



Lake Michigan Committee March 19, 2012

# Status and Trends of Prey Fish Populations in Lake Michigan, 2011<sup>1</sup>

Charles P. Madenjian, David B. Bunnell, Timothy J. Desorcie, Margret A. Chriscinske, Melissa J. Kostich, and Jean V. Adams
U. S. Geological Survey
Great Lakes Science Center
1451 Green Road
Ann Arbor, Michigan 48105

## **Abstract**

The Great Lakes Science Center (GLSC) has conducted lake-wide surveys of the fish community in Lake Michigan each fall since 1973 using standard 12-m bottom trawls towed along contour at depths of 9 to 110 m at each of seven index transects. The resulting data on relative abundance, size structure, and condition of individual fishes are used to estimate various population parameters that are in turn used by state and tribal agencies in managing Lake Michigan fish stocks. All seven established index transects of the survey were completed in 2011. The survey provides relative abundance and biomass estimates between the 5-m and 114-m depth contours of the lake (herein, lake-wide) for prey fish populations, as well as burbot, yellow perch, and the introduced dreissenid mussels. Lake-wide biomass of alewives in 2011 was estimated at 7.64 kilotonnes (kt) (1 kt = 1000 metric tons), which was 19% higher than the 2010 estimate. Adult alewife abundance has remained low during 2004-2011 and the age distribution of the adult population was truncated during 2009-2011 compared with previous years. Lake-wide biomass of bloater in 2011 was estimated at 3.70 kt, which was 52% lower than the 2010 estimate. Rainbow smelt lake-wide biomass equaled 0.47 kt in 2011, which was 38% lower than the 2010 estimate. Deepwater sculpin lake-wide biomass equaled 1.86 kt, which was 29% lower than the 2010 estimate. Slimy sculpin lake-wide biomass remained relatively high in 2011 (1.93 kt), but was still 30% lower than the 2010 level. Ninespine stickleback lake-wide biomass equaled 0.04 kt in 2011, which was the lowest value in the time series. Estimated biomass of round goby decreased by 78% between 2010 and 2011, from 8.51 to 1.83 kt. Burbot lake-wide biomass (2.00 kt in 2011) has shown a recent increase. Numeric density of age-0 yellow perch (i.e., < 100 mm) equaled only 1 fish per ha, which is indicative of a relatively poor year-class. Lake-wide biomass estimates of dreissenid mussels increased by more than fourfold from 12.18 kt in 2010 to 52.70 kt in 2011. Overall, the total lake-wide prey fish biomass estimate (sum of alewife, bloater, rainbow smelt, deepwater sculpin, slimy sculpin, round goby, and ninespine stickleback) in 2011 was 17.47 kt, which represented the lowest total biomass of the time series.

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The Great Lakes Science Center (GLSC) has conducted daytime bottom trawl surveys in Lake Michigan during the fall annually since 1973. From these surveys, the relative abundance of the prey fish populations are measured, and estimates of lake-wide biomass available to the bottom trawls (for the region of the main basin between the 5-m and 114-m depth contours) can be generated (Hatch et al. 1981; Brown and Stedman 1995). Such estimates are critical to fisheries managers making decisions on stocking and harvest rates of salmonines and allowable harvests of fish by commercial fishing operations.

The basic unit of sampling in our surveys is a 10-minute tow using a bottom trawl (12-m headrope) dragged on contour at 9-m (5 fathom) depth increments. At most survey locations, towing depths range from 9 or 18 m to 110 m. Age determinations are performed on alewives (*Alosa pseudoharengus*, using otoliths) and bloaters (*Coregonus hoyi*, using scales) from our bottom trawl catches (Madenjian et al. 2003; Bunnell et al. 2006a). Although our surveys have included as many as nine index transects in any given year, we have consistently conducted the surveys at seven transects. These transects are situated off Manistique, Frankfort, Ludington, and Saugatuck, Michigan; Waukegan, Illinois; and Port Washington and Sturgeon Bay, Wisconsin (Figure 1). All seven transects were completed in 2011.

Lake-wide estimates of fish biomass require (1) accurate measures of the surface areas that represent the depths sampled and (2) reliable measures of bottom area swept by the trawl. A complete Geographical Information System (GIS) based on depth soundings at 2-km intervals in Lake Michigan was developed as part of the acoustics study performed by Argyle et al. (1998). This GIS database was used to estimate the surface area for each individual depth zone surveyed by the bottom trawls. Trawl mensuration gear that monitored net configuration during deployment revealed that fishing depth (D, in meters) influenced the bottom area swept by the trawl. We have corrected the width (W, in meters) of the area sampled according to  $W = 3.232 + 7.678(1 - e^{-0.044*D})$ , as well as the actual time (AT, in minutes) spent on the bottom according to AT = tow time -0.945 + (0.056D), based on trawl measurements made during June 2009 (Madenjian et al. 2010a). These relationships, along with boat speed, were used to estimate bottom area swept.

To facilitate comparisons of our estimates of fish abundance with abundance estimates in other lakes and with hydroacoustic estimates of abundance, we report both numeric (fish per hectare [ha]) and biomass (kg per ha) density. A weighted mean density over the entire range of depths sampled (within the 5-m to 114-m depth contours) was estimated by first calculating mean density for each depth zone, and then weighting mean density for each depth zone by the proportion of lake surface area assigned to that depth zone. Standard error (SE) of mean density was estimated by weighting the variances of fish density in each of the depth zones by the appropriate weight (squared proportion of surface area in the depth zone), averaging the weighted variances over all depth zones, and taking the square root of the result. Relative standard error (RSE) was calculated by dividing SE by mean fish density and multiplying this ratio by 100 to yield a percentage. SE and RSE for the estimate of lake-wide biomass were calculated in a manner analogous to that for calculating SE and RSE for the estimate of mean numeric or biomass density. For this report, we provide plots of prey fish RSE for numeric density only, as RSE for biomass density exhibited a similar trend.

### NUMERIC AND BIOMASS DENSITY

By convention, we classify "adult" prey fish as age 1 or older, based on length-frequency: alewives  $\geq 100$  mm total length (TL), rainbow smelt (Osmerus mordax)  $\geq 90$  mm TL, bloaters  $\geq 120$  mm TL, and yellow perch (Perca flavescens)  $\geq 100$  mm TL. We assume all fish smaller than the above length cut-offs are age-0. Catches of age-0 alewife, bloater, and rainbow smelt are not necessarily reliable indicators of future year-class strengths for these populations, because their small size and position in the water column make them less vulnerable to bottom trawls. Nevertheless, during the bloater recovery in Lake Michigan that began in the late 1970s, our survey contained unusually high numbers of age-0 bloaters, indicating some correspondence between bottom trawl catches and age-0 abundance in the lake. Catch of age-0

yellow perch is likely a good indicator of year-class strength, given that large catches in the bottom trawl during the 1980s corresponded to the strong yellow perch fishery.

