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Status of Pelagic Prey Fish in Lake Michigan, 2001-2004

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ABSTRACT

Acoustic surveys were conducted in the fall during the years 2001-2004 to estimate prey fish biomass in Lake Michigan. Surveys conducted in 2001-2003 were limited in coverage, but regions included in the 2004 lakewide survey represented ~94% of the lake area. Midwater trawling during the surveys provided measures of species and size composition of the fish community for use in scaling acoustic data and providing species-specific abundance estimates. Alewives (*Alosa pseudoharengus*) were the largest proportion of the catch in all years but 2003. No trends were observed in the proportion (by weight) of any species in the trawl catch, but acoustic estimates of total biomass and alewife biomass exhibited a decreasing trend across years. The decrease in total biomass was driven primarily by a decline in alewife biomass. Alewife biomass and variance estimates from the acoustic surveys were similar to estimates derived from the USGS fall bottom trawl survey. The decline in alewife biomass over time was of similar magnitude for both the acoustic and bottom trawl surveys, suggesting that the decrease in the acoustic estimates of biomass was not an artifact of the limited spatial coverage in 2001-2003. Two alewife year classes (2002 and 2003) made up a large portion of the midwater catch of yearling-and-older alewives at age one. Even though the highest young-of-the-year alewife biomass occurred in 2002, only the 2003 year class made up a significant portion of the total catch beyond age 0, suggesting the 2003 year class may dominate the alewife population for the next several years. The 95% confidence interval for lakewide biomass of alewives in 2004 was 18-32 kt, with a mean of 25 kt.

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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 by GLSC 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*) and rainbow smelt (*Osmerus mordax*). 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. 2005a), the initiation of a lakewide fall acoustic prey fish survey was critical. The cooperative survey of Lake Michigan was initiated in 2001 and the survey was first completed according to protocol in 2003. Surveys were conducted in 2001-2004, with 2004 representing an expanded effort and the most extensive coverage to date. This report is focused on results of the acoustic surveys of Lake Michigan prey fish conducted in 2001-2004. This effort has been a joint venture between USGS, MDNR, IDNR, INHS, and WDNR and was based on guidelines and recommendations outlined in Argyle et al. (1998).

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 employed in 2004, which included two additional strata (north and

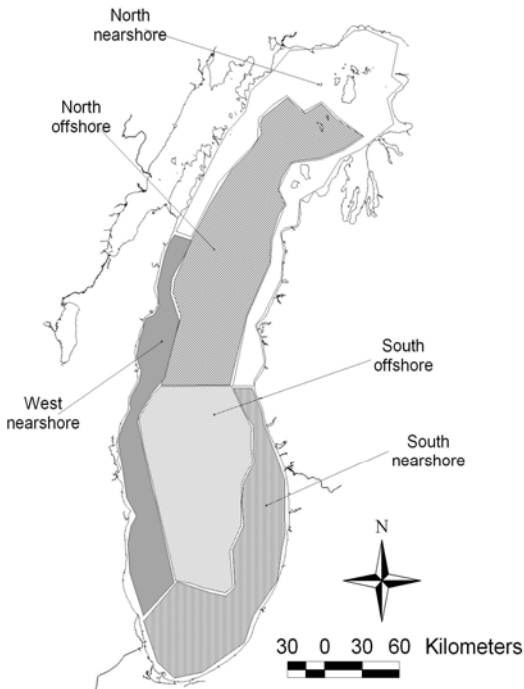


Figure 1. Map of Lake Michigan showing strata used in design and analysis of the lakewide acoustic survey conducted in 2004.

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 also differed in that they were evenly spaced parallel transects as recommended for open seas by Simmonds et al. (1992).

Data Collection and Processing

Acoustic data were collected with Biosonics dual (MDNR) and split beam (USGS) 120 kHz echosounders. The dual beam transducer (6.6 x 20° half-power beam widths) was housed in the sea chest of the S/V Steelhead, with sound energy transmitted through a rubber-compound window. This window has little effect on beam transmission or receive-sensitivity at the frequency used for this survey (Fleischer et al. 2002). The split beam transducer (6.8° half-power beam width) was deployed on a

towfish suspended abeam ship from a crane and towed at a depth of ~ 1 m on the R/V Kiyi and Sturgeon (2003 and 2004). In 2001-2002 the towfish was suspended from a davit or cleat (S/V Sculpin and S/V Barney Devine). With the exception of the dual beam unit in 2001, both 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 (33 mm diameter) with theoretical target strength (TS) of -40.6 dB. 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.

