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Status and Trends of Prey Fish Populations in Lake Michigan, 2006[1]

David B. Bunnell, Charles P. Madenjian, Jeffrey D. Holuszko, Timothy J. Desorcie, 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 2006. 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 and round gobies. Lake-wide biomass of alewives in 2006 was estimated at 9.86 kilotonnes (kt) (1 kt = 1000 metric tons), which was 26% lower than 2005. Lake-wide biomass estimates of bloater (13.30 kt) and rainbow smelt (2.39 kt) in 2006 were 46% and 69%, respectively, lower than in 2005. Bloater biomass has declined drastically since 1989 and the 2006 estimate is the lowest since 1978. Abundance of age-0 bloaters (< 120 mm) in 2004-2006, however, has been higher than in the previous 10-year period, perhaps signaling a bloater recovery. The 2006 rainbow smelt lake-wide biomass estimate was similar to the previous 10-year period; the 2005 estimate was the highest since 1993. Deepwater sculpin lake-wide biomass (22.86 kt in 2006) has not shown a pronounced temporal trend during 1990-2006. Slimy sculpin lake-wide biomass has been increasing since 2001, and biomass in 2006 (8.16 kt) was the highest in the overall time series. Ninespine stickleback lake-wide biomass remained relatively high in 2006 (4.05 kt), as the species has generally increased in abundance from 1996-present compared to 1973-1995. Burbot lake-wide biomass (2.05 kt in 2006) has remained fairly constant since 2002. After a record-high 2005 year-class, numeric density of age-0 yellow perch (i.e., < 100 mm) remained relatively high (5.2 fish per ha) compared to the 1996-2004 period. Lake-wide biomass of dreissenid mussels has been increasing since 2003, and the 2006 estimate (212.27 kt) was a nearly 3-fold increase over the 2005 estimate. Round goby were first captured in 2003 and have since been increasing in abundance. Round goby abundance in 2006 (27.7 fish per ha) was a 16-fold increase over the 2005 estimate. Overall, the total lake-wide prey fish biomass estimate (sum of alewife, bloater, rainbow smelt, deepwater sculpin, slimy sculpin, and ninespine stickleback) was 60.62 kt, which was the lowest observed since the survey began in 1973.

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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 (using otoliths) and bloaters (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 2006.

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. Since 1998, we have corrected the width (W, in meters) of the area sampled according to $W = 9.693 - (43.93/D)$, as well as the actual time (AT, in minutes) spent on the bottom according to $AT = \text{tow time} - 3.875 + D^{0.412}$ (Fleischer et al. 1999). 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.

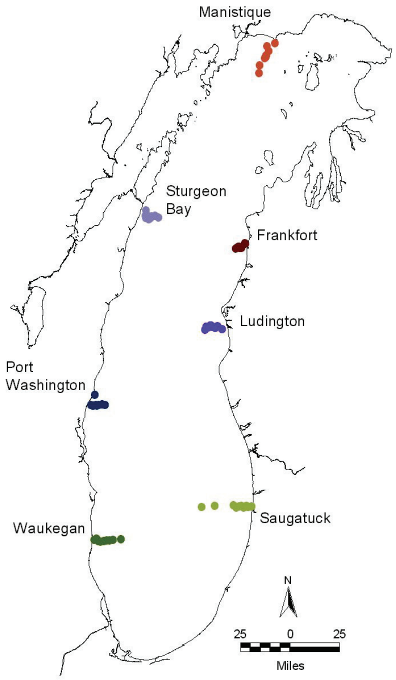

Figure 1. Established sampling locations for GLSC bottom trawls in Lake Michigan.

NUMERIC AND BIOMASS DENSITY

By convention, we classify "adult" prey fish as age 1 or older, based on length-frequency: alewives ≥ 100 mm total length (TL), rainbow smelt ≥ 90 mm TL, bloaters ≥ 120 mm TL, and yellow perch ≥ 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. Catches of age-0 yellow perch are 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.