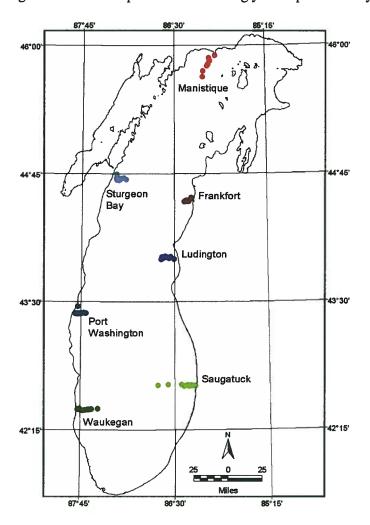


Figure 1. Established sampling locations for GLSC bottom trawls in Lake Michigan.

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

Adult alewife biomass density increased from 1.3 kg per ha in 2010 to 1.7 kg per ha in 2011 (Figure 2b). This 30% increase was likely due to the 2010 year-class of alewives becoming recruited to the age-1 and older population. The 2010 year-class was the largest year-class of alewives produced in Lake Michigan

since 2001 (Warner et al. 2012). Numeric density of adult alewives increased by more than a factor of two between 2010 and 2011 (Fig. 2a). The overall temporal trends in adult alewife density primarily reflected an increase in predation by salmonines on alewives during the 1970s and 1980s, followed by relatively high predation maintained by salmonines on alewives from the early 1980s to the present time (Madenjian et al. 2002, 2005a).

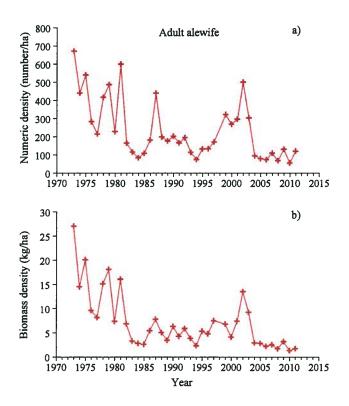


Figure 2. Density of adult alewives as number (a) and biomass (b) per ha in Lake Michigan, 1973-2011.

Adult alewife density has remained at low levels during 2004-2011, with relatively little year-to-year variability (Figure 2). This continued depression of adult alewife abundance may reflect a recently intensified amount of predation exerted on the alewife population by Chinook salmon due to three factors: (1) activation of a new source of wild recruitment to the Chinook salmon population in Lake Huron, and presumably Lake Michigan as well, during the late 1990s and/or early 2000s, (2) increased importance of alewives in the diet of Chinook salmon in Lake Michigan between the 1990s and the 2000s, and (3) a decrease in the energy density of adult alewives during the late 1990s. The complete collapse of alewives in Lake Huron during 2002-2004 was associated with the new production of wild Chinook salmon smolts in tributaries to Georgian Bay of Lake Huron (Johnson et al. 2010; Marklevitz et al. 2011). Movement of Chinook salmon from Lake Huron to Lake Michigan has been documented (Adlerstein et al. 1997). Percentage of alewives in the diet of large Chinook salmon, on a weight basis, has increased from about 80% during the mid 1990s to over 95% during 2009-2010 (Jacobs et al., in review). Owing to a 23% decrease in the energy density of adult alewives during the late 1990s, Chinook salmon in Lake Michigan during the 2000s had to consume a 22% greater biomass of alewives to maintain their growth rate (Madenjian et al. 2006).

Nearly 80% of the alewives in the bottom trawl catch during 2011 belonged to the 2010 year-class (Figure 3). Only 0.1% of the alewives were age-6 fish, and no age-7 or older alewives were caught in the bottom trawls during 2011. Similarly, during 2009 and 2010, only 0.5% and 0.1%, respectively, of the alewives caught in the bottom trawls were age-6 fish, and no age-7 or older alewives were caught. In

contrast, during most years prior to 2000, age-7, age-8, and sometimes age-9, alewives were observed in the bottom trawl catch (Madenjian et al. 2003; Bunnell et al. 2007). Thus, the alewife age distribution was truncated during 2009-2011 compared with previous years.

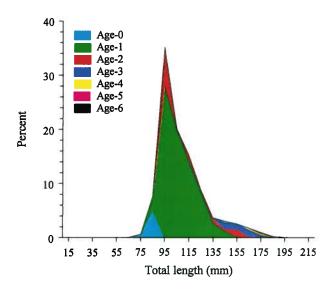


Figure 3. Age-length distribution of alewives caught in bottom trawls in Lake Michigan, 2011.

Low adult alewife density maintained over an eight-year period and truncation of the adult alewife age distribution were characteristics of the alewife population in Lake Huron prior to its collapse during 2003-2004. The bottom trawl estimates of adult alewife biomass density in Lake Huron remained at a low level during the eight-year period between 1995 and 2002, followed by a complete collapse of the adult alewife population in 2003 (Riley et al. 2012). Further, adult alewife age distribution became truncated during 1995-2002, with maximum age of alewife observed in the bottom trawl catch decreasing from 9 to 5 (Schaeffer et al. 2005).

During 1973-2011, RSE for adult alewife numeric density averaged 24% (Figure 4a). RSE has generally increased during 1999-2011 (mean= 35%) relative to earlier years (mean=19%) which suggested that adult alewives are more patchily distributed in recent years than in earlier ones.

Our results for temporal trends in adult alewife density were in partial agreement with results from the lake-wide acoustic survey, in that adult alewife abundance during 2004-2011 was relatively low compared with adult alewife abundance during the mid 1990s based on the acoustic survey of Lake Michigan (Warner et al. 2012). Agreement between gear provided further support for the contention that adult alewife abundance has substantially dropped between the 1990s and the 2004-2011 period. However, Warner et al. (2012) did report a substantial increase in adult alewife density during 2007-2010 that was not detected by the bottom trawl survey.

<u>Bloater</u> - Bloaters are eaten by salmonines in Lake Michigan, but are far less prevalent in salmonine diets than alewives (Warner et al. 2008). Over 30% of the diet of large (≥ 600 mm) lake trout at Saugatuck and on Sheboygan Reef was composed of adult bloaters during 1994-1995, although adult bloaters were a minor component of lake trout diet at Sturgeon Bay (Madenjian et al. 1998). When available, juvenile bloaters have been a substantial component of salmon and nearshore lake trout diets, particularly for

intermediate-sized fish (Elliott 1993; Rybicki and Clapp 1996). The bloater population in Lake Michigan also supports a valuable commercial fishery.