Acoustic analyses 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 a transect, with locations typically chosen as fishing sites when there was uncertainty about the composition of fish aggregations observed acoustically. All but three of the tows made were at a fixed depth. Three tows were made in a

stepped-oblique fashion in 2004. These tows were treated as two tows with identical catch but different fishing depths. A trawl with a 5 m headrope and 6.35 mm bar mesh cod end was fished from the S/V Steelhead, while on the USGS vessels (R/V Siscowet, R/V Kiyi and R/V Sturgeon) a trawl with a 15 m headrope and 6.35 mm cod end was used. Trawl depth was monitored using warp length and trigonometry (S/V Steelhead) or a net monitoring system (USGS).

Fish processing varied among vessels and years. 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 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 young-of-the-year (YOY) and yearling-and-older (YAO) groups using a cutoff length (minimum length of age 1 alewives – two standard deviations) in each year. This length was determined from fish caught in the USGS bottom trawl survey and aged using otoliths. 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 (Table 1).

Catch and acoustic data were assigned to one of three depth layers (<20 m, 20-50m, and >50 m). These layers were loosely based on thermocline depth and fish distribution. Trawls were assigned to these layers based on fishing depth. Trawl data were geographically linked with acoustic

transect data by assigning catch composition and sizes from each tow to the corresponding transect and depth layer. In the case of stepped oblique tows, the tow was treated as two separate tows with identical catch composition and mean fishing depth equal to the mean headrope depth of each step. Catch composition, mean length, and mean mass were calculated for each layer of each 500 m transect segment from trawling conducted on that transect. When this was not possible, the mean from the respective depth layers in the stratum in which the transect was located was used. 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 some estimate of species composition for this area, the mean of catch proportions in this stratum during 2002-2004 were used. Mean mass of fish for this stratum was taken from data collected in the north stratum by MDNR in 2001. 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 mean of data from this layer was calculated from tows made by USGS in 2002-2003.

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

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

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

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

$$(1) \text{ Absolute density (fish} \cdot \text{ha}^{-1}) = 10^4 \times \frac{ABC}{\sigma}$$

where ABC = area backscattering coefficient ($\text{m}^2 \cdot \text{m}^2$) 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 invertebrates such as *Mysis relicta*, as aggregations of *Mysis* have TS similar to individual young-of-year (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 absolute 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 (-62 to -54 dB) published by Rudstam et al. (2003).

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. Total alewife density was subdivided into YOY and YAO density by multiplying total alewife density by the numeric proportions of alewives in each age group. Biomass (kg/ha) for the different

groups was then estimated as the product of density and mean species or age-specific mean mass as determined from trawling. Mean and relative standard error ($\text{RSE} = (\text{SE}/\text{mean}) \times 100$) 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 (corresponding to a 500 m transect segment) 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. The methods presented here differed from those employed in 2003 (Warner 2004) and were expected to give results for the 2003 survey that were different but more accurate than previously presented by better accounting for spatial variability. To examine distribution of total fish biomass, YOY alewife biomass, and YAO alewife biomass, strata estimates were compared within years using ANOVA and Tukey pairwise comparisons (when more than two strata were surveyed). These calculations were made using transect means as the elementary sampling unit within each region.

RESULTS

Abundance, biomass, and age

Alewife – Alewives were the dominant species observed in midwater tows, representing between 48 and 90% (mean = 64.3%, relative standard error, RSE

=6.0%) of the catch by weight with no apparent trend during 2001-2004. Alewives were most common (90% by weight, RSE=24%) in the catch in 2002, with some alewives present in all tows with non-zero catch. Alewives were least common (48% by weight, RSE=78%) in the catch in 2003. Acoustic estimates of density of alewives varied between 1,069 fish/ha (RSE = 13.0%) in 2003 and 2,722 fish/ha (RSE=21.4%) in 2002 (Figure 2). Relative biomass of alewives varied between 5.1 kg/ha (RSE = 16.4%) in 2004 and 16.8 kg/ha (RSE =25.8%) in 2002 (Figure 2). Density of YOY alewives ranged from 587 fish/ha (RSE = 35.0%) in 2003 to 2,133 fish/ha (RSE = 21.5%) in 2002. Biomass of YOY alewives ranged from 0.5 kg/ha (RSE = 38.6%) in 2001 to 4.6 kg/ha in (RSE = 29.0%) in 2002. The high RSE in 2003 was likely the result of a large-scale distribution pattern caused by an upwelling along the western shoreline.

