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Status of Pelagic Prey Fishes in Lake Michigan, 1992-2005

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ABSTRACT

Acoustic surveys were conducted in the fall during the years 1992-1996 and 2001-2005 to estimate prey fish biomass in Lake Michigan. Midwater trawling during the surveys provided a measure of species and size composition of the fish community for use in scaling acoustic data and providing species-specific abundance estimates. The 2005 survey included 31 transects and 62 midwater tows. Alewives were the dominant species in the 2005 trawl catch by mass, followed by rainbow smelt then bloater. Alewife, rainbow smelt, bloater, and yellow perch all produced abundant young in 2005, with YOY alewife density highest since 1995. Bloater and yellow perch YOY were more abundant in 2005 than in any other year of the survey. Numeric density of YOY alewife in 2001-2005 was positively correlated with May-August surface water temperature (r^2=0.95). Total prey biomass (alewife, rainbow smelt, bloater, sticklebacks, and yellow perch) was 2.2x higher in 2005 (69 kt) than in 2004, but was only ~40% of 2001 biomass. Of the lakewide prey fish total of 69 kt, 49% was alewife. In 2005, there was evidence of spatial structure at multiple scales, with small-scale autocorrelation in density occurring up to ~5 km accompanied by large-scale (regional) differences in distribution. The regional differences consisted of spatial segregation among species and between size groups within species in 2004-2005. Numeric fish density was again highest in offshore regions (north and south offshore), but biomass density was highest in nearshore areas (depths <100 m).

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The U.S Geological Survey Great Lakes Science Center (GLSC) has been conducting forage fish surveys using bottom trawls in Lake Michigan since the early 1960s. Acoustic surveys were first conducted by GLSC in Lake Huron in the 1970s (Argyle 1982). The first acoustic surveys of Lake Michigan were undertaken in the late 1980s (Argyle 1992) and continued through the 1990s (Argyle et al. 1998). Based on work during this period, Argyle et al. (1998) recommended implementation of an annual fall lakewide acoustic survey as a tool to improve and enhance forage fish assessment capabilities.

In light of the drastic changes in the Lake Michigan food web during the last 30 years (Madenjian et al. 2002) and the continuing influence of humans through introduction of exotic species, pollution, fishing, and fish stocking, enhancement of long-term data on prey fish dynamics is critical. The traditional GLSC prey fish monitoring method (bottom trawl) is inadequate for fish located off bottom (Fabrizio et al. 1997). In particular, bottom trawls do not adequately sample young-of-the-year (YOY) alewives (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*), or bloater (*Coregonus hoyi*). Alewives are and have been the primary prey of introduced salmonines in the Great Lakes (Stewart and Ibarra 1991; Madenjian et al. 1998). Alewife dynamics typically reflect occurrences of strong year classes. Much of the biomass making up a strong year class is not recruited to bottom trawls in its first fall of life, and significant predation by salmonines may occur on YOY and yearling alewives before they are recruited to the bottom trawl (R. Claramunt, Michigan Department of Natural Resources, Charlevoix, MI, unpublished data). The dynamic nature of the Lake Michigan food web and the potential for high levels of predation on YOY and yearling alewives warrant an increased focus on abundance, distribution, and survival of alewives throughout all stages of life.

Given the importance of accurate estimates of prey fish abundance for salmonine management (Madenjian et al. 2005), the initiation of a lakewide fall acoustic prey fish survey was critical. A cooperative survey based on recommendations in Argyle et al. (1998) was initiated in 2001 and the survey was first completed according to protocol in 2003. In 2004-2005, survey effort was expanded and resulted in the most extensive coverage to date. Because of similarities in the sampling protocol and fish community structure during 2001-2005, statistical analyses in this report were focused on data collected during that period. Data collected in 1992-1996 are shown for comparison. Because of the ability of acoustic equipment to count organisms far off bottom, this type of sampling is ideal for highly pelagic fish like YOY alewives. Acoustic sampling can provide abundance data that can be related to other variables to provide predictions about factors influencing year class strength. Environmental features can influence recruitment, and Madenjian et al. (2005) demonstrated that alewife recruitment to age 3 was positively correlated with spring-summer water temperatures. We use acoustic data from 2001-2005 to test the hypothesis that YOY fish density is positively related to spring-summer water temperatures.