According to the bottom trawl survey results, biomass density of adult bloater decreased by 51% between 2010 (2.1 kg per ha) and 2011 (1.0 kg per ha) (Figure 5a). Similarly, adult bloater numeric density decreased from 89 fish per ha in 2010 to 31 fish per ha in 2011. RSE for adult bloater numeric density has averaged 23% during 1973-2011, but RSE for 2011 was 44% following a general trend of increasing RSE since 1999 (Figure 4a).

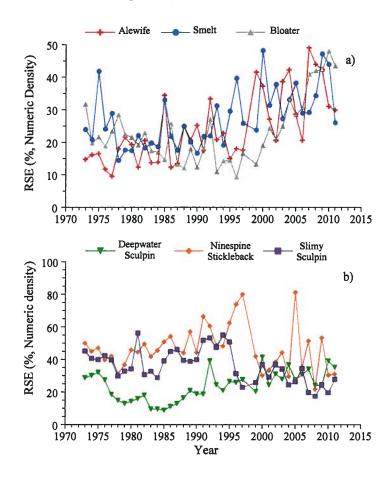


Figure 4. RSE for numeric density of Lake Michigan prey fishes, 1973-2011. Panel (a) provides estimates for adult alewife, adult rainbow smelt, and adult bloater. Panel (b) provides estimates for deepwater sculpin, slimy sculpin, and ninespine stickleback.

Adult bloater numeric and biomass densities have shown an overall declining trend since 1989 (Figure 5a). These declines are attributable to relatively poor recruitment since 1992 (Madenjian et al. 2002, Bunnell et al. 2006a, Bunnell et al. 2009a). Reduction in size-specific fecundity, owing to lower observed condition with the decline of *Diporeia* spp., was not responsible for this poor recruitment (Bunnell et al. 2009a). Although fecundity in 2006 was 24% lower than in the late 1960s (when adult condition was 69% higher), this reduction does not explain why bloater recruitment has been so consistently low.

Madenjian et al. (2002) proposed that the Lake Michigan bloater population may be cycling in abundance, with a period of about 30 years. There are signs of modest increases in recruitment in recent years. Numeric density of age-0 bloaters (< 120 mm TL) in 2005, 2008, and 2009 were 34, 27, and 29 fish per ha, respectively (Figure 5b). Although these densities pale in comparison to those observed between 1980 and 1990 (mean = 449 fish per ha), they are an order of magnitude greater than all of the other densities since 1992 (mean = 2 fish per ha). The increased bloater recruitment during the late 2000s

did not appear to be due to an increase in adult bloater energy density, because bloater energy density did not appreciably change between the 1998-2001 and 2008-2009 periods (Pothoven et al. 2012). Corresponding to the increased bloater recruitment during the late 2000s, adult bloater biomass density in Lake Michigan did show an overall increasing trend during 2008-2011, despite the decline between 2010 and 2011. Adult bloater biomass density has also shown an increasing trend during 2008-2011 in Lake Huron, where adult bloater density was estimated to increase by more than twofold between 2010 and 2011 (Riley et al. 2012). Given the broad-scale, long-term synchrony between bloater populations in Lake Michigan and Lake Huron (Madenjian et al. 2008; Bunnell et al. 2010), we may expect similar temporal trends in both lakes during the 2010s.

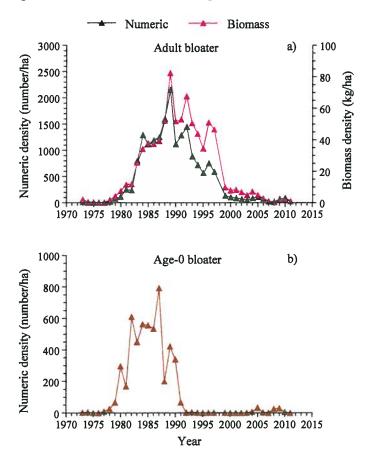


Figure 5. Panel (a) depicts numeric and biomass density of adult bloater in Lake Michigan, 1973-2011. Panel (b) depicts numeric density of age-0 bloater in Lake Michigan, 1973-2011.

Similar to the results from the bottom trawl survey, results from the acoustic survey in Lake Michigan indicated increased age-0 bloater abundance during the late 2000s (Warner et al. 2012). In addition, both the acoustic survey and bottom trawl survey documented roughly an order of magnitude decrease in the biomass density of adult bloaters in Lake Michigan between the 1992-1996 period and the 2000s.

Rainbow smelt – Adult rainbow smelt is an important diet constituent for intermediate-sized (400 to 600 mm) lake trout in the nearshore waters of Lake Michigan (Stewart et al. 1983; Madenjian et al. 1998). Overall, however, rainbow smelt are not eaten by Lake Michigan salmonines to the same extent as alewives. The rainbow smelt population supports commercial fisheries in Wisconsin and Michigan waters (Belonger et al. 1998; P. Schneeberger, Michigan Department of Natural Resources, Marquette, MI, personal communication).

Adult rainbow smelt biomass density decreased from 0.17 kg per ha in 2010 to 0.12 kg per ha in 2011 (Figure 6a). Adult rainbow smelt numeric density decreased from 24 fish per ha in 2010 to 13 fish per ha in 2011. These 2011 levels of rainbow smelt density were relatively low in the context of the entire time series. Adult rainbow smelt numeric density was highest from 1981 to 1993, but then declined between 1993 and 2001, and has remained at a relatively low density, except in 2005, since 2001. Causes for the decline remain unclear. Consumption of rainbow smelt by salmonines was higher in the mid 1980s than during the 1990s (Madenjian et al. 2002), yet adult and age-0 (< 90 mm TL) rainbow smelt abundance remained high during the 1980s (Figure 6b). Age-0 rainbow smelt has been highly variable since 2002. Age-0 numeric density in 2011 was 40 fish per ha, which was considerably lower than the average density for the entire time series of 188 fish per ha. RSE for adult rainbow smelt numeric density averaged 27% from 1973-2011, and RSE for 2011 was 26% (Figure 4a).

