Acoustic measures of the relationship between winter severity and overwinter mortality of alewives

David Warner[1]
Mark Cornwell[2]

ABSTRACT

Freshwater alewives have been shown to be quite sensitive to cold water, and evidence exists to suggest that entire year classes have died in severe winters. Although a number of factors influence alewife survival rates, it is likely that overwinter mortality is substantial in most years. In spite of the apparent importance of overwinter mortality, estimates of overwinter mortality rates for this species do not exist. In this study, acoustic methods were used to estimate overwinter mortality of alewives in a lake dominated by this species by comparing abundances in fall and the subsequent spring in five years. Overwinter mortality rates were quite variable, with daily instantaneous rates between 0.0022-0.0079, corresponding to percent mortality between 38-83%. These mortality estimates were similar in magnitude to annual estimates for adult alewives in Lake Michigan during the 1960s. Daily instantaneous mortality rates presented here were also similar to daily instantaneous rates of juvenile Pacific herring. Daily instantaneous mortality during winter was positively correlated with an index of winter severity (cumulative freezing degree days), but was not related to mean length in fall, nor to summer water temperature. Because abundance data from fall and subsequent spring acoustic surveys presented here were separated by nearly half a year, we suggest that overwinter mortality is a significant portion of annual natural mortality even under mild winter conditions.

INTRODUCTION

Alewives (*Alosa pseudoharengus*) are an important introduced prey species in many U.S. lakes including New York State's Finger Lakes and Lakes Ontario, Michigan, and Huron. Alewives have proven to be the predominant prey item of introduced salmonids and lake trout (*Salvelinus namaycush*) (Stewart and Ibarra 1991; Madenjian 1998). Although this result is consistent with the intentions behind the stocking of non-native salmonids, the variability in alewife abundance has resulted in a salmonid management situation dependent on the unpredictable alewife stocks.

---

[1] Corresponding author. U.S.G.S Great Lakes Science Center, 1451 Green Road, Ann Arbor M.I. 48105. dmwarner@usgs.gov.

[2] State University of New York at Oneonta Biological Field Station, 5838 State Highway 80, Cooperstown, N.Y. 13326.

A variety of mechanisms are believed to exert some control on alewife abundance, including predation, water temperature, and intraspecific competition. Several authors have proposed that low water temperatures negatively affect alewife growth, survival, and abundance with the implication that winter conditions contribute significantly to mortality of alewives (Brown 1972; Colby 1973; Eck 1985; Bergstedt 1989). Other studies have suggested that summer water temperatures during the first year of life are as important or more important to recruitment processes than winter severity or length (Henderson and Brown 1985; Madenjian et al. submitted). Perhaps more realistically, O'Gorman et al. (in press) and Madenjian et al. (submitted) demonstrated with long-term data sets that both physical (thermal conditions) and biological (predation) processes influence alewife recruitment and survival in the Laurentian Great Lakes. However, one common factor in many studies of alewife dynamics has been the contribution of winter conditions to alewife mortality, and laboratory work has clearly demonstrated that low water temperatures negatively affect alewives (Colby 1973). In spite of this knowledge, there are no estimates of overwinter mortality rates for alewives in the literature. In this study we used fall and subsequent spring acoustic abundance to estimate daily instantaneous mortality during five winters between 1996 and 2003. The acoustic estimates were compared to annual estimates based on catch data. We also examined the relationship between thermal conditions and over-winter mortality. Acoustic methods for estimating fish abundance have been widely used in the Great Lakes and elsewhere since the early 1990s. Although acoustic survey data have previously been used to estimate mortality of juvenile Pacific herring (Stokesbury et al. 2002), this work is the first to use acoustics (or any other method) to estimate over-winter mortality of alewives in freshwater. This approach may prove to be a valuable tool for the study of prey fish dynamics in systems like the Great Lakes.

METHODS

Measures of climactic conditions included estimates of cumulative heating degree-days (hdd) between May and September of each year and cumulative freezing degree-days (fdd) between December and May. Water temperature was measured approximately fortnightly at 2 m intervals with a Hydrolab Scout II® or Surveyor 4®. Heating degree-days were estimated by subtracting 10º from mean water temperature in the top 20 m of the water column, plotting this difference versus day of year, and integrating the area under the curve. Freezing degree days were estimated from daily air temperature data recorded at a National Weather Service monitoring station located approximately 500 m from the west shore of the lake. Freezing degree-days were defined as the difference between mean temperature for each day and 0° C. For example, a mean daily temperature of -5° C was equivalent to 5 fdd. Days on which the mean temperature was above freezing received a score of zero fdd. The cumulative value was the summation of fdd observed between 1 December and 1 May of the subsequent year.