METHODS

Sampling Design

Acoustic survey design has developed a great deal in the past ten years with a focus on understanding the assumptions and biases of different designs (Rivoirard et al. 2000). Classical variance estimates are biased if sample sites are not randomly selected (Rivoirard et al. 2000), but in practice this randomization can be difficult to achieve. The initial Lake Michigan survey adopted by the Lake Michigan Committee (Fleischer et al. 2001) was a stratified quasi-random design with three strata (north, south-central, and west) and unequal effort allocated among strata. The location of strata and number of transects within each stratum was determined from a study of geographic distribution of species and the variability of fish abundance within the strata (Argyle et al. 1998). A modified stratification (Figure 1) was developed in 2004 (Warner et al. 2005), which included two additional strata (north and

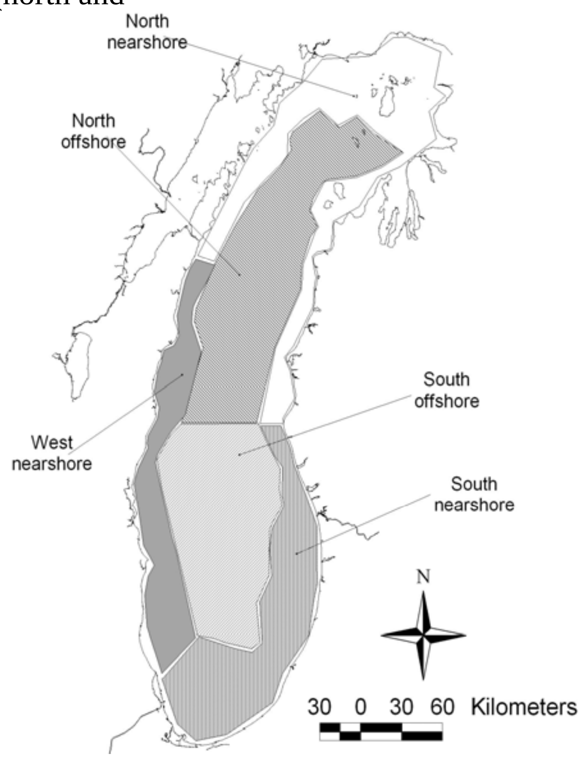

Figure 1. Map of Lake Michigan showing strata used in design and analysis of the lakewide acoustic survey conducted in 2004.

south offshore). Even though the initial three strata were retained, their size was modified based on data collected in 2003 as well as NOAA CoastWatch Great Lakes node maps of sea surface temperature from 2001-2003. The transects sampled in 2004-2005 also differed in that they were evenly spaced parallel transects as recommended for open seas by Simmonds et al. (1992).

Data Collection and Processing

From 1992-1996, data were collected using Biosonics dual beam echosounders (120 kHz). Sampling was conducted between September and November with acoustic data collection initiated ~1 hour after sunset and ending ~1 hour before sunrise. The dual beam transducers were either deployed using a towfish suspended abeam ship from a crane and towed at a depth of ~1 m or housed in the sea chests of the R/V Grayling and S/V Steelhead. With the sea chest, sound energy was transmitted through a rubber-compound window. This window had little effect on beam transmission or receive-sensitivity at the frequency used for this survey (Fleischer et al. 2002). Beginning in 2001, acoustic data were collected with Biosonics dual (MDNR) and split beam (USGS) 120 kHz echosounders. Beginning in 2005, acoustic equipment on the S/V Steelhead was upgraded and as a result, only split beam transducers were used (6.8° half-power beam width). The upgrade to the S/V Steelhead included modifications to transducer placement. Beginning in 2005, the split beam transducer was mounted on the hull rather than in the sea chest. This eliminated maintenance problems with the sea chest and prevented the necessity of testing the new transducer's receive and transmit sensitivities through the rubber window. Between 2001-2004, transducer deployment on the USGS vessels was accomplished using a towfish suspended abeam ship from a crane and towed at a depth of ~1 m. In 2005, it was suspended on a large aluminum pipe through a sonar tube, which allowed an increase in survey speed from 6 to ~12 km/hr. Acoustic surveys in 2001-2005 occurred during August–

September with sampling initiated ~1 hour after sunset and ending ~1 hour before sunrise.

With the exception of the dual beam unit in 2001, acoustic systems were calibrated in the field according to methods described in Foote et al. (1987) and MacLennan and Simmonds (1992) during the survey using tungsten carbide spheres. Because of low variability with the dual beam echosounder, we used the mean calibration of offsets for later years in 2001. Calibration offsets were applied to echo integration and target strength data during processing. The dual beam echosounder was susceptible to noise at depths >80 m. To compensate for high noise levels in deep water, a time-varied threshold was applied to target strength variables. Echo integration thresholds for data collection were -80 or -85 dB, depending on depth conditions. The same thresholds were applied to single target data. A -80 dB echo integration threshold was employed during analyses.

