted and weighed in aggregate. Large catches (> ca. 20 kg) were subsampled; a random sample was sorted, counted, and weighed, and the remainder of the catch was weighed for extrapolation of the sample.

Actual time on bottom for each trawl increased with depth (Fabrizio et al. 1997), so trawl catch rates were adjusted for trawl fishing time according to the following equation:

$$C_t = \frac{10N}{K_t T},$$

where C_t is the catch per 10 min (CPE) on bottom for trawl type t, N is the catch, T is tow time, and K_t is a correction factor that varies with fishing depth (D in m) and trawl type such that K_{12} =

0.00400D + 0.8861 for the 12-m trawl and K_{21} = 0.00385D + 0.9149 for the 21-m trawl. Catches were expressed in terms of density or biomass (number/ha and kg/ha) by dividing the CPE by the area swept by the trawl. The area swept was estimated as the product of the distance towed (speed multiplied by tow time) and the trawl width. Trawl width estimates were depth-specific and were based on trawl mensuration data collected from the R/V *Grayling* in 1991, 1998, and 2005. Catches of Alewife *Alosa pseudoharengus*, Rainbow Smelt *Osmerus mordax*, and Bloater *Coregonus hoyi* were partitioned into length-based age classes for analysis. Year-specific length cutoffs were determined from length-frequency data and then used to apportion the catches into age-0 fish (young-of-the-year, or YOY) and those age-1 or older (yearling and older, or YAO). Lastly, fish catches were weighted by the area of the main basin of Lake Huron that occurred in each depth range.

To make density estimates from the 12-m headrope (1973-1991) and 21-m headrope (1992-2021) trawls comparable, we multiplied density estimates from the 12-m trawl (1976-1991) by species-specific fishing power corrections (FPCs) developed from a comparative trawl experiment (Adams et al. 2009). We applied FPCs greater than 1.0 to the density and biomass of Alewife, Rainbow Smelt (YAO only), Bloater, and FPCs less than 1.0 to the density and biomass of Deepwater Sculpin *Myoxocephalus thompsonii*. Catches of Trout-perch *Percopsis omiscomaycus* were not significantly different between the two trawls. Insufficient data were available to estimate FPCs for Ninespine Stickleback and YOY Rainbow Smelt, so density estimates were not corrected for these species.

Trawl surveys on Lake Huron are typically conducted between early October and mid-November. In 1992 and 1993, however, trawl surveys occurred in early- to mid-September, and these data were not used in this report because the distribution of many offshore species in the

Great Lakes is seasonally variable (Dryer 1966, Wells 1968) and data collected in September may not be comparable to the rest of the time series. In 1998, sampling was conducted in a non-standard manner, and these data were also excluded. The fall survey was not conducted in 2000 and was not completed in 2008. We did not use data prior to 1976 because all ports and depths in Lake Huron were not consistently sampled until 1976.

Acoustic-midwater trawl survey design and methods—The pelagic prey fish survey in Lake Huron is based on a stratified-random design with acoustic transects in five geographic strata: main-basin east, main-basin west, main-basin south, Georgian Bay, and the North Channel. Within each stratum, the first transect is selected randomly each year based on latitude and longitude; subsequent transects are spaced equidistant (north-south or east-west) from the first within the constraints of the stratum boundary. Effort (number of transects per stratum) is reallocated each year based on stratum area and variability of total biomass in each stratum from previous surveys (Adams et al. 2006). For the purposes of this report, acoustic strata are hereafter referred to as "regions." For analyses, each transect was divided into 3,000 m horizontal units and 10 m depth layers. Transects were typically 20 km in length. These divisions comprise the elementary sampling units (ESUs) within which fish density is summarized along transects.