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, deepwater sculpin, emerald shiner, lake trout, and yellow perch (Smith 1970; Wells and McLain 1973; Madenjian et al. 2005c; Bunnell et al. 2006b). Additionally, alewife has remained the most important constituent of salmonine diet in Lake Michigan for the last 35 years (Jude et al. 1987; Stewart and Ibarra 1991; P. Peeters, Wisconsin Department of Natural Resources, Sturgeon Bay, WI, personal communication; R. Elliott, U. S. Fish and Wildlife Service, Green Bay, WI, personal communication). Most of the alewives consumed by salmonines in Lake Michigan are eaten by chinook salmon (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.

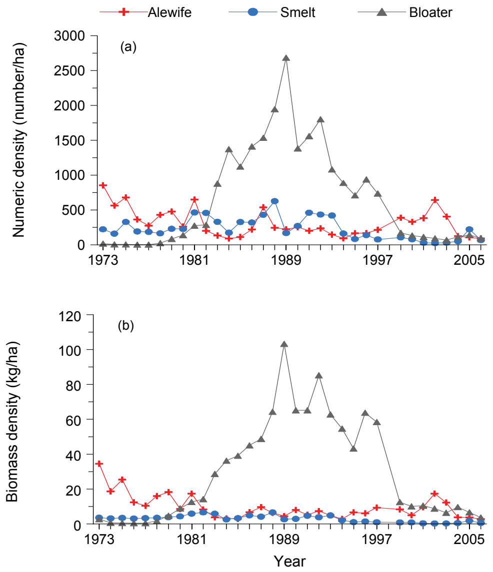

Figure 2. Density of adult alewives, rainbow smelt and bloaters as number (a) and mass (b) of fish per ha in Lake Michigan, 1973-2006.

Adult alewife numeric density has been declining since 2002. Numeric density of adult alewives in Lake Michigan was 92 fish per ha in 2006 and 105 fish per ha in 2005 (Figure 2a; Appendix 1). Alewife biomass densities were 26% lower in 2006 (2.8 kg per ha) than in 2005 (3.7 kg per ha; Figure 2b). Only in 1984 was adult alewife biomass density less than that observed in 2006. Given that predation by salmon and trout appears to be the most important factor regulating alewife abundance in Lake Michigan (Madenjian et al. 2002, 2005a), a recent increase in chinook salmon biomass may be a likely cause for the recent pronounced decrease in adult alewife numeric density since 2002. In addition, energy density of adult alewives in Lake Michigan decreased by 23% between the 1979-1981 and 2002-2004 periods (Madenjian et al. 2006). The decrease in adult alewife energy density is believed to have occurred in 1995 in response to decreasing abundance of the amphipod *Diporeia*. The decrease in *Diporeia* abundance during the 1990s was strongly linked to the dreissenid mussel invasion of the lake (Nalepa et al. 2006).

During 1973-2006, RSE for adult alewife numeric density averaged 21% (Figure 3a). RSE has generally increased during 1999-2006 relative to earlier years, which suggests that adult alewives are more patchily distributed in recent years than in earlier ones.