Data structure differed between the early (1990s) and later (2001-2005) portions of the time series. Analyses of the 1990s acoustic data are described in detail in Argyle et al. (1998) and Fleischer et al. (1997) but a brief description will be included here. Transects consisted of elementary sampling units that were 10 m deep and spanned the distance between 10 m bottom contours. To insure consistency with the current stratification, samples with bottom depths >100 m were considered offshore. Analyses of data collected from 2001-2005 were conducted with Echoview 3.25. Each transect was subdivided in ~500 m horizontal segments that were 10 m deep. The decision to use the 500 m segments as the elementary sampling unit (ESU) was based on the need to balance the number of pings and targets in each cell with efforts to capture spatial variability.

Midwater trawls were employed to identify species in fish aggregations observed with echosounders and to provide size composition data. Tows targeted aggregations of fish observed in echograms while sampling and fishing locations were typically chosen when there was uncertainty about the composition of fish aggregations observed acoustically. A trawl with a 5 m headrope and 6.35 mm bar mesh cod end was fished from the S/V Steelhead in all years, while on the USGS vessel R/V Grayling, a variety of trawls were used. On the USGS vessels R/V Siscowet, R/V Kiyi and R/V Sturgeon, a trawl with ~15 m headrope and 6.35 mm cod end was used. In the 1990s, trawl depth was monitored using net sensors. Similar sensors were used in 2001-2005 (except 2002 on USGS vessel, 2001-2004 on MDNR vessel). In cases without trawl sensors, warp length and angle were used to estimate fishing depth.

Fish were measured (nearest mm) either in the field or frozen in water and measured upon return to the laboratory. Lengths of large catches (>100 fish) were taken from a random subsample. Fish were weighed in groups (total catch weight per species, nearest 2 g) in the field or individually in the laboratory (nearest 0.1 g). Total catch weight was recorded as the sum of weights of individual species. For a small number of tows with only numbers and lengths by species, a weight-length regression was used to estimate catch weights for each species from lengths and numbers caught. Alewives caught in trawls were separated into YOY and YAO groups using a cutoff length of 100 mm. Rainbow smelt were separated using a length of 90 mm, while for bloater this length was 120 mm. The number of midwater tows made in each year and region varied, with most effort occurring in the north nearshore region where most transects were located (Data from 2001-2005 shown in Table 1).

Catch and acoustic data were assigned to one of three depth layers (<20 m, 20-50 m, and >50 m). These layers were loosely based on thermocline depth and fish distribution. Trawl data were linked with acoustic transect data by assigning catch composition and sizes from each tow to the corresponding transect, depth layer, and bottom depth, and region. Catch composition, mean length, and mean mass were calculated for each layer of each ESU from trawling conducted on that transect. When this was not possible, we used the mean from the respective depth layers in the stratum in which a transect was located. If data from a layer were absent from a stratum, the mean of the layer in the remainder of the lake was used. In 2001, trawl data were not available for the western stratum. To provide an estimate of species composition and size for this area, the mean of catch proportions and sizes in this stratum during 2003-2005 were used. In 2004, there were no tows with fishing depth >50 m and non-zero catch. To provide an estimate of species composition and size for this layer in 2004, the stratum (region) means of data from this layer was calculated from tows made in 2003-2005.

Estimates of Abundance

Acoustic density estimates for each transect were made for two groups: all targets and those that corresponded to fish targets. An estimate of absolute density (including all targets) was made using the formula

$$(1)\ Total\ \ density\ \ (\#\cdot ha^{-1}) = 10^{4} \times \frac{ABC}{\sigma}$$

where 10^4 = conversion factor ($m^2 \cdot ha^{-1}$), *ABC* = area backscattering coefficient ($m^2 \cdot m^2$) and σ = the mean backscattering cross section (m^2) of all targets between -76 and -20 dB, a range including all fish catchable with our trawl. The estimate from equation 1 provided density for all targets, potentially including

Table 1. Number of midwater tows with non-zero catch made during acoustic surveys in each region and year.