Otsego Lake is located in Otsego County, N.Y. and is a 1,700 ha dimictic lake with an average depth of 20 m and a maximum depth of 51 m (Harman et al. 2002). The prey fish community has been dominated by alewives since the early 1990s, which has been reflected in trawl and gill net catches that have been 90-95% alewives on average since the mid 1990s (Warner et al. 2002). Acoustic surveys of the entire lake (Figure 1) were conducted during late summer or fall in five years. Five additional surveys were conducted in each subsequent spring season. Surveys consisted of 8-10 parallel transects in an east-west direction. Mean density was likely not affected by the survey design and any differences in density reflected true changes in fish density (Rivoirard et al. 2000). Acoustic data were collected using either a 70 kHz Simrad EY500 split beam echosounder (0.2 or 0.6 ms pulse length, 11.1° half-power beam width) or a Biosonics DE6000 split beam echosounder (0.3 ms pulse length, 6.8° half-power beam width). Thresholds of –80 dB (echo integration) and –70 to –76 dB (single target detection) were employed to reduce scattering from any invertebrates that may have been present. The echosounders were calibrated just prior to the survey except for the September 1996 survey. Calibration of the sounder occurred approximately one month after the survey in this case. Calibrations indicated that the effect of the beam angle on a standard target was well described by the beam pattern function applied (typical maximum deviation of 0.6 dB after accounting for the beam pattern within the 6 dB compensation angle). Comparisons of data from the 70 and 120 kHz echosounders by Rudstam et al. (1999) indicated that results for both target strength (TS) and fish density were similar. Acoustic sampling was accompanied by fishing to estimate the length distributions, identify scatterers in the water column, and to obtain bony structures for age estimation. Monofilament gill nets effective at catching alewives between 50-200 mm with relatively even selectivity (Warner et al. 2002) were deployed prior to the surveys and retrieved after the surveys. Nets were constructed of bar mesh of 6.25, 8, 10, 12.5, 15, and 18.75 mm with one mesh size per panel. Vertical distribution of the catch from these nets was used as a correction factor to compensate water column density for the portion of the water column (upper 2 m) not sampled by the vertically oriented transducer. This correction factor was based on the assumption that the ratio of the catch in the top 2 m to the total catch was equivalent to the ratio of fish density in the top 2 m to the fish density in the depth range fished by the nets. If 30% of the catch was from the top 2 m, 0.3 times the acoustic density in the depth range of the nets was added to the density of the water column >2m. Catch data were also used to develop a length-age key and catch curve to estimate mortality. Paired sagittal otoliths were removed from alewives captured in October 2002. Otoliths pairs from 30 fish per year were used to estimate age, with most otoliths coming from the dominant size group in the catch.

Otoliths were examined using a dissecting microscope and reflected light. Age composition of the catch was determined using the length-age key to develop a catch curve, which represents the age composition of the catch with the difference between catch levels of subsequent ages representing the mortality between those two ages. The natural logarithm of the catch at age was plotted against age, and the slope of a linear regression line for these data was used as the annual mortality rate.