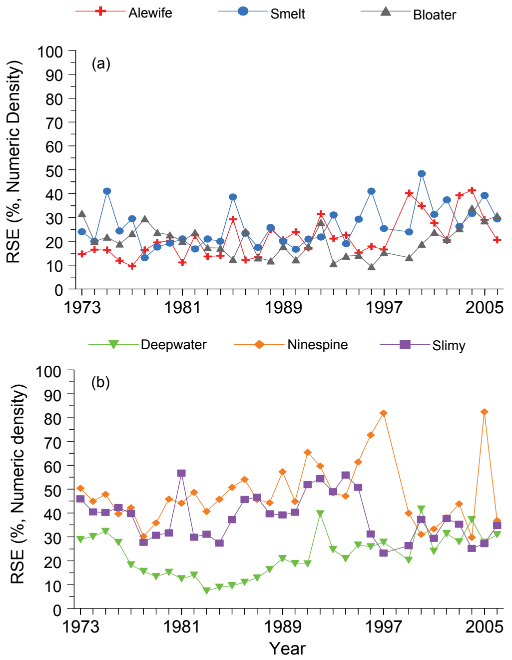

Figure 3. RSE for numeric density of Lake Michigan prey fishes, 1973-2006. Panel (a) provides estimates for adult alewife, adult rainbow smelt, and adult bloater. Panel (b) provides estimates for deepwater sculpin, slimy scuplin, and ninespine stickleback.

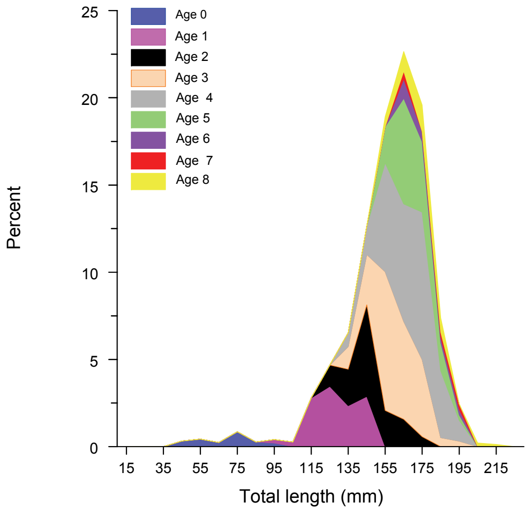

Figure 4. Age-length distribution of alewives caught in bottom trawls in Lake Michigan, 2006. The 2002 and 1998 year-classes are age-4 and age-8 fish respectively.

The catch of adult alewives comprised several year-classes, primarily 2001-2003 (Figure 4). During 1999-2004, the 1998 year-class dominated the adult catch (Madenjian et al. 2005b). In 2005, the 2002 year-class dominated the adult catch. The 2005 year-class, which was estimated to be one of the strongest year classes since 1995 by the Lake Michigan acoustic survey (Warner et al. 2006), comprised a considerable proportion of the 105-135 mm size classes.

Bloater - Bloaters are eaten by salmonines in Lake Michigan, but are far less prevalent in salmonine diets than alewives. 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.

In 2006, adult bloater numeric density was 3.7 kg per ha, a 44% decline from 2005, and the lowest observed since 1978 (Figure 2). RSE for adult bloater numeric density has averaged 20% from 1973-2006, but RSE for 2006 was 31% following a general trend of increasing RSE since 1999 (Figure 3a).

Overall, adult bloater numeric and biomass density has been declining since 1989 (Figure 2). This decline was attributable to relatively poor recruitment during 1992-2003 (Madenjian et al. 2002, 2005b). Madenjian et al. (2002) proposed that the Lake Michigan bloater population may be cycling in abundance, with a period of about 30 years. Numeric density of age-0 bloaters (< 120 mm TL) was 4.9 fish per ha in 2006, which was considerably lower than 42.1 fish ha observed in 2005 (Figure 5a). When the bloaters began their last recovery in 1977 (Eck and Wells 1987), numeric density of age-0 bloaters more than doubled each year between 1976 and 1980 (Figure 5a). Evidence for a recovery appeared promising in 2005, when the density of age-0 bloaters showed two consecutive years of 4-fold increases. The low estimate in 2006, however, casts doubt on the strength of a bloater recovery. On the other hand, biomass density of adult bloater in 2006 (3.7 kg per ha) is within the range that occurred between 1976 and 1980 (0.40-8.94 kg per ha), which suggests that spawning stock size remains sufficient for a recovery. In addition, bloater sex ratio is becoming increasingly balanced (65% female in 2006), which correlates with strong bloater recruitment success (Bunnell et al. 2006a). If adult bloater biomass continues to decline, strong year classes must occur in the next 2-3 years to ensure a bloater recovery.