	Region[1]				
Year	NN	SN	WN	NO	SO
2001	13				
2002	14		6		
2003	19	4	11		
2004	16	6	5	5	4
2005	19	11	10	11	11

[1]NN=north nearshore, SN=south nearshore, WN= west nearshore, NO=north offshore, SO=south offshore.

invertebrates such as *Mysis relicta*, as aggregations of *Mysis* have TS similar to individual YOY rainbow smelt (-70 to -64 dB, Rudstam et al. 2003; D.M. Warner, unpublished data). To maintain consistency with acoustic surveys of Lake Michigan in the 1990s (Argyle et al. 1998), targets <-60 dB were excluded. To accomplish this, density of fish targets was estimated by multiplying total density (equation 1) by the proportion of the total number of targets that were between -60 and -20 dB. This threshold should have included targets corresponding to the smallest YOY alewives (2-3 cm) at most orientations based on in situ TS-length relations (-60 to -52 dB) published by Warner et al. (2002). This threshold likely resulted in underestimation of rainbow smelt density given expected target strengths published by Rudstam et al. (2003).

Numeric densities (fish/ha) of the different species were estimated as the product of fish density and the proportion by weight in the catch at that location. Proportion by weight was used to reduce the influence of trawl contamination that occurs because closing nets were not used. This approach had minimal effect on the density of the most abundant species (alewife) relative to using numeric proportions. Total alewife, smelt, and bloater density was subdivided into YOY and YAO density by multiplying total density for these species by the numeric proportions of alewives in each age group. Biomass density (kg/ha) for the different groups was then estimated as the product of density and species or age-specific mean mass as determined from trawling. Mean and relative standard error (RSE = (SE/mean) x 100) for density and biomass in the survey area were estimated using stratified cluster analysis methods featured in the statistical routine SAS PROC SURVEYMEANS (SAS Institute Inc. 2004). This program is designed to analyze survey data and enables the use of stratification and clustering to estimate means and variances. Cluster sampling techniques are appropriate for acoustic data, which represent a continuous stream of autocorrelated data (Williamson 1982; Connors and Schwager 2002). Density and biomass values for each ESU in each stratum were weighted by dividing the stratum area (measured using GIS) by the number of ESUs in the stratum. The contribution of each stratum to the overall survey mean was dependent on the area of the stratum.

Spatial structure of the data were described using empirical variograms and general linear models. Along-transect variograms were constructed for data collected in 2005 to detect the range of spatial autocorrelation of total fish density (numeric and biomass). To examine large-scale distribution of fish in 2004-2005, stratum estimates were compared within and between years using general linear models and Tukey pairwise comparisons using transect mean densities as the elementary sampling unit in a stratum.

Relationships between lakewide mean YOY alewife, rainbow smelt, and bloater density and water temperature were examined using acoustic data and Great Lakes Surface Environmental Analyses data (GLSEA, NOAA CoastWatch Great Lakes Node, http://coastwatch.glerl.noaa.gov/statistic/statistic.html). The GLSEA data were condensed to the mean of daily surface water temperatures between 1 April and 1 August in each year.

RESULTS

Alewife – Alewife were the dominant species observed in midwater tows in 2005, representing 73% (relative standard error, RSE=5%) of the catch by weight. Mean numeric density of alewives was 3,519 fish/ha (RSE=18%) in 2005, nearly 2x higher than in 2004 (Figure 2). Mean biomass density of alewives was 6.9 kg/ha (RSE=8%), which was lower than in three of the last four years.

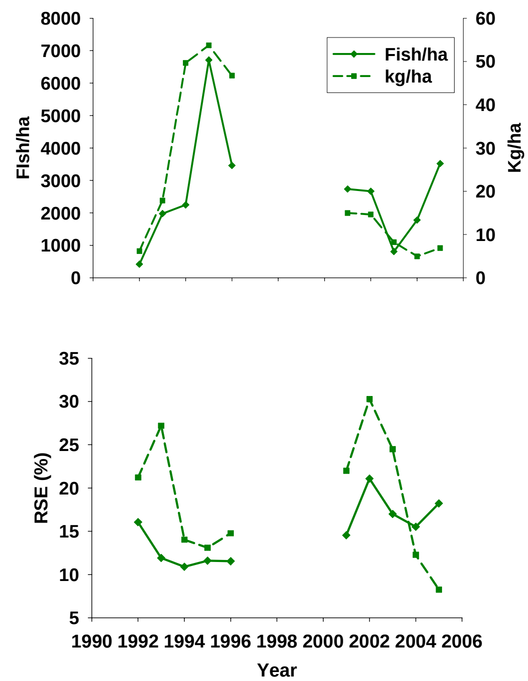

Figure 2. Acoustic estimates of alewife density in Lake Michigan, fall 1992-2005 (upper panel) shown with relative standard error of the estimates (RSE, lower panel).