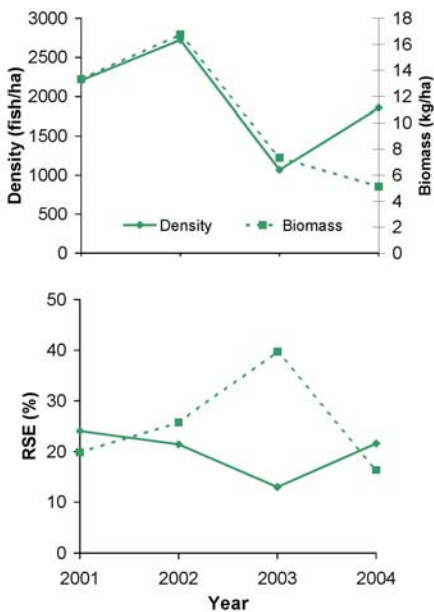


Figure 2. Acoustic estimates of density and biomass of alewives in Lake Michigan in fall 2001-2004 (upper panel) shown with relative standard error of the estimates (RSE, lower panel).

The length composition of alewives caught was indicative of uneven representation of age classes in the catch. In all years YOY alewives made up 38% or more of the catch by number, with much higher representation of YOY in 2001-2003 (77-91% of total alewife catch) compared to 2004 (38%, Figure 3). Only two year-classes made up at least 10% of the total alewife catch (numerically) in more than one year, and only one of these (2003) was hatched during the years 2001-2004. The 1998 year-class was present through 2004, making up ~20% of the catch at age three in 2001, and ~10% at age four in 2002. Examination of the age-length composition of YAO alewives (Figure 4) revealed that both the 2002 and 2003 year classes were a large component of the YAO catch and may represent year classes that will dominate the alewife population for the next 3-4 years. However, only the 2003 year class was a significant portion of total catch (45%) after age 0.

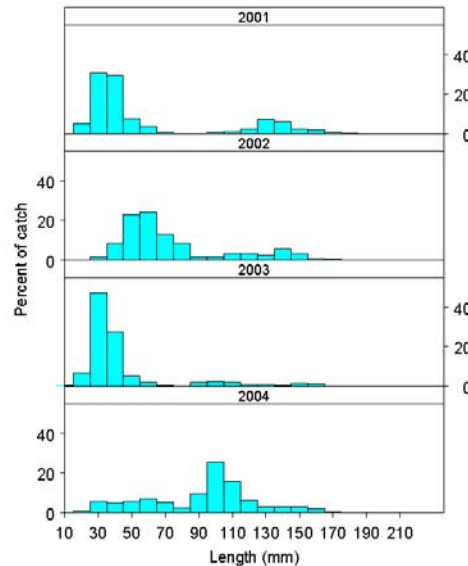


Figure 3. Length-frequency distribution of alewives caught with midwater trawls during Lake Michigan acoustic surveys in 2001-2004.

Rainbow smelt – Rainbow smelt were the second most dominant species in the midwater catch during 2001-2004 and

represented between 5 and 25% (mean =20.7%, RSE =14.9%) of the catch by weight. The proportion of rainbow smelt in the catch did not exhibit any trend in 2001-2004, nor did density and biomass. Density of rainbow smelt varied between 157 fish/ha (RSE =28.1%) in 2002 and 831 fish/ha (RSE = 22.7 %) in 2001 (Figure 5). Relative biomass of rainbow smelt was lowest in 2004 (1.2 kg/ha, RSE=46.0%) and highest in 2003 (4.6 kg/ha, RSE=61.7%).