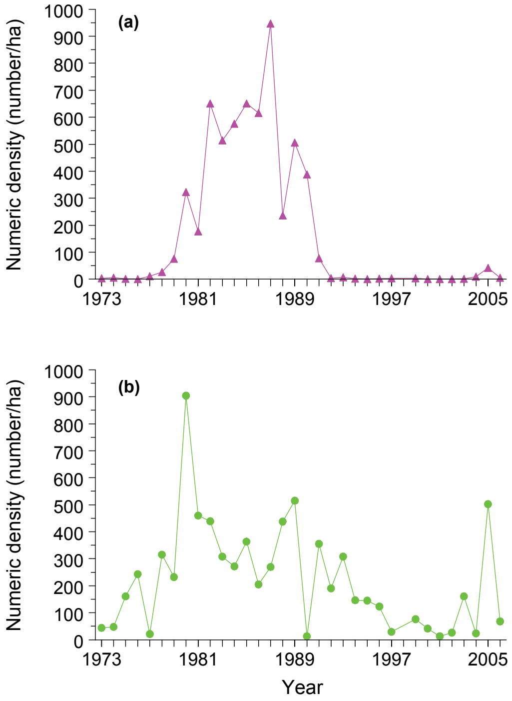

Figure 5. Numeric density of age-0 bloaters (a) and age-0 rainbow smelt (b) in Lake Michigan, 1973-2006.

Rainbow smelt – Adult rainbow smelt is an important diet item 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).

In 2006, adult rainbow smelt numeric density was 67 fish per ha, a 70% decline from 2005 (Figure 2a). Overall, however, the 2006 estimate is just below the average rainbow smelt numeric density for 1994–2006 (83 fish per ha). Biomass density decreased from 1.9 to 0.6 kg per ha between 2005 and 2006 (Figure 2b). RSE for adult rainbow smelt numeric density averaged 26% from 1973-2006, and RSE for 2006 was 29% (Figure 3a). Across the time series, adult rainbow smelt numeric density was highest from 1981 to 1993, and has remained at a relatively low density from 1994 to present. Causes for the decline remain unclear. Consumption of 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 (Figures 2, 5b).

Sculpins – From a biomass perspective, the cottid populations in Lake Michigan proper are dominated by deepwater, and to a lesser degree, slimy sculpins. Spoonhead sculpins, 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).

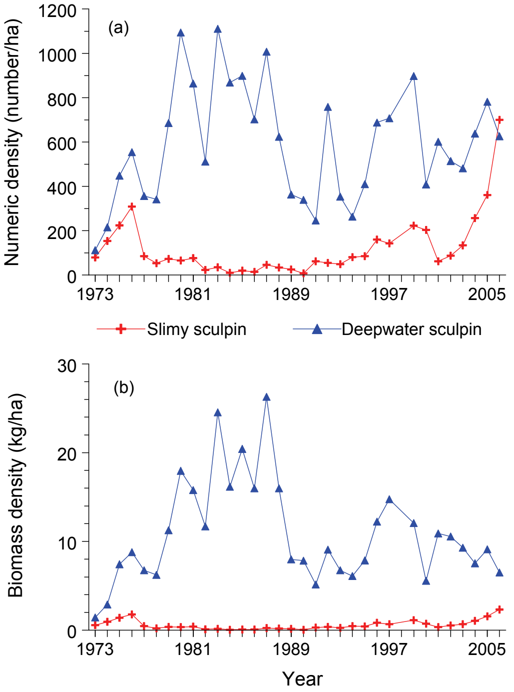

Figure 6. Density of slimy and deepwater sculpins as number (a) and mass (b) of fish per ha in Lake Michigan, 1973-2006.