Mean numeric density of YOY alewives in 2005 was 3,385 fish/ha (RSE=19%). Numeric density of YOY alewife in 2005 was second only to density in 1995 and was more than 2x higher than in 2004 and 1.6x higher than in 2002; the second highest value in 2001-2005 (Figure 3). Mean biomass density of YOY alewives in 2005 was 3.2 kg/ha (RSE=11%), 1.7x higher than in 2004. Mean numeric density of YAO alewives in 2005 was 133 fish/ha (RSE=14%), with the value in 2005 continuing the downward trend from ~600 fish/ha in 2001. Mean biomass density of YAO alewives in 2005 was 3.6 kg/ha (RSE=16%), 1.4x higher than 2004.

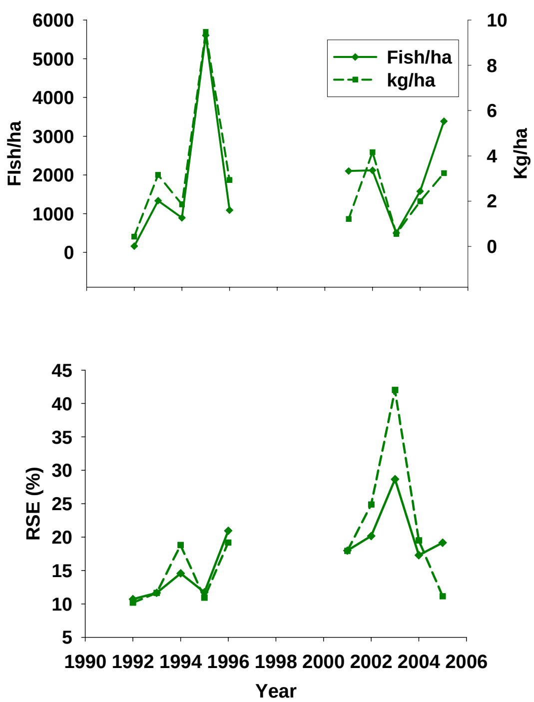

Figure 3. Acoustic estimate of YOY alewife density in Lake Michigan, 1992-2005 (upper panel) shown with relative standard error of the estimates (RSE, lower panel)

As in previous years, small alewives dominated the catch and the length composition of alewives caught in 2005 was indicative of uneven representation of age classes. Very few fish were >100 mm total length (Figure 4). This was especially prominent in 2005, and age estimation using otoliths revealed that virtually all of the alewives caught in 2005 were YOY. Ages were estimated for 61 alewives between 69 and 126 mm. At least six fish were aged per 10 mm length bin from 70-120 mm. These data revealed that most fish between 90 and 100 mm were age 1. We re-analyzed the acoustic data using 90 mm as the YOY cutoff to compare biomass density with the value estimated using the 100 mm cutoff. We found that YOY alewife biomass density was reduced 3% by using the 90 mm cutoff.

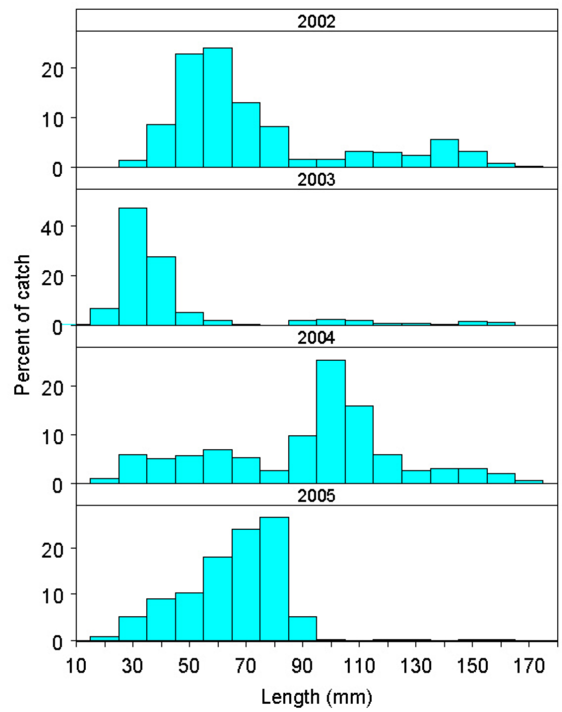

Figure 4. Length-frequency distribution of alewives caught with midwater trawls during Lake Michigan acoustic surveys in 2002-2005.