During 2004-2005 and 2007-2008 acoustic data were collected during September through early October with a BioSonics split-beam 120 kHz echosounder deployed from the Research Vessel (R/V) *Sturgeon*. During 2006, acoustic data were collected during August with a 70 kHz echosounder and a transducer deployed via towfish from the R/V *Grayling*. During 2009, the survey was performed with a 38 kHz echosounder because the 120 kHz transducer failed field calibration tests. Because the 38 kHz echosounder results in higher fish density estimates than the 120 kHz, we chose to exclude 2009 data from this report until appropriate corrections can be applied to the 38 kHz data from that survey. In 2010-2021, we used both a 38 and 120 kHz echosounder to facilitate frequency comparisons, but only 120 kHz data are presented in this report. During 2011-2012 and 2014-2021, the survey was carried out jointly between USGS-GLSC and the United States Fish and Wildlife Service (USFWS) to increase spatial coverage. USFWS used 70 kHz and 120 kHz split-beam echosounders (Simrad EK60) deployed from the *M/V Spencer F. Baird* to sample transects located in the MW region. In all years, sampling was initiated one hour after sunset and ended no later than one hour before sunrise. A threshold equivalent to uncompensated target strength (TS) of - 66 decibels (dB) was applied to S_v data.

Fish were collected using a 16.5-m headrope midwater trawl with 76, 38, 25, and 6.35 mm stretch meshes (USGS) and a 19.8-m headrope midwater trawl with 200, 150, 100, 75, 50, and 38 mm stretch mesh with a cod-end liner having 3.175 mm stretch mesh (USFWS). Midwater trawl locations and depths were chosen to target fish aggregations. Multiple tows per transect were conducted when fish were present at multiple depths so that trawl data within a region were available from each scattering layer formed by fish. At a minimum, a single midwater trawl was conducted on each transect except in rare instances when very few fish targets were detected. Trawl fishing depth was monitored using Netmind™ (2004-2015) and Marport M3 (2016-2021) systems (USGS) and a Simrad PI44 catch monitoring system (USFWS). In 2021, midwater trawling depths ranged from 3 to 100 m (mean = 29 m, mode = 13 m). Most midwater trawl tows were of 20-minute duration, with tow times extended up to 25 or 30 minutes when few fish were present. All fishes captured in the midwater trawl tows were identified, counted, and weighed in aggregate by species. Total length in millimeters was measured on a random subsample (100-200 fish) per species per tow. Individual fishes were assigned to two size categories based on the following length cutoffs: Alewife =100 mm; Rainbow Smelt *Osmerus mordax* = 90 mm; Bloater *Coregonus hoyi* = 100 mm, and Cisco *Coregonus artedi* = 200 mm.

Density (fish/ha) of individual species was estimated for each transect as the product of acoustic fish density and the proportion of each species (by number) in the midwater trawl catches at that location. Total density per species was subdivided into length classes (for applicable species) by multiplying total density by the numeric proportions of each size group. Biomass (kg/ha) of each species was estimated for each transect as the product of density and size-specific mean mass estimated from fish lengths in trawls, and length-weight relationships. The arithmetic mean and standard error are presented for total and species-specific density and biomass estimates for the survey area.

Acoustic estimates of fish density presented in this report from 2004-2021 were derived using the NearD method (Yule et al. 2013). Previous analyses of the acoustic and midwater trawl data from USGS surveys of Lake Huron have relied on the Hierarchical Averaging Method (Warner et al. 2009). Both methods rely on the composition of midwater trawl catch (for acoustic data < 50 m below the surface) or target strength (for acoustic data ≥ 50 m below the surface) to apportion density to species. However, one notable difference between hierarchical averaging and NearD is that only trawls from the same geographic stratum can be used for a given acoustic sample with NearD. This approach more accurately reflects spatial patterns in fish density and biomass for evaluation of long-term trends in the fish community. Numeric fish density estimates and biomass density were generated using the *estimateLake()* function in the EchoNet2Fish R package (Adams 2008, R Core Team 2021). This function calculates numeric fish density estimates and apportions them to user-defined fish groups using catch data.

[1] The data associated with this report are currently under review and will be publicly available in 2022 at the following location: 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] Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.