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 are only a minor part of adult lake trout diets. Deepwater sculpin is an important diet item 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 decreased slightly to 626 fish per ha in 2006, compared with 781 fish per ha in 2005 (Figure 6a). Overall, deepwater sculpin numeric density has trended slightly upwards since 1990, with considerable variation. Deepwater sculpin biomass density also decreased from 9.1 to 6.5 kg per ha between 2005 and 2006 (Figure 6b). Biomass density has trended neither upward nor downward since the early 1990s. This leveling off during the 1990s coincided with a leveling off of burbot abundance. RSE for deepwater sculpin numeric density was 31% in 2006, which follows a general trend of slightly increasing RSE since 1983 (Figure 3b).

Numeric density of slimy sculpins in Lake Michigan increased from 362 fish per ha in 2005 to 701 fish per ha in 2006 (Figure 6a). RSE for slimy sculpin numeric density was 35% in 2006, which was lower than its average RSE of 40% from 1973-2006 (Figure 3b). Overall, slimy sculpin numeric density has been increasing since 1990. This increase may have actually begun in 1986, when an emphasis was first placed on stocking lake trout on offshore reefs rather than stocking lake trout in areas closer to shore in Lake Michigan. The GLSC bottom trawl survey does not cover the rocky, offshore reefs that have been heavily stocked with lake trout since 1986. Thus, the observed increase during the 1990s in slimy sculpin abundance detected in the GLSC bottom trawl survey was likely attributable to the 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). The effect of the decrease in *Diporeia* abundance on the slimy sculpin population remains to be determined.

Analysis of bottom trawl survey data indicates that alewives interfering with deepwater sculpin reproduction and predation by burbot on deepwater sculpins are the most important factors affecting deepwater sculpin abundance in Lake Michigan (Madenjian et al. 2005c). The survey data provided no evidence that slimy sculpins negatively affected deepwater sculpin abundance.

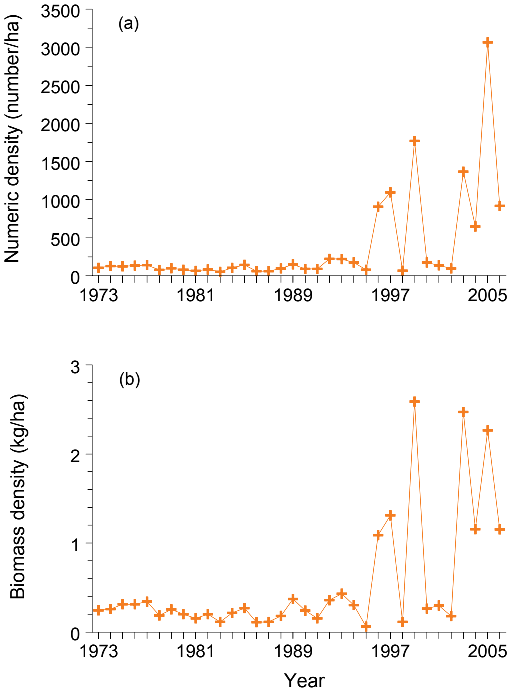

Figure 7. Density of ninespine sticklebacks as number (a) and mass (b) of fish per ha in Lake Michigan, 1973-2006.

<u>Ninespine stickleback</u> – Given the increasing abundance of ninespine stickleback in Lake Michigan and its occasional occurrence in the diets of salmonines and lake trout, we added this species to our annual report. Two stickleback species occur in Lake Michigan. Ninespine stickleback is native, whereas threespine stickleback 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 preyfishes, 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 7a). Densities increased dramatically in 1996-1997, and have since been highly variable. Their recent increase coincides with the expansion of dreissenid mussels in the lake, but mechanisms underlying the population increase of ninespine stickleback are unknown.

Numerically, ninespine stickleback has been the most abundant species in the bottom trawl survey since 2003. Its numeric density estimate of 919 fish per ha in 2006 was very close to the mean numeric density of 931 fish for the 1996-2006 period (Figure 7a). Even with the recent numeric increase, the biomass density of ninespine stickleback remains far below that of all other prey fish species, except rainbow smelt. Biomass density was estimated to be 1.2 kg per ha in 2006 (Figure 7b). RSE for ninespine stickleback numeric density was 37% in 2006, which was lower than its average RSE of 48% from 1973-2006 (Figure 3b). RSE generally decreased in the late 1990s and early 2000s, which coincided with their increase in numeric density.