Rainbow smelt – Rainbow smelt were the second most dominant species in the midwater catch in 2005 and represented 38.0% (RSE=18%) of the catch by weight. The proportion of rainbow smelt in the catch did not exhibit any trend in 2001-2004, nor did density. Mean numeric density of rainbow smelt in 2005 was 1,041 fish/ha (RSE=12%, Figure 5). Mean biomass density of rainbow smelt in 2005 was 5.8 kg/ha (RSE=19%), which was nearly 7x higher than in 2004. Mean numeric density of YOY rainbow smelt in 2005 was 459 fish/ha (RSE=14%) and was almost identical to the 2004 value. Mean biomass density of YOY rainbow smelt in 2005 was 0.3 kg/ha (RSE=38%) and was 3x higher than in 2004. Mean numeric density of YAO rainbow smelt in 2005 was 582 fish/ha (RSE=18%) and was 5.6x higher than in 2004. Mean biomass density of YAO rainbow smelt in 2005 was 5.5 kg/ha (RSE=19%) and was 7.4x higher than in 2004. For the first time since 1993, YAO smelt biomass density was higher than YAO alewife biomass density.

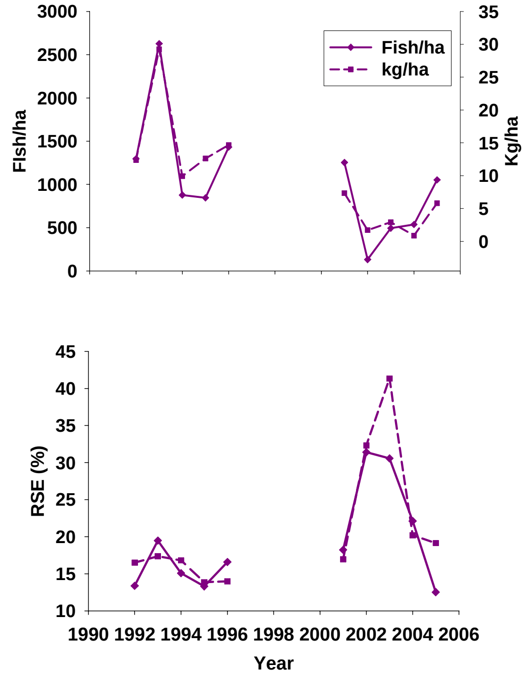

Figure 5. Acoustic estimates of rainbow smelt density in Lake Michigan in fall 1992-2005 (upper panel) shown with relative standard error of the estimates (RSE, lower panel).

Bloater – Bloater were the third most common species caught, composing 14.8% of the midwater catch by weight (RSE=27%). The proportion of bloaters in the catch was more variable than that of alewives and rainbow smelt. Mean numeric density of bloaters in 2005 was 435 fish/ha (RSE=12%, Figure 6) and was higher than in the previous four years. Mean biomass density of bloaters in 2005 was 0.87 kg/ha (RSE=23%) and was 1.6x higher than in 2004. Mean numeric density of YOY bloaters in 2005 was 414 fish/ha (RSE=12%), 16.6x higher than in 2004 and the highest value observed in the 1992-2005 period. Mean biomass density of YOY bloater was 0.3 kg/ha (RSE=11%), 5x higher than in 2004 and the second highest value observed in 1992-2005 (the highest occurred in 1993). Mean numeric density of YAO bloater in 2005 was 21 fish/ha (RSE=41%), while mean biomass density was 1.0 kg/ha (RSE=36%). Bloater

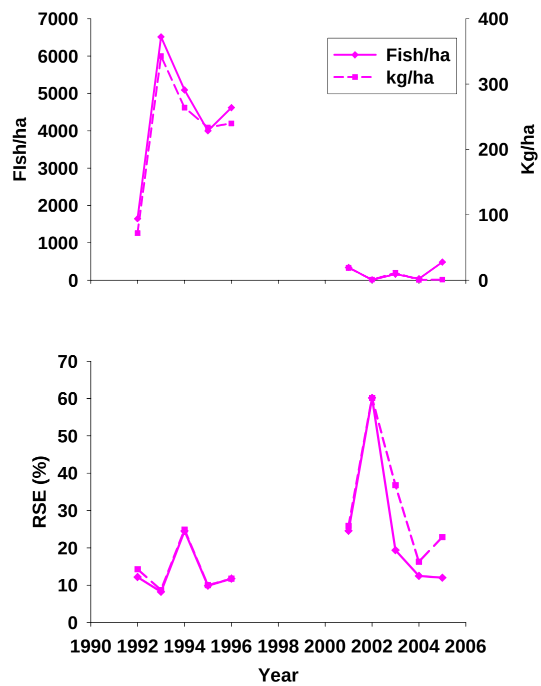

Figure 6. Acoustic estimates of density of bloater in Lake Michigan in fall 1992-2005 (upper panel) shown with relative standard error of the estimates (RSE, lower panel).

abundance remained much lower than in the 1990s, but the high abundance of YOY bloater in 2005 was evidence of a strong year class.