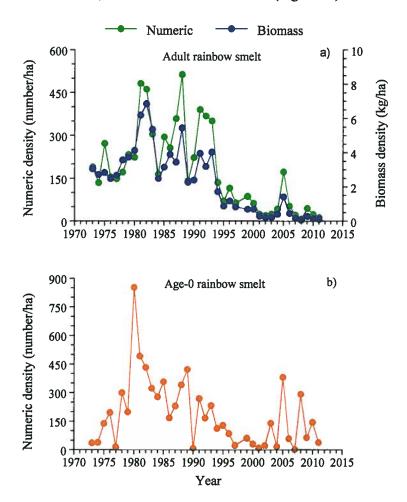


Figure 6. Panel (a) depicts numeric and biomass density of adult rainbow smelt in Lake Michigan, 1973-2011. Panel (b) depicts numeric density of age-0 rainbow smelt in Lake Michigan, 1973-2011.

Temporal trends in rainbow smelt biomass from the acoustic and bottom trawl surveys in Lake Michigan have been similar since 2001. The bottom trawl survey has documented relatively low rainbow smelt biomass during 2001-2011, with a minor peak in 2005 (Figure 6b). Similarly, biomass of rainbow smelt in the acoustic survey was relatively low during 2001-2011, with a minor peak during 2005-2006 (Warner et al. 2012). Results from both the acoustic and bottom trawl surveys indicated that rainbow smelt biomass in Lake Michigan during 1992-1996 was roughly four times higher than rainbow smelt biomass during 2001-2011.

<u>Sculpins</u> – From a biomass perspective, the cottid populations in Lake Michigan proper have been dominated by deepwater sculpins, and to a lesser degree, slimy sculpins (*Cottus cognatus*). Spoonhead sculpins (*Cottus ricei*), once fairly common, suffered declines to become rare to absent by the mid 1970s (Eck and Wells 1987). Spoonhead sculpins are still encountered in Lake Michigan, but in small numbers (Potter and Fleischer 1992).

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

Numeric density of deepwater sculpins in Lake Michigan was only 61 fish per ha in 2011, which was the lowest value in the time series (Figure 7a). Likewise, biomass density of deepwater sculpins in Lake Michigan was only 0.5 kg per ha, the lowest value in the time series. During 1990-2006, both deepwater sculpin biomass density and numeric density trended neither downward nor upward. However, deepwater sculpin catch in our bottom trawls dropped suddenly and drastically during 2007-2009, and the decline has continued through 2011. Madenjian and Bunnell (2008) demonstrated that deepwater sculpins have been captured at increasingly greater depths since the 1980s. Therefore, one potential explanation for the recent declines in deepwater sculpin densities is that an increasing proportion of the population is now occupying depths deeper than those sampled by our survey (i.e., 110 m). Furthermore, because the deepwater sculpin occupies deeper depths than any of the other prey fishes of Lake Michigan, a shift to waters deeper than 110 m would seem to be a reasonable explanation for the recent declines in deepwater sculpin densities. Previous analysis of the time series indicated deepwater sculpin density is negatively influenced by alewife (predation on sculpin larvae) and burbot (predation on juvenile and adult sculpin, Madenjian et al. 2005b). Based on bottom trawl survey results, neither alewife nor burbot increased in abundance during 2007-2009 to account for this decline in deepwater sculpins. Which factor or factors could have driven the bulk of the deepwater sculpin population to move to waters deeper than 110 m during 2007-2011? This proposed shift to deeper water by deepwater sculpins coincided with the population explosion of the profundal form of the quagga mussel (Dreissena bugensis) in Lake Michigan waters of depths between 60 and 90 m (Bunnell et al. 2009b; T. Nalepa, NOAA Great Lakes Environmental Research Laboratory, personal communication). Perhaps some consequences of the colonization of deeper waters by quagga mussels prompted a move of deepwater sculpins to deeper water. If this hypothesis were correct, then a substantial decline in quagga mussel abundance in the 60-m to 90m deep waters could lead to a shift of deepwater sculpins back to shallower waters. RSE for deepwater sculpin numeric density in 2011 was 35%, which was well above the average of 24% for the entire time series (Figure 4b).

Numeric density of slimy sculpins in Lake Michigan decreased from 267 fish per ha in 2010 to 105 fish per ha in 2011, which represented a 61% decrease (Figure 7b). Biomass density of slimy sculpins decreased from 0.78 kg per ha in 2010 to 0.55 kg per ha in 2011, which represented a 30% decrease. RSE for slimy sculpin numeric density was 28% in 2011, which was lower than its average RSE of 36% from 1973-2011 (Figure 4b). Overall, slimy sculpin numeric density has generally increased since around 1990, with considerable interannual variation. This increase was likely attributable to greater emphasis on stocking lake trout on offshore reefs beginning in 1986 (Madenjian et al. 2002). Diporeia has dominated the diet of slimy sculpins in Lake Michigan since the 1970s (Madenjian et al. 2002), and Diporeia abundance in Lake Michigan has declined during the 1990s and 2000s (Nalepa et al. 2006). To date, this decrease in Diporeia abundance does not appear to have had a negative effect on slimy sculpin abundance in Lake Michigan. Despite the decline between 2010 and 2011, slimy sculpin abundance in Lake Michigan during 2011 remained relatively high.

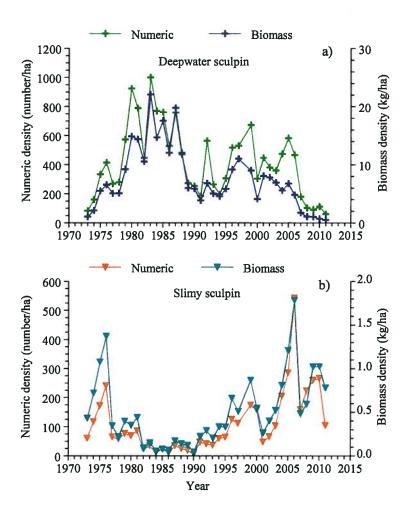


Figure 7. Numeric and biomass density for deepwater (a) and slimy sculpin (b) in Lake Michigan, 1973-2011.