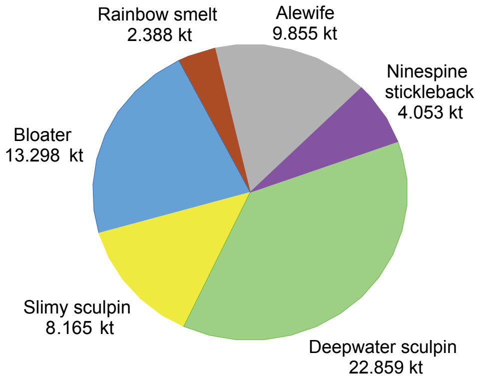

Figure 8. Estimated lake-wide biomass of prey fishes in Lake Michigan, 2006, based on the bottom trawl survey.

LAKE-WIDE BIOMASS

We estimated a total lake-wide biomass of prey fish available to the bottom trawl in 2006 of 60.62 kilotonnes (kt) (1 kt = 1000 metric tons) (Figure 8, Appendix 1). Total prey fish biomass was the sum of the population biomass estimates for alewife, bloater, rainbow smelt, deepwater sculpin, slimy sculpin, and ninespine stickleback. Deepwater sculpins constituted 38% (22.86 kt), bloaters constituted 22% (13.30 kt), and alewives constituted 16% (9.86 kt) of the total prey fish biomass in Lake Michigan in 2006.

Total prey fish biomass in Lake Michigan has trended downward since 1989, and is largely a result of the tremendous decrease in bloater biomass (Figure 9). The current bloater biomass is about 4% of the peak value in 1989. Total prey fish biomass did increase slightly between 2000 and 2002 due to an increase in alewife biomass, in particular, the exceptionally large 1998 alewife year-class (Figure 9). The decline in total prey fish biomass between 2002 and 2005 was primarily due to a decrease in alewife biomass. The decline between 2005 and 2006, however, was due to large decreases in lake-wide biomass for all species (ranging from 26% for alewife to 69% for rainbow smelt) except slimy sculpin, which increased by 50% relative to 2005. The total lake-wide biomass of prey fish available to the bottom trawl in 2006 was the lowest biomass recorded in our time series.

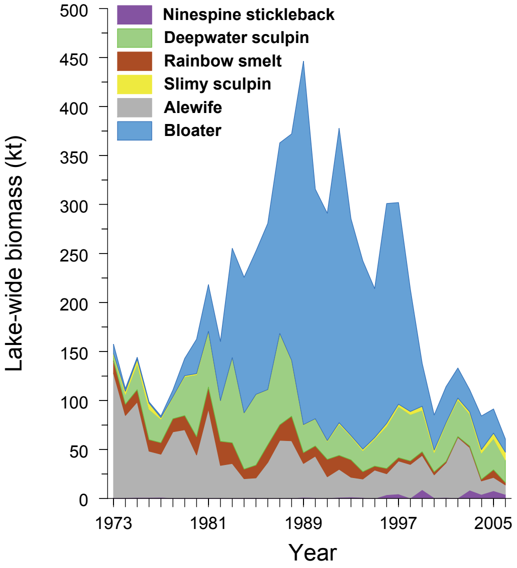

Figure 9. Estimated lake-wide biomass of prey fishes in Lake Michigan, 1973-2006, based on bottom trawl surveys.

OTHER SPECIES OF INTEREST

Burbot – 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.