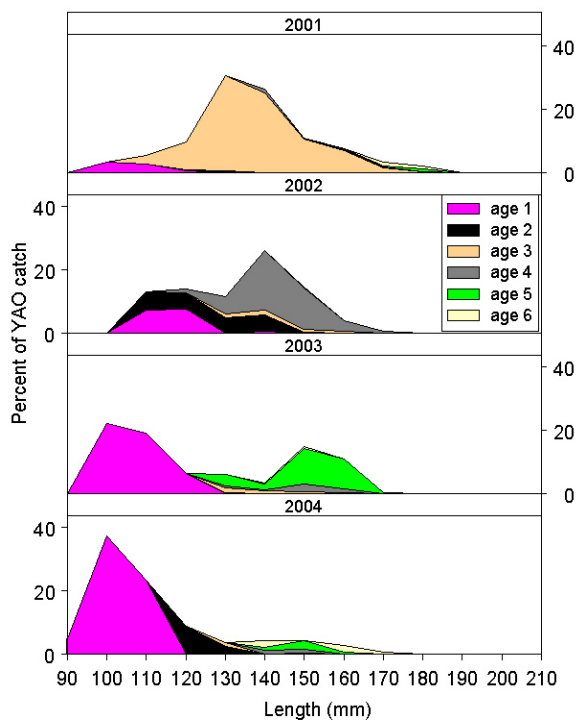


Figure 4. Age-length composition of YAO alewives captured in Lake Michigan with midwater trawls during acoustic surveys conducted in 2001-2004.

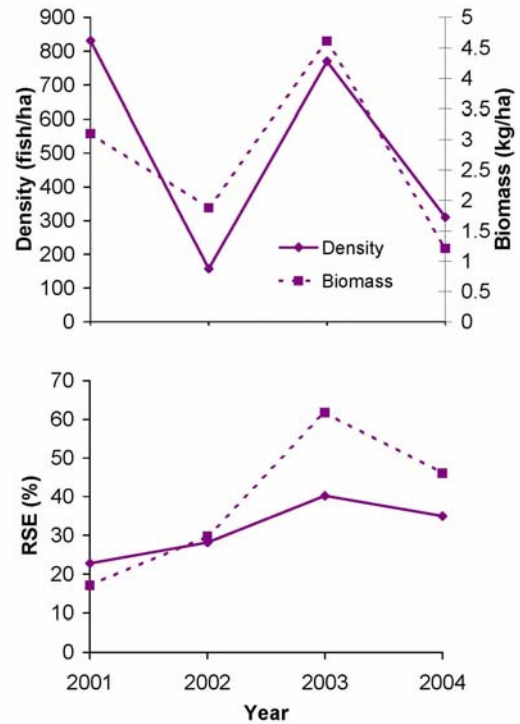


Figure 5. Acoustic estimates of density and biomass of rainbow smelt in Lake Michigan in fall 2001-2004 (upper panel) shown with relative standard error of the estimates (RSE, lower panel).

Bloater – Bloater (*Coregonus hoyi*) were the third most common species caught, comprising between 3.1 and 21.8% of the midwater catch by weight (mean =9.6%, RSE=27.1%). Of alewives, rainbow smelt, and bloaters, the proportion of bloaters in the catch was the most variable. It is unclear whether this is a result of patchy distribution or inconsistency in the efficiency of the trawls. Density of bloaters varied between 7 fish/ha (RSE = 59.9%) in 2002 and 182 fish/ha (RSE =33.5%, Figure 6) in 2001. Relative biomass of bloaters ranged from 0.69 kg/ha (RSE = 59.9%) in 2002 to 4.6 kg/ha (RSE = 18.8%) in 2003.

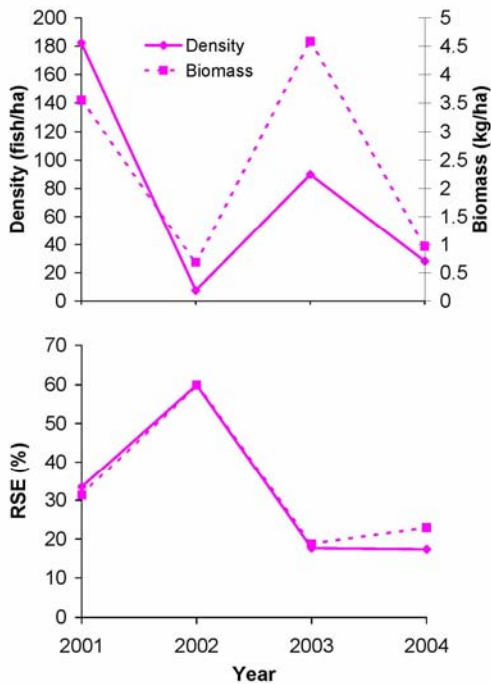


Figure 6. Acoustic estimates of relative density and biomass of bloaters in Lake Michigan in fall 2001-2004 (upper panel) shown with relative standard error of the estimates (RSE, lower panel).