Ninespine stickleback - Two stickleback species occur in Lake Michigan. Ninespine stickleback (Pungitius pungitius) is native, whereas threespine stickleback (Gasterosteus aculeatus) is non-native and was first collected in the GLSC bottom trawl survey during 1984 (Stedman and Bowen 1985). Ninespine stickleback is generally captured in greater densities than the threespine, especially in recent years. Relative to other prey fishes, ninespine sticklebacks are of minor importance to lake trout and other salmonines. In northern Lake Michigan, for example, sticklebacks occur infrequently in the diet of lake trout (Elliott et al. 1996). Numeric density of ninespine stickleback remained fairly low from 1973-1995 (Figure 8a). Densities increased dramatically in 1996-1997, and have since been highly variable. Numeric density of ninespine stickleback in 2011 was only 6 fish per ha, the lowest value in the time series. Similarly, biomass density in 2011 was only 0.01 kg per ha, the lowest value in the time series. Thus, ninespine stickleback abundance has remained relatively low during 2008-2011. RSE for ninespine stickleback numeric density was 31% in 2011, which was below the long-term average RSE of 47% from 1973-2011 (Figure 4b). An analysis of ninespine stickleback densities in lakes Michigan and Superior revealed that the increase in Lake Michigan coincided with the expansion of dreissenid mussels in the lake (Madenjian et al. 2010b). One proposed mechanism for the increase in ninespine stickleback occurring during the dreissenid mussel expansion of the 1990s was that the concomitant increase in the prevalence of the green alga Cladophora improved spawning habitat quality for ninespine sticklebacks, resulting in increased ninespine stickleback recruitment. One plausible explanation for the low ninespine stickleback abundance during 2008-2011 may be that predation on ninespine sticklebacks in Lake Michigan has increased during the past few years, coincident with the depressed abundance of alewives

during 2004-2011. With reduced alewife abundance, some piscivores may have begun to incorporate ninespine sticklebacks to a greater degree into their diets. The decrease in ninespine stickleback abundance in Lake Superior between the 1978-1999 and 2000-2007 periods was attributed to increased predation by lake trout (Madenjian et al. 2010b).

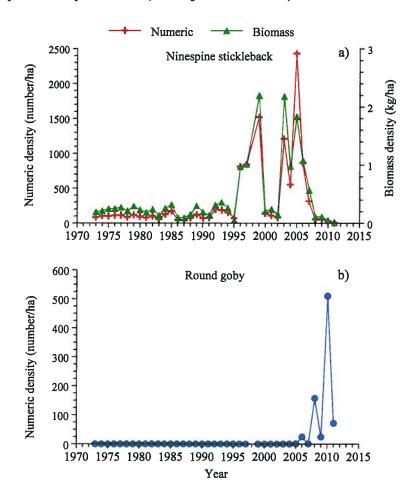


Figure 8. Panel (a) depicts numeric and biomass density of ninespine sticklebacks in Lake Michigan, 1973-2011. Panel (b) depicts numeric density of round goby in Lake Michigan, 1973-2011.

Round goby – The round goby (*Neogobius melanostomus*) is an invader from the Black and Caspian seas. Round gobies have been observed in bays and harbors of Lake Michigan since 1993, and were captured by Michigan DNR personnel in the southern main basin of the lake as early as 1997 (Clapp et al. 2001). Round gobies were not captured in the GLSC bottom trawl survey until 2003, however. By 2002, round gobies had become an integral component of yellow perch diet at nearshore sites (i.e., < 15 m depth) in southern Lake Michigan (Truemper et al. 2006). Round gobies also had become an important constituent of the diet of burbot in northern Lake Michigan by 2005 (Hensler et al. 2008; Jacobs et al. 2010).

According to our bottom trawl survey, round goby numeric density has shown an overall increasing trend during 2003-2011, but with high inter-annual variability (Figure 8b). Round goby numeric density decreased from 510 fish per ha in 2010 to 72 fish per ha in 2011. Round gobies have now been captured at all transects, at depths ranging 9 to 110 m, and will likely continue to contribute to the diets of Lake Michigan piscivores into the future. Given the importance of round gobies in the diet of burbot, an offshore predator, and in the diets of yellow perch and smallmouth bass (*Micropterus dolomieu*),

nearshore predators, we may expect round goby abundance in Lake Michigan to level off in the upcoming years as predatory control begins to be exerted.

#### LAKE-WIDE BIOMASS

We estimated a total lake-wide biomass of prey fish available to the bottom trawl in 2011 of 17.47 kilotonnes (kt) (1 kt = 1000 metric tons) (Figure 9, Appendix 1). Total prey fish biomass was the sum of the population biomass estimates for alewife, bloater, rainbow smelt, deepwater sculpin, slimy sculpin, ninespine stickleback, and round goby. Percentages of the total prey fish biomass (and biomass estimates) for the prey fish species were: alewife 44% (7.64 kt), bloater 21% (3.70 kt), slimy sculpin 11% (1.93 kt), deepwater sculpin 11% (1.86 kt), round goby 10% (1.83 kt), rainbow smelt 3% (0.47 kt), and ninespine stickleback <1% (0.04 kt).

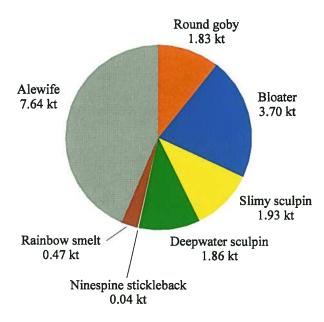


Figure 9. Estimated lake-wide (i.e., 5-114 m depth region) biomass of prey fishes in Lake Michigan, 2011 based on the bottom trawl survey.

Total prey fish biomass in Lake Michigan has trended downward since 1989 (Figure 10). This decline was largely driven by the dramatic decrease in bloater biomass. During 2002-2011, decreases in alewife and deepwater sculpin biomasses also contributed to the continued decrease in total prey fish biomass. Total prey fish biomass in 2011 was 17.47 kt, which was the lowest value in the time series and represented a 40% decrease from the total prey fish biomass estimated for 2010 of 29.13 kt. Total prey fish biomass first dropped below 30 kt in 2007, and has remained below 30 kt since that time.

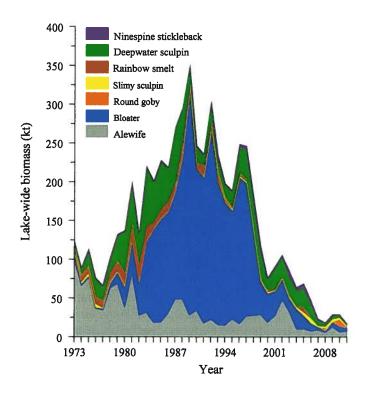


Figure 10. Estimated lake-wide (i.e., 5-114 m depth region) biomass of prey fishes in Lake Michigan, 1973-2011, based on the bottom trawl survey.

### OTHER SPECIES OF INTEREST

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

Burbot collected in the bottom trawls are typically large individuals (>350 mm TL); juvenile burbot apparently inhabit areas not covered by the bottom trawl survey.