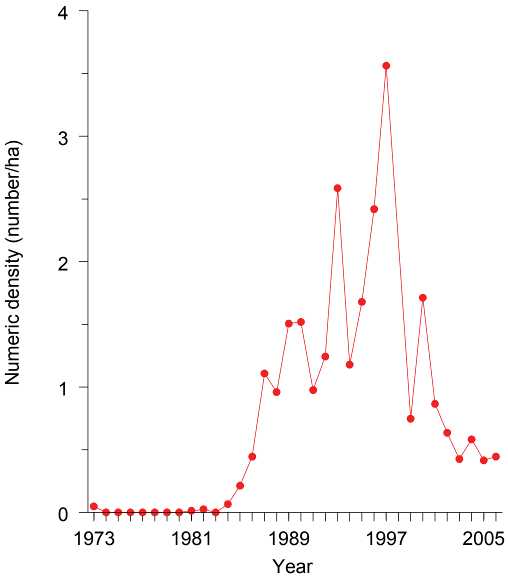

Figure 10. Numeric density of burbot in Lake Michigan, 1973-2006.

Burbot numeric density in 2006 (0.44 fish per ha) was similar to that of 2005 (0.42 fish per ha) (Figure 10). After a period of low numeric density in the 1970s, burbot showed a strong recovery in the 1980s. Densities increased through 1997, although we interpret the trend as a leveling off between 1990 and 2001. Since 2001, however, burbot densities decreased, perhaps partly due to increased predation by sea lampreys. Lake-wide estimates of spawning sea lampreys have generally been increasing since 2000 (D. Lavis, U. S. Fish and Wildlife Service, Ludington, MI, personal communication).

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 11). This huge year-class was likely attributable to a sufficient abundance of female spawners and favorable weather. The 2006 year-class was the second strongest since 1995 (after 2005), In addition, numeric density of “adult” yellow perch (i.e., ≥ 100 mm) was the highest observed since 2000, which suggests that a considerable part of the record 2005 year-class survived overwinter. Most researchers believe that the poor yellow perch recruitment that occurred during 1989-2004 (Figure 11) was a combination of several factors: poor weather conditions, low abundance of female spawners, and possibly a low availability of zooplankton for yellow perch larvae (Makauskas and Clapp 2000).

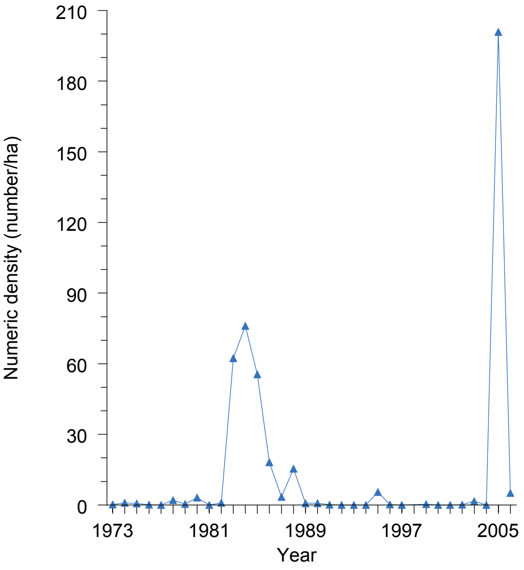

Figure 11. Numeric density of age-0 yellow perch in Lake Michigan, 1973-2006.

Round goby – The round goby 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 first caught in the GLSC bottom trawl survey in 2003, and have been caught in each subsequent year. Prior to 2006, total catches for years 2003, 2004, and 2005 were 23, 26, and 37 round gobies, respectively. They also were limited to three ports (Manistique, Saugatuck, and Ludington) and the four shallowest depths (9, 18, 27, and 37 m) sampled. In 2006, numeric density of round gobies increased to 27 fish per ha (Figure 12a), which was a 17-fold increase over 2005. This large increase, however, was driven by two large catches at Ludington: 422 fish at 18 m and 379 fish at 27 m. All other catches were five fish or fewer. In addition to the increase in numeric density, round gobies also were captured at two new ports (Sturgeon Bay and Waukegan) and at even greater depths (46 and 64 m at Manistique). Hence, this invader appears to be increasing its distribution and abundance in Lake Michigan. With additional years of continued surveillance, results from the GLSC bottom trawl survey should help detect significant effects of round gobies on the Lake Michigan fish community.