Distribution

Alewife distribution was patchy (Figure 7), but there also appeared to be large-scale (regional) differences in abundance during surveys. In 2004 there was significant variation in total biomass, YOY alewife biomass, and YAO biomass among regions ($P < 0.05$). In 2004, total fish biomass was significantly higher in the north nearshore region compared to the north offshore and south offshore regions ($P < 0.05$). Biomass of YOY alewives was highest in the south offshore region and was significantly higher in this region compared to the north nearshore region (Tukey pairwise comparison, $P < 0.05$). Furthermore, YAO alewife biomass was significantly higher in the north nearshore region compared to the south offshore region (Tukey pairwise

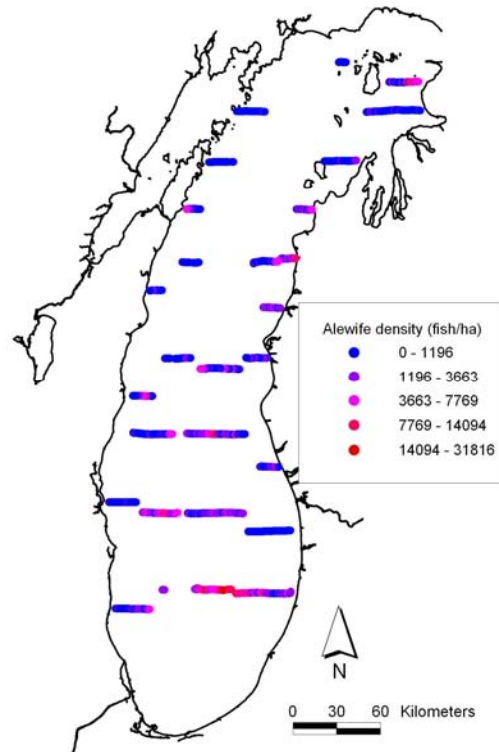


Figure 7. Map of Lake Michigan showing alewife density along acoustic transects in 2004. Each symbol represents a 500 m horizontal segment of the water column.

comparison, $P < 0.05$). The region with the highest biomass of YOY alewives (south offshore) had the lowest biomass of YAO alewives, and the region with the highest biomass of YAO alewives (north nearshore) had the second lowest biomass of YOY alewives. Significant variation in total biomass and YOY alewife biomass among regions was not observed in 2001-2003. However, in 2003 significant regional variation in YAO alewife biomass was observed; the highest biomass occurred in the south nearshore region, and it was significantly higher in this region than in the west nearshore region.

CONCLUSIONS

The four years of acoustic abundance data presented here indicate that there has been a relatively large decrease in pelagic fish biomass (Figure 8) and in alewife biomass.

This conclusion assumes that differences in biomass were not the result of differences in distribution of fish, as only part of the lake was surveyed in 2001-2003. Mean biomass in both the north and west nearshore regions was lower in 2004 than in 2001, and biomass in the south nearshore region (sampled only in 2003-2004) was lower in 2004 than in 2003 (Figure 9), suggesting biomass has decreased in multiple areas of the lake. Furthermore, the decrease in the south nearshore mirrored that in the west nearshore. A similar pattern was observed for alewife biomass. Given a decreasing trend in alewife biomass observed in the USGS bottom trawl survey, it is reasonable to assume that even if there has been a large-scale re-distribution of fish, there has also been a large-scale decrease in total forage fish and alewife biomass. This decrease in total biomass was in large part driven by a decrease in abundance of the 1998 alewife year class.