After a period of low numeric density in the 1970s, burbot showed a strong recovery in the 1980s (Figure 11). Densities increased through 1997, and we interpret the decline between 1997 and 2002 as a leveling off in response to density-dependent forces. Burbot numeric densities appeared to be relatively stable during 2003-2008, but trawl survey results from 2010 and 2011 suggested a very recent increase in burbot abundance. Burbot numeric density increased from 0.47 fish per ha in 2010 to 0.63 fish per ha in 2011. Perhaps this increase in burbot abundance has been in response to the increasing densities of round gobies, which appear to be a favored prey of burbot.

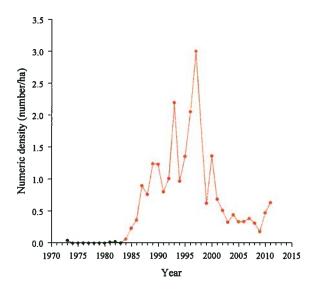


Figure 11. Numeric density of burbot in Lake Michigan, 1973-2011.

Yellow perch – The yellow perch population in Lake Michigan has supported valuable recreational and commercial fisheries (Wells 1977). GLSC bottom trawl surveys provide an index of age-0 yellow perch numeric density, which serves as an indication of yellow perch recruitment success. The 2005 year-class of yellow perch was the largest ever recorded (Figure 12). This huge year-class was likely attributable to a sufficient abundance of female spawners and favorable weather. Numeric density of the 2011 year-class was only 1 fish per ha, an indication of a weak year-class. Most researchers believe that the poor yellow perch recruitment during the 1990s and early 2000s was due to a combination of several factors, including poor weather conditions and low abundance of female spawners (Makauskas and Clapp 2000).

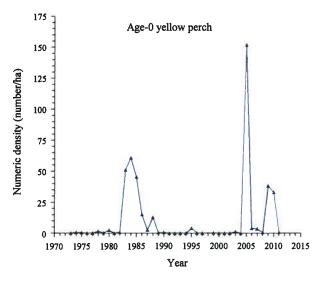


Figure 12. Numeric density of age-0 yellow perch in Lake Michigan, 1973-2011.

<u>Dreissenid mussels</u> – The first zebra mussel (*Dreissena polymorpha*) noted in Lake Michigan was found in May 1988 (reported in March 1990) in Indiana Harbor at Gary, Indiana. By 1990, adult mussels had been found at multiple sites in the Chicago area, and by 1992 were reported to range along the eastern and

western shoreline in the southern two-thirds of the lake, as well as in Green Bay and Grand Traverse Bay (Marsden 1992). In 1999, catches of dreissenid mussels in our bottom trawls became significant and we began recording weights from each tow. Lake Michigan dreissenid mussels include two species: the zebra mussel and the quagga mussel. The quagga mussel is a more recent invader to Lake Michigan than the zebra mussel (Nalepa et al. 2001). According to the GLSC bottom trawl survey, biomass density of dreissenid mussels was highest in 2007 (Figure 13a), which followed an exponential like increase between 2004 and 2006 (Bunnell et al. 2009b). Over this same period of dreissenid mussel increases, prey fish biomass was declining, which led to a dramatic increase in the percentage of dreissenids in the total bottom trawl catch (Figure 13b). Some authors have attributed the recent decline in prey fish to food-web changes induced by the expansion of dreissenids (Nalepa et al. 2009). However, Bunnell et al. (2009b) proposed that the bulk of the decline in total prey fish biomass may be better explained by factors other than food-web-induced effects by dreissenids, including poor fish recruitment (that preceded the mussel expansion), shifts in fish habitat, and increased fish predation by Chinook salmon.

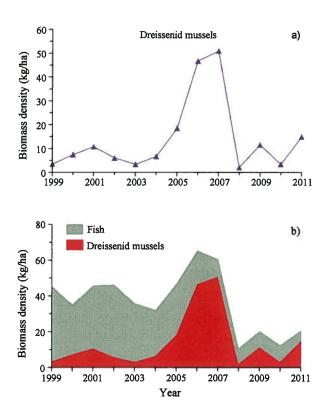


Figure 13. Panel (a) depicts biomass density of dreissenid mussels in the bottom trawl in Lake Michigan, 1999-2011. Panel (b) depicts biomass of dreissenids and total fish biomass estimated by the bottom trawl between 1999 and 2011.

The biomass density of dreissenid mussels in 2011 was 14.97 kg per ha, which was equal to 29% of the peak biomass density estimated for 2007 (Figure 13a). A comparison of the biomass density of dreissenid mussels (14.97 kg per ha) with biomass density of all of the fish (5.80 kg per ha) caught in the bottom trawl indicated that 28% and 72% of the biomass in Lake Michigan during 2011 estimated from the bottom trawl survey corresponded to fish and dreissenid mussels, respectively (Figure 13b). Some of the temporal trends in dreissenid mussel biomass density shown in Figure 13a were difficult to explain. The exceptionally high biomass densities recorded in 2006 and 2007 were attributable to the expansion of quagga mussels into deeper (> 60 m) waters of Lake Michigan. However, there was no clear explanation for the drastic drop in dreissenid mussel biomass density between 2007 and 2008. According to the results of the benthic macroinvertebrate survey led by Tom Nalepa at NOAA-GLERL, quagga mussel biomass density in Lake Michigan appears to have peaked sometime between 2008 and 2010. This

peaking may be in response to the exceeding of the carrying capacity, and a decline in quagga mussel biomass density may be expected in upcoming years.

### CONCLUSIONS AND PROGNOSIS

Our bottom trawl estimate of total prey fish biomass in 2011 was the lowest since our survey began in 1973, and follows five years of sustained, near-record low, biomass. These relatively low prey fish biomass estimates for 2007-2011 were probably due to a suite of factors. We can clearly identify two of these factors as: (1) an apparently prolonged period of relatively low bloater year-class strength during 1992-2011, and (2) intensified predation on alewives by Chinook salmon during the 2000s. Adult alewife density has been maintained at a relatively low level over the last eight years and the age distribution of the adult alewife population has been truncated during the past three years compared with previous years; similar characteristics were shown by the Lake Huron alewife population just prior to its collapse during 2003-2004. Whether or not the alewife population in Lake Michigan will undergo a complete collapse over the next few years will depend on several factors, such as the number of Chinook salmon inhabiting Lake Michigan during next few years, whether or not the adult alewife population can produce a strong year-class in 2012, and environmental effects on alewife survival. Assessing and quantifying the bottomup effects on prey fish biomass in Lake Michigan will likely require additional years of surveillance, across-lake comparisons, and food-web analyses. Will the bottom trawl estimates of total prey fish biomass in Lake Michigan ever exceed 100 kt in upcoming years? The answer to this question hinges on the ability of the bloater population to show a substantial recovery in the near future. During the late 1980s and early 1990s, bloater lake-wide biomass estimates were substantially greater than 100 kt (Figure 11). A bloater recovery of sufficient magnitude would ensure lake-wide biomass estimates of prey fish eventually surpassing 100 kt.