Other species – Unlike previous years, in 2005 relatively high numbers of YOY or juvenile yellow perch (*Perca flavescens*) were captured in offshore waters (up to 60 km). These yellow perch were between 44 and 90 mm in length, with all but one < 76 mm. Numeric density of yellow perch was 62 fish/ha (RSE=15%). Biomass density was lower than any other species at 0.02 kg/ha (RSE=53%). Yellow perch have been observed in offshore areas recently (Dettmers at al. 2005), but with lengths < 30 mm.

Sticklebacks (*Pungitius pungitius* and *Gasterosteus aculeatus*) were more abundant in 2005 than in 2001-2004. However, they represent only a small portion total biomass (~4%). Numeric density of sticklebacks was 380 fish/ha (RSE=29%). Biomass density of sticklebacks was 0.57 kg/ha (RSE=27%).

Distribution

Biomass density of a number of species as well as total biomass density exhibited spatial structure at multiple scales. Directional empirical variograms revealed that acoustic densities 5-7 kilometers apart along a transect were correlated for most species/age groups. In addition, there appeared to be large-scale (regional) differences in abundance during 2004-2005. These differences were identified by comparing stratum densities within and between years using general linear models. Factors included year, region, and the year x region interaction. Tukey pair-wise comparisons were used where necessary. The large-scale patterns identified differed by species and sometimes age groups. For example, YOY alewife biomass density was highest in the south offshore region, while YAO alewife biomass density was highest in the north nearshore region. Figure 7 shows total alewife biomass density concentrated in several areas. Additionally, for YOY alewife there was a significant year x region interaction ($P<0.05$), while for YAO alewife this interaction was not significant ($P>0.05$). This difference suggests that regional patterns were not consistent between years for YOY while distribution of YAO biomass density was similar in both years. In general, the biomass density in the offshore regions (particularly south offshore) was primarily YOY fish. Linkage of these distribution patterns to recruitment success may be possible with additional sampling.

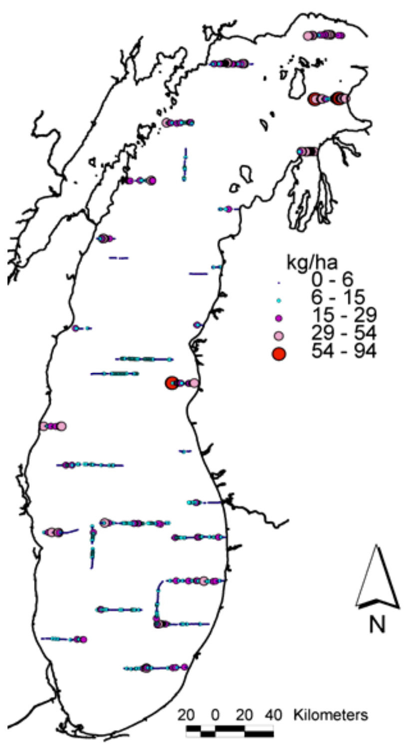

Figure 7. Map of Lake Michigan showing alewife density along acoustic transects in 2005. Each symbol represents a 500 m horizontal segment of the water column.

Year class strength and water temperature

Both YOY fish densities and surface water temperatures varied in 2001-2005. However, there was a much wider range of variation in fish density than in temperature.

Mean surface water temperature was higher in 2005 than in the previous four years and was the highest observed since 1998. Numeric density of YOY alewife in 2001-2005 was significantly positively correlated with April-July surface water temperature (r^2=0.95, P=0.004, Figure 8). Biomass density of YOY alewife, like numeric and biomass density for YOY of other species, was not correlated with surface water temperature (Table 2).

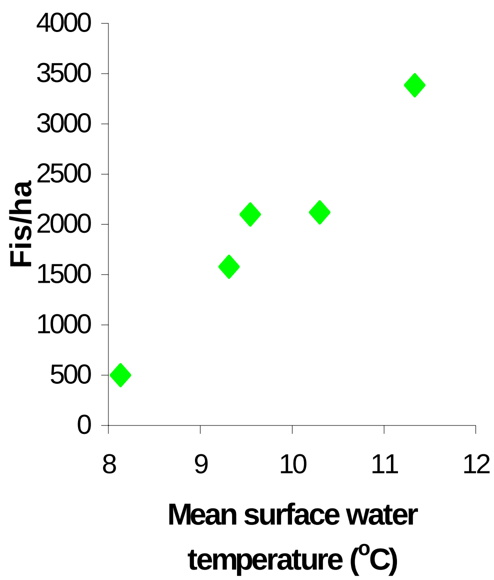

Figure 8. Plot of mean numeric density of YOY alewife versus mean 1 April-31 July surface water temperature in Lake Michigan.