To provide some idea of the effect of increased spatial coverage on patterns in alewife biomass estimates, the survey data from were analyzed including all regions surveyed and with only the north and west nearshore regions. This resulted in four years of data with two strata, two with three strata (2003-2004), and one year (2004) with lakewide coverage (Figure 10). In 2003 and 2004, inclusion of additional portions of the lake resulted in lower mean biomass/ha but also resulted in lower RSE. This indicated that expansion of the data from the two regions surveyed in 2001-2003 to a lakewide absolute biomass estimate was not appropriate because addition of other regions within a given year resulted in different mean densities. However, trends remained relatively similar regardless of which areas were included in mean relative biomass estimates. If accurate lakewide biomass estimates are required

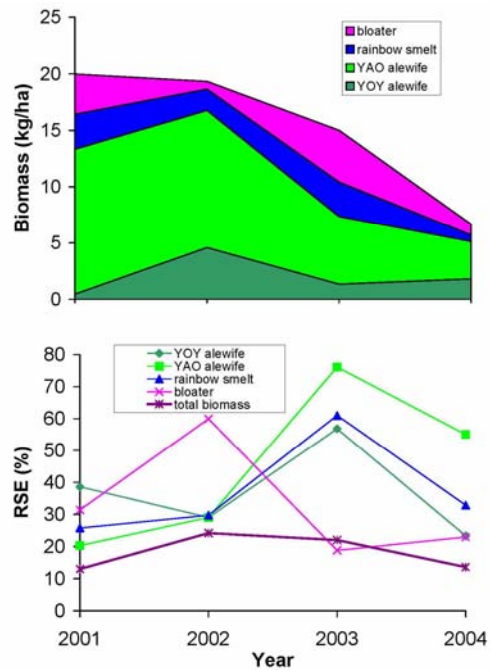


Figure 8. Acoustic estimates of relative biomass of YOY alewives, YAO alewives, rainbow smelt, and bloater in Lake Michigan, 2001-2004 (upper panel) shown with RSE of the estimates (lower panel).

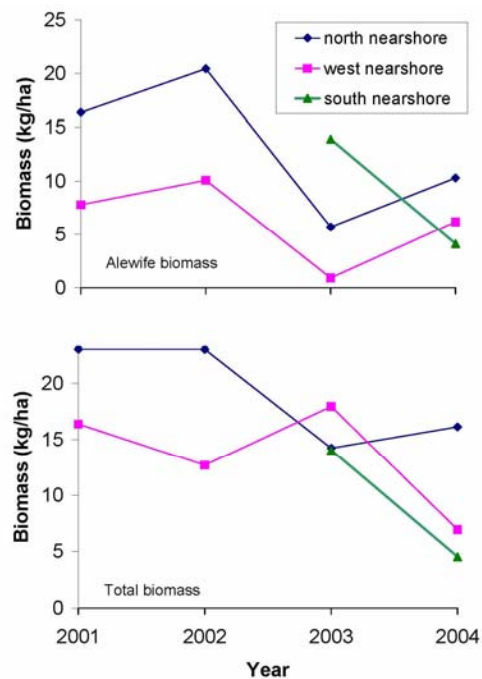


Figure 9. Annual mean relative alewife and total biomass in different regions of Lake Michigan in fall 2001-2004.

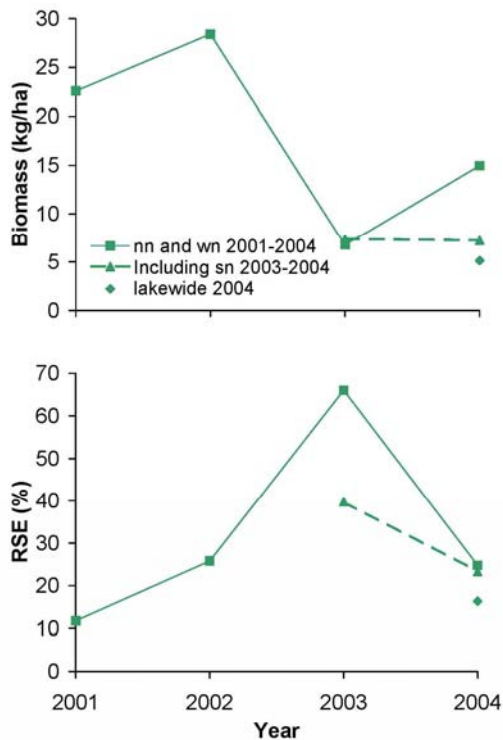


Figure 10. Comparison of mean relative alewife biomass (upper panel) estimated from only north and west nearshore data in 2001-2004 with estimates that included the south nearshore region (2003-2004) and all surveyed regions (2004). Relative standard errors of the estimates are shown as well (lower panel).