The GLFC Fish Community Objective for planktivores is not being fully achieved according to the bottom trawl survey results. The Objective calls for a lake-wide biomass of 500-800 kt, and the total prey fish biomass estimated by the bottom trawl survey was only 17 kt. The Objective also calls for a diversity of prey species. Based on Figure 9, the prey fish community is quite diverse, with five different species each contributing at least 10% to the total prey fish biomass.

# REFERENCES

Adlerstein, S. A., E. S. Rutherford, D. Clapp, J. A. Clevenger, and J. E. Johnson. 2007. Estimating seasonal movements of Chinook salmon in Lake Huron from efficiency analysis of coded wire tag recoveries in recreational fisheries. N. Am. J. Fish. Manage. 27:792-803.

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

Belonger, B. B. T. Eggold, P. Hirethota, S. Hogler, B. Horns, T. Kroeff, T. Lychwick, S. Marcquenski, P. Peters, S. Surendonk, and M. Toneys. 1998. Lake Michigan Management Reports, Wisconsin Department of Natural Resources. Lake Michigan Committee Meetings, Great Lakes Fishery Commission, Thunder Bay, Ontario, March 16-17, 1998.

Brown, E. H., Jr., and R. M. Stedman. 1995. Status of forage fish stocks in Lake Michigan, 1994. Pages 81-88 in Minutes of Great Lakes Fishery Commission, Lake Michigan Committee Meeting, Milwaukee, Wisconsin, March 29-30, 1995.

Bunnell, D. B., C. P. Madenjian, and T. E. Croley II. 2006a. Long-term trends of bloater recruitment in Lake Michigan: evidence for the effect of sex ratio. Can. J. Fish. Aquat. Sci. 63:832-844.

Bunnell, D. B., C. P. Madenjian, and R. M. Claramunt. 2006b. Long-term changes of the Lake Michigan fish community following the reduction of exotic alewife (*Alosa pseudoharengus*). Can. J. Fish. Aquat. Sci. 63:2434-2446.

- Bunnell, D. B., C. P. Madenjian, J. D. Holuszko, T. J. Desorcie, and J. V. Adams. 2007. Status and Trends of Prey Fish Populations in Lake Michigan, 2006. A report to the Great Lakes Fishery Commission, Lake Michigan Committee, Ypsilanti, Michigan, March 20, 2007.
- Bunnell, D. B., S. R. David, and C. P. Madenjian. 2009a. Decline in bloater fecundity in southern Lake Michigan after decline of *Diporeia*. J. Great Lakes Res. 35:45-49.
- Bunnell, D. B., C. P. Madenjian, J. D. Holuszko, J. V. Adams, and J. R. P. French III. 2009b. Expansion of *Dreissena* into offshore waters of Lake Michigan and potential impacts on fish populations. J. Great Lakes Res. 35:74-80.
- Bunnell, D. B., J. V. Adams, O. T. Gorman, C. P. Madenjian, S. C. Riley, E. F. Roseman, and J. S. Schaeffer. 2010. Population synchrony of a native fish across three Laurentian Great Lakes: evaluating the effects of dispersal and climate. Oecologia 162:641-651.
- 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.
- Eck, G. W., and L. Wells. 1987. Recent changes in Lake Michigan's fish community and their probable causes, with emphasis on the role of the alewife *Alosa pseudoharengus*. Can. J. Fish. Aquat. Sci. 44(Suppl. 2):53-50.
- Elliott, R. F. 1993. Feeding habits of chinook salmon in eastern Lake Michigan. M. S. Thesis, Michigan State University, East Lansing, MI. 108 pp.
- Elliott, R. F., and eight coauthors. 1996. Conducting diet studies of Lake Michigan piscivores- a protocol. U.S. Fish and Wildlife Service, Fishery Resources Office, Report 96-2, Green Bay, Wisconsin.
- 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.
- Fratt, T. W., D. W. Coble, F. Copes, and R. E. Brusewitz. 1997. Diet of burbot in Green Bay and western Lake Michigan with comparison to other waters. J. Great Lakes Res. 23:1-10.
- Hatch, R. W., P. M. Haack, and E. H. Brown, Jr. 1981. Estimation of alewife biomass in Lake Michigan, 1967-1978. Trans. Am. Fish. Soc. 110:575-584.
- Hensler, S. R., D. J. Jude, and J. He. 2008. Burbot growth and diet in Lakes Michigan and Huron: an ongoing shift from native species to round gobies. Pages 91-107 in V. L. Paragamian and D. H. Bennett (ed) Burbot: Ecology, Management, and Culture. American Fisheries Society, Symposium 59, Bethesda, MD.
- 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.
- Jacobs, G. R., C. P. Madenjian, D. B. Bunnell, D. M. Warner, and R. M. Claramunt. in review. Chinook salmon foraging patterns in a changing Lake Michigan. Trans. Am. Fish. Soc.
- Johnson, J. E., S. P. DeWitt, and D. J. A. Gonder. 2010. Mass-marking reveals emerging self regulation of the Chinook salmon population in Lake Huron. N. Am. J. Fish. Manage. 30:518-529.
- Jude, D. J., F. J. Tesar, S. F. DeBoe, and T. J. Miller. 1987. Diet and selection of major prey species by Lake Michigan salmonines, 1973-1982. Trans. Am. Fish. Soc. 116:677-691.
- 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., T. J. DeSorcie, and R. M. Stedman. 1998. Ontogenic and spatial patterns in diet and growth of lake trout from Lake Michigan. Trans. Am. Fish. Soc. 127: 236-252.
- 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. 60:736-753.
- Madenjian, C. P., J. D. Holuszko, and T. J. Desorcie. 2003. Growth and condition of alewives in Lake Michigan, 1998-2001. Trans. Am. Fish. Soc. 132:1104-1116.