CONCLUSIONS

Prey fish biomass in Lake Michigan remains at levels much lower than in the 1990s. The large difference in biomass from the 1990s resulted primarily from the decrease in bloater and alewife abundance. Together, these species have made up the majority of the biomass observed during acoustic surveys. Although both species remain at low abundance relative to the 1990s, both appear to have produced strong year classes in 2005. Strong alewife and bloater year classes appear to have been accompanied by strong rainbow smelt and yellow perch year classes. Both YOY bloater and YOY yellow perch were observed in greater numbers than in any previous acoustic survey.

Table 2. Results of linear regression (F statistic, r^2, and P) relating density of YOY alewife, rainbow smelt, and bloater in Lake Michigan 2001-2005 to mean surface water temperatures (1 April to 1 August) for each year.

Species	#/ha	kg/ha
alewife	61, 0.95, 0.004	5.8, 0.66, 0.1
rainbow smelt	0.05, 0.02, 0.8	1.3, 0.08, 0.3
bloater	3.3, 0.5, 0.2	2.4, 0.44, 0.2

Total pelagic prey biomass in the area surveyed in 2005 was 69 kt (95% CI 55-83 kt). Alewife composed 49% of this biomass, with rainbow smelt making up another 41%. Estimated biomass of age 2 and 3 Chinook salmon in 2001-2004 was between 12.3 and 17.2 kt. These estimates were derived by multiplying numeric abundance from the catch-at-age model of Benjamin and Bence (2003) by weight at age 2 and 3 Chinook salmon sampled at the Little Manistee and Strawberry creek weirs and the MDNR vessel survey. Given the biomass estimates for Chinook, there was between two and five times more alewife biomass than Chinook biomass in 2001-2004. Chinook biomass declined 30% from 2003 to 2004, and 2003 was the first year in which the ratio of alewife to Chinook biomass was <5.

Mechanisms regulating recruitment of pelagic prey species in the Great Lakes are varied and may be biotic or abiotic, extrinsic or intrinsic (Lantry 2000; Hoff 2004; Madenjian et al. 2005; Bunnell et al. 2006). For some species like alewife, we can predict recruitment relatively well (Madenjian et al. 2005); for other species, we can't. Acoustic surveys in 2004 and 2005 have provided YOY and YAO prey biomass density estimates with a low level of associated uncertainty for most species/ages (Table 3). In addition to providing abundance estimates, the recent surveys have provided information on fish distribution that was not previously available. We have observed evidence of spatial segregation of species and age groups within species that are likely to lead to differences in spatial overlap with prey, predators, and competitors. Acoustic surveys are uniquely suited to the study of these differences. Additional sampling in the future can improve our understanding of the factors contributing to high YOY abundance for a number of species. We have demonstrated this possibility by showing that YOY alewife density is correlated with surface water temperature.

There are currently 10 years of fall acoustic data available for Lake Michigan. Recent total biomass estimates are very different from those in the 1990s. Furthermore, the 1990s acoustic biomass estimates were on average 5.5x greater than the bottom trawl estimates, while acoustic estimates from 2001-2005 are 0.88 times bottom trawl estimates (D Warner, unpublished data). It is unclear why these differences exist. It is possible that there were density-dependent behaviors that reduced availability of fish to the bottom trawl in the 1990s. However, Fabrizio et al. (1997) found that acoustic sampling provided lower biomass estimates than bottom trawling for bloater, which made up the majority of lakewide pelagic biomass in the 1992-1996 period. Because of this uncertainty it is important to continue concurrent bottom trawl and acoustic sampling in the future.

Table 3. Biomass density, RSE, and 95% CI for biomass density of YOY, YAO, total alewife, rainbow smelt, and bloater estimated from acoustic and midwater trawl data collected in Lake Michigan in 2005.

Species	Biomass density (kg/ha)	RSE (%)	95% CI
YOY alewife	3.2	11	(2.6, 3.9)
YAO alewife	3.6	16	(2.7, 4.7)
alewife	6.9	8	(5.9, 7.8)
rainbow smelt	5.8	19	(4.0, 7.7)
YOY bloater	0.33	11	(0.26, 0.39)
bloater	0.87	23	(0.5, 1.2)
total	14.1	12	(11.3, 16.9)

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