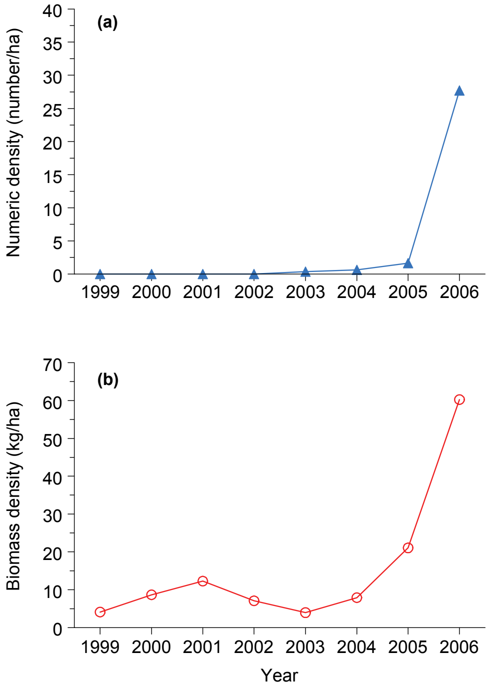

Figure 12. Estimated lake-wide numeric density of round goby (a) and biomass of density dreissenid mussels (b) in Lake Michigan, 1999-2006, based on bottom trawl surveys.

<u>Dreissenid mussels</u> – The first zebra mussel 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 2006 (Figure 12b), exhibiting a nearly 3-fold increase over 2005. Since 2003, biomass density has more than doubled in each subsequent year. This increase in abundance is likely due to the greater proportion of quagga mussels in Lake Michigan (T. Nalepa, NOAA Great Lakes Environmental Research Laboratory, Ann Arbor, MI, personal communication). Relative to the zebra mussel, quagga mussels can reproduce at lower temperatures (Roe and MacIsaac 1997) and, in turn, greater depths. As a result the distribution of dreissenid mussels likely increased as a result of the quaggas. Unfortunately, the increase in dreissenid mussels has been associated with the decline in the amphipod *Diporeia* in Lake Michigan, although the mechanism by which dreissenid mussels are negatively affecting *Diporeia* remains unidentified (Madenjian et al. 2002; Nalepa et al. 2006).

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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 2006. Estimates are based on the bottom trawl survey. Standard error enclosed in parentheses. NA denotes that estimate is not available.

Taxon	Numeric density (fish per ha)	Biomass density (kg per ha)	Lake-wide biomass (kt)
age-0 alewife	2.79 (1.39)	0.006 (0.003)	0.023 (0.010)
adult alewife	91.57 (18.89)	2.792 (0.590)	9.833 (2.077)
age-0 bloater	4.88 (1.55)	0.042 (0.014)	0.146 (0.049)
adult bloater	93.57 (28.76)	3.735 (1.246)	13.152 (4.387)
age-0 rainbow smelt	67.79 (34.68)	0.082 (0.025)	0.287 (0.090)
adult rainbow smelt	67.47 (19.85)	0.597 (0.201)	2.101 (0.709)
deepwater sculpin	626.23 (194.10)	6.491 (1.795)	22.859 (6.321)
slimy sculpin	700.50 (243.68)	2.318 (0.748)	8.165 (2.634)
ninespine stickleback	918.84 (337.61)	1.15 (0.410)	4.053 (1.430)
burbot	0.44 (0.24)	0.581 (0.287)	2.046 (1.011)
age-0 yellow perch	5.16 (3.55)	0.017 (0.012)	0.059 (0.041)
round goby	27.69 (19.55)	0.23 (0.15)	0.803 (0.543)
dreissenid mussels	NA	60.277 (30.950)	212.273 (108.995)