- Madenjian, C. P., T. O. Höök, E. S. Rutherford, D. M. Mason, T. E. Croley II, E. B. Szalai, and J. R. Bence. 2005a. Recruitment variability of alewives in Lake Michigan. Trans. Am. Fish. Soc. 134:218-230.
- Madenjian, C. P., D. W. Hondorp, T. J. Desorcie, and J. D. Holuszko. 2005b. 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, J. D. Holuszko, T. J. Desorcie, and J. V. Adams. 2010a. *Status and Trends of Prey Fish Populations in Lake Michigan*, 2009. A report to the Great Lakes Fishery Commission, Lake Michigan Committee, Windsor, Ontario, March 23, 2010.
- Madenjian, C. P., D. B. Bunnell, and O. T. Gorman. 2010b. Ninespine stickleback abundance in Lake Michigan increases after invasion of dreissenid mussels. Trans. Am. Fish. Soc. 139:11-20.
- Makauskas, D., and D. Clapp. 2000. Status of yellow perch in Lake Michigan and Yellow Perch Task Group progress report. In Minutes of 2000 Annual Meeting of the Lake Michigan Committee. Great Lakes Fishery Commission, Ann Arbor, Michigan.
- Marsden, J. E. 1992. The zebra mussel invasion. Aquaticus 23:19-27.
- Marklevitz, S. A. C., B. J. Fryer, D. Gonder, Z. Yang, J. Johnson, A. Moerke, and Y. E. Morbey. 2011. Use of otolith chemistry to discriminate juvenile Chinook salmon (*Oncorhynchus tshawytscha*) from different wild populations and hatcheries in Lake Huron. J. Great Lakes Res. 37:698-706.
- Nalepa, T. F., D. W. Schloesser, S. A. Pothoven, D. W. Horndorp, D. L. Fanslow, M. L. Tuchman, and G. W. Fleischer. 2001. First finding of the amphipod *Echinogammarus ischmus* and the mussel *Dreissena bugensis* in Lake Michigan. J. Great Lakes Res. 27:384-391.
- Nalepa, T. F., D. L. Fanslow, A. J. Foley III, G. A. Lang, B. J. Eadie, and M. A. Quigley. 2006. Continued disappearance of the benthic amphipod *Diporeia* spp. in Lake Michigan: is there evidence for food limitation? Can. J. Fish. Aquat. Sci. 63:872-890.
- Nalepa, T. F., D. L. Fanslow, G. A. Lang. 2009. Transformation of the offshore benthic community in Lake Michigan: recent shift from the native amphipod *Diporeia* spp. to the invasive mussel *Dreissena rostriformis bugensis*. Freshwater Biol. 54:466-479.
- Potter, R. L. and G. W. Fleischer. 1992. Reappearance of spoonhead sculpins (*Cottus ricei*) in Lake Michigan. J. Great Lakes Res. 18:755-758.
- Pothoven, S. A., D. B. Bunnell, C. P. Madenjian, O. T. Gorman, and E. F. Roseman. 2012. Energy density of bloaters in the upper Great Lakes. Trans. Am. Fish. Soc. 131: in press.
- Riley, S. C., E. F. Roseman, T. P. O'Brien, J. V. Adams, A. L. Fingerle, and J. G. Londer. 2012. Status and Trends of the Lake Huron Offshore Demersal Fish Community, 1976-2011. A report to the Great Lakes Fishery Commission, Lake Huron Committee, Windsor, Ontario, March 20, 2012.
- Rybicki, R.W. and D. F. Clapp. 1996. Diet of chinook salmon in eastern Lake Michigan. Michigan Department of Natural Resources, Fisheries Technical Report, Ann Arbor, MI.
- Schaeffer, J. S., E. F. Roseman, S. C. Riley, C. S. Faul, T. P. O'Brien, and A. Fouilleroux. 2005. *Status and Trends of the Lake Huron Deepwater Fish Community*, 2004. A report to the Great Lakes Fishery Commission, Lake Huron Committee, Ypsilanti, Michigan, March 2005.
- Smith, S. H. 1970. Species interactions of the alewife in the Great Lakes. Trans. Am. Fish. Soc. 99:754-765.
- Stedman, R. M., and Bowen, C. A. 1985. Introduction and spread of the threespine stickleback (*Gasterosteus aculeatus*) in lakes Huron and Michigan. J. Great Lakes Res. 11:508-511.
- Stewart, D. J., and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978-88. Can. J. Fish. Aquat. Sci. 48:909-922.
- Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetics model for lake trout, *Salvelinus namaycush*: application to the Lake Michigan population. Can. J. Fish. Aquat. Sci. 40:681-698.

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.

Van Oosten, J., and H. J. Deason. 1938. The food of the lake trout (*Cristivomer namaycush*) and of the lawyer (*Lota maculosa*) of Lake Michigan. Trans. Am. Fish. Soc. 67:155-177.

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, T. P. O'Brien, S. H. Farha, and J. S. Schaeffer. 2012. Status of Pelagic Prey Fishes and Pelagic Macroinvertebrates in Lake Michigan, 1992-2011 A report to the Great Lakes Fishery Commission, Lake Michigan Committee, Windsor, Ontario, March 19, 2012.

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

Wells, L., and A. L. McLain. 1973. Lake Michigan: man's effects on native fish stocks and other biota. Great Lakes Fishery Commission. Technical Report 20. 56 p.

Appendix 1. Mean numeric and biomass density, as well as lake-wide biomass (defined as biomass available to the bottom trawls for the region of the main basin between the 5-m and 114-m depth contours), estimates for various fishes and dreissenid mussels in Lake Michigan during 2011. Estimates are based on the bottom trawl survey. Standard error enclosed in parentheses. NA denotes that estimate is not available.

Taxon	Numeric density	Biomass density	Lake-wide
	(fish per ha)	(kg per ha)	biomass (kt)
age-0 alewife	79.51	0.43 <b>8</b>	1.542
	(40.17)	(0.222)	(0.781)
adult alewife	121.71	1.732	6.100
	(36.49)	(0.505)	(1.780)
age-0 bloater	0.25	0.002	0.007
	(0.13)	(0.001)	(0.004)
adult bloater	31.16	1.048	3.694
	(13.57)	(0.446)	(1.571)
age-0 rainbow smelt	39.66	0.017	0.060
	(25.44)	(0.011)	(0.038)
adult rainbow smelt	13.04	0.116	0.408
	(3.40)	(0.030)	(0.106)
deepwater sculpin	61.42	0.527	1.856
	(21.59)	(0.181)	(0.637)
slimy sculpin	104.89	0.547	1.927
	(29.22)	(0.201)	(0.706)
ninespine stickleback	6.30	0.012	0.042
	(1.96)	(0.003)	(0.011)
burbot	0.63	0.569	2.002
	(0.25)	(0.254)	(0.896)
age-0 yellow perch	0.91	0.005	0.018
	(0.54)	(0.004)	(0.013)
round goby	72.07	0.520	1.831
	(25.27)	(0.174)	(0.614)
dreissenid mussels	NA	14.965 (3.389)	52.702 (11.936)