to accurately describe more than trends, it will be necessary to conduct the surveys on a lakewide scale (as in 2004). Unlike previous surveys, the survey design implemented in 2004 provided an estimate of lakewide alewife biomass in Lake Michigan, but this estimate only applies to the area ~5 m below the surface to ~1 m above bottom and is subject to a number of assumptions. Given the variable distribution of alewife in Lake Michigan, forage fish surveys that exclude sampling in large areas will not provide accurate estimates of absolute alewife biomass. The area surveyed in 2004 (~94% of the main basin) was more than twice the area surveyed in previous

years and provided a more accurate estimate of lakewide biomass of alewife (25 kt, 95% CI = 18-32 kt) with a high degree of associated certainty (Table 2).

Table 2. Relative biomass, RSE, and 95% CI for biomass for YOY, YAO, total alewife, rainbow smelt, and bloater estimated from acoustic and midwater trawl data collected in Lake Michigan in 2004.

Species	Biomass (kg/ha)	RSE (%)	95% CI
YOY alewife	1.8	23	(0.9, 2.7)
YAO alewife	3.1	24	(1.7, 4.9)
alewife	5.1	16	(3.4, 6.9)
rainbow smelt	0.58	33	(0.2, 1.0)
bloater	0.97	23	(0.5, 1.4)

Interpretation of the data presented here in the context of predator-prey relations or relative to other biomass indices was complicated by the limited spatial scale of the survey in some years. As a result, the biomass estimates for years in which the survey covered only part of the lake are best considered as relative indices of forage fish abundance for the entire lake. Comparison of the acoustic biomass indices and their associated RSE with data from the USGS bottom trawl survey (Madenjian et al. 2005b) indicated that not only did similar patterns occur in biomass estimates from both surveys, patterns in variability (RSE) were similar as well (Figure 11). Adult alewife estimates from the bottom trawl survey ranged from 3.9 to 17.4 kg/ha, while acoustic estimates ranged from 3.3 to 12.8 kg/ha. The two surveys differ drastically in the estimates of YOY alewife biomass, with bottom trawl estimates of YOY alewife biomass ranging from 0.007 to 0.5 kg/ha while acoustic estimates ranged from 0.5 to 4.6 kg/ha. Given the similarities in biomass magnitude and trend observed in the two

surveys, it is reasonable to conclude that alewife and total preyfish biomass have declined since 2001. Furthermore, both surveys indicate this decline was likely caused by decreasing abundance of the 1998 year class. Although acoustic surveys indicate there was relatively good survival of the 2003 alewife year class, abundance of this year class was low relative to the 1998 year class.

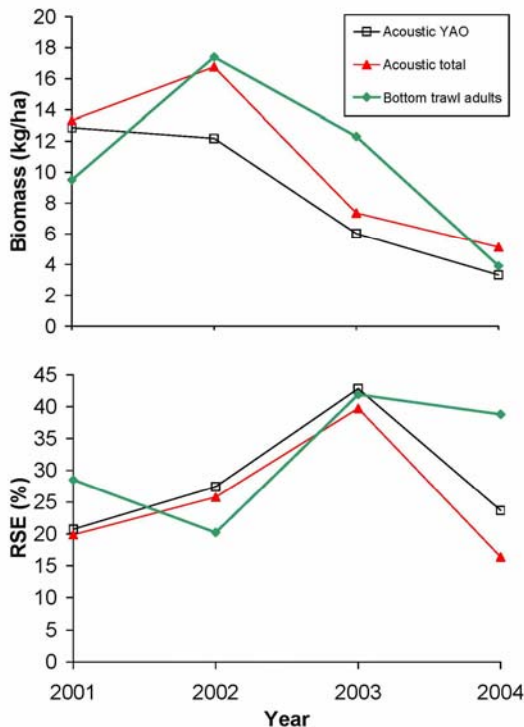


Figure 11. Comparison of bottom trawl estimates of relative biomass of adult alewives in Lake Michigan in 2001-2004 with acoustic estimates of YAO and total alewife biomass (upper panel). Relative standard errors of the estimates are shown as well (lower panel).

REFERENCES

Argyle, R. L. 1982. Alewives and rainbow smelt in Lake Huron: midwater and bottom aggregations and estimates of standing stocks. *Transactions of the American Fisheries Society* 111: 267-285.

Argyle, R. L. 1992. Acoustics as a tool for the assessment of Great Lakes forage fishes. *Fisheries Research* 14: 179-196.

Argyle, R. L., G. W. Fleischer, G. L. Curtis, J. A. 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 Resource Division, Great Lakes Science Center, 1451 Green Road, Ann Arbor, MI USA.

Connors, M. E., and S. J. Schwager. 2002. The use of adaptive cluster sampling for hydroacoustic surveys. *ICES Journal of Marine Science* 59: 1314-1325

Fabrizio, M. C., J. V. Adams, and G. L. Curtis. 1997. Assessing prey fish populations in Lake Michigan: comparison of simultaneous acoustic-midwater trawling with bottom trawling. *Fish Research* 33: 37-54.

Fleischer, G. W., R. L. Argyle, R. T. Nester, and J. J. Dawson. 2002. Evaluation of a rubber-compound diaphragm for acoustic fisheries surveys: Effects on dual-beam signal intensity and beam patterns. *Journal of Sound and Vibration* 258: 763-772.

Fleischer, G. W., J. Dettmers, and R. M. Claramunt. 2001. Original Acoustics LWAP Adopted by the Lake Michigan Technical Committee at the Summer 2001 Meeting in Sturgeon Bay, Wisconsin.

Foote, K. G., H. P. Knudsen, G. Vestnes, D. N. MacLennan, and E. J. Simmonds. 1987. Calibration of acoustic instruments for fish density estimation. 1987. International Council for the Exploration of the Sea Cooperative Research Report number 144.

MacLennan, D.N., and E. J. Simmonds. 1992. Fisheries Acoustics. Chapman and Hall. London.

Madenjian, C. P., T. O. Hook, 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. *Transactions of the American Fisheries Society* 134: 218-230.

Madenjian, C. P., T. J. DeSorcie, and J. D. Holuszko. 2005b. Status and trends of prey fish populations in Lake Michigan, 2004. A report to the Great Lakes Fishery Commission, Lake Michigan Committee, Ypsilanti, MI March 24 2004.

Madenjian, C. P., and 14 coauthors. 2002. Dynamics of the Lake Michigan food web, 1970-2000. *Canadian Journal of Fisheries and Aquatic Sciences*. 59: 736-753.

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. *Transactions of the American Fisheries Society* 127: 236-252.

Rivoirard, J., J. Simmonds, K. G. Foote, P. Fernandes, and N. Bez. 2000. Geostatistics for Estimating Fish Abundance, Blackwell Science. Oxford.

Rudstam, L. G., S. L. Parker, D. W. Einhouse, L. Witzel, D. M. Warner, J. Stritzel, D. L. Parrish, and P. Sullivan. 2003. Application of in situ target strength to abundance estimations in lakes- examples from rainbow smelt surveys in Lakes Erie

and Champlain. *ICES Journal of Marine Science* 60: 500-507.

SAS Institute Inc. 2004. SAS OnlineDoc®9.1.2. Cary, NC: SAS Institute Inc.

Simmonds, E. J., N. J. Williamson, F. Gerlotto, and A. Aglen. 1992. Acoustic survey design and analysis procedure: a comprehensive review of current practice. ICES Cooperative Research Report # 187. Copenhagen

Stewart, D. J., and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978-1988. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 909-922.

Warner, D.M. 2004. Status of Pelagic Prey Fish in Lake Michigan, 2003. A report to the Great Lakes Fishery Commission, Lake Michigan Committee, Ypsilanti, MI March 24 2004.

Warner, D. M., L. G. Rudstam, and R. A. Klumb. 2002. In situ target strength of alewives in freshwater. *Transactions of the American Fisheries Society* 131: 212-223.

Williamson, N. J. 1982. Cluster sampling estimation of the variance of abundance estimates derived from quantitative echo sounder surveys. *Canadian Journal of Fisheries and Aquatic Sciences* 39: 228-231.