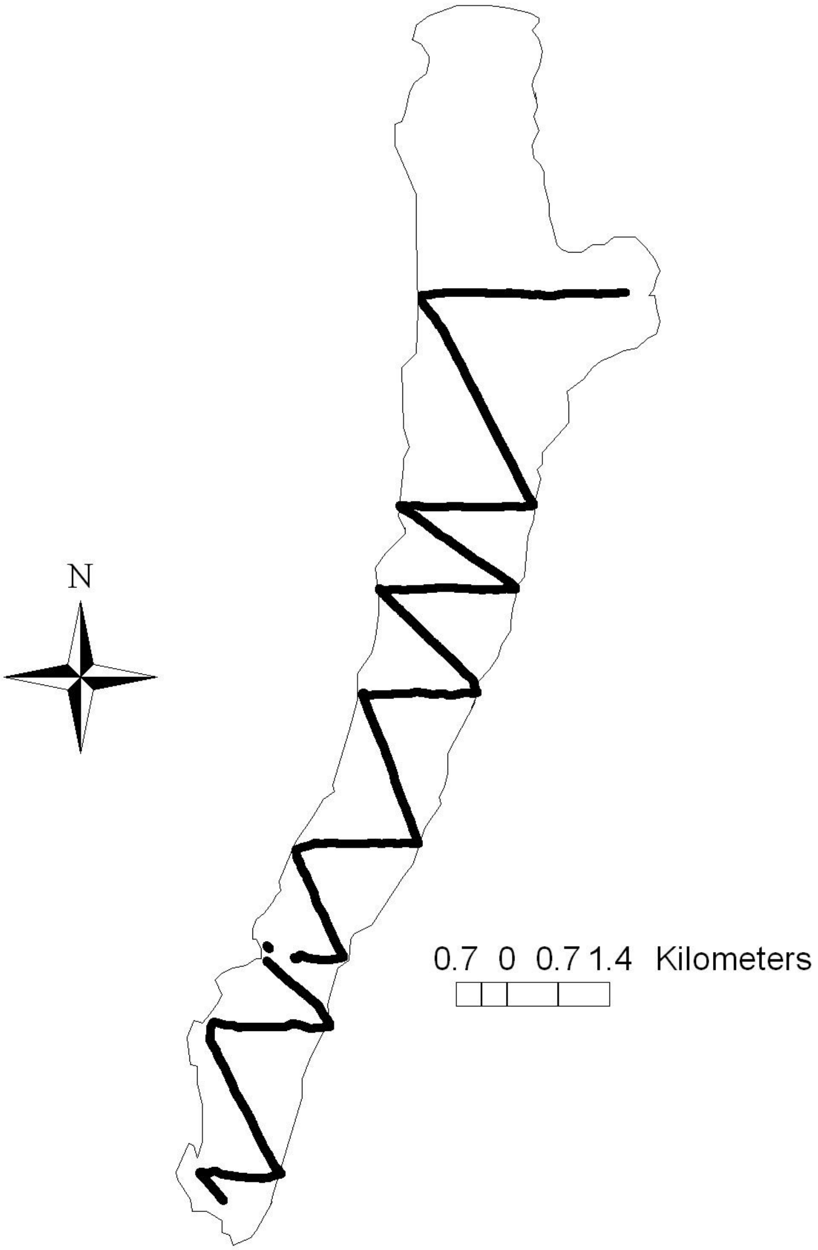

Figure 1. Acoustic survey track from Otsego Lake on 14 October 2002.

Acoustic data were analyzed with Echoview 3.0. Echo integration occurred over entire transects with an epilimnetic layer (2-12 m) and a hypolimnetic layer (12-50 m). Target strength (TS) frequency distributions based on accepted single targets (range –76 to –20 dB) were tabulated in 1-dB bins for each of these cells. For both 70 and 120 kHz data, single target acceptance criteria were set to accept targets with echo length between 0.8 and 1.8 times the pulse length with a phase deviation of 4 steps (Simrad 1996). Maximum beam compensation for accepted targets was 6 dB. Single targets were detected from 70 kHz data using the single target detection algorithm implemented by the EY500 (Simrad 1996), while 120 kHz data employed the Simrad (1996) algorithm implemented in Echoview 3.0. Absolute fish density was calculated for each cell using the formula

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

where ABC = area backscattering coefficient ($m^2 \cdot m^2$) and σ = mean backscattering area (m^2) calculated over the full TS range for each survey. Water column density for each transect was the sum of densities in the epilimnetic and meta-hypolimnetic layers.

Absolute density represented the total density of all scatterers present during the survey and likely included some invertebrates and bubbles. Because there is a lower limit to acoustic size of alewives, these fish likely represented only a proportion of total scatterers. This proportion was estimated from the expected TS range of alewives present during each survey as predicted with an in situ TS-length equation based on fish from Otsego and several other lakes (Warner 2002). The TS range in fall was wider (-64 to –37 dB) than that in spring (-61 to –37 dB) because smaller alewives were present in fall and some fish may not have been fully recruited to the fishing gear (gill nets) because of size selectivity observed with these nets (Warner et al. 2002). One-way ANOVA was used to test for significant differences in logarithmically (base 10) transformed mean density between fall and subsequent spring surveys.

Daily instantaneous mortality for the period between late summer/fall surveys and subsequent spring surveys was estimated using observed mean lake-wide fish densities (fish $\cdot ha^{-1}$). Mortality estimates were made using the formula

$$-\frac{LN(N_{t+1}) - LN(N_t)}{t}$$

where $LN(N_{t+1})$= the natural logarithm of mean spring density, $LN(N_t)$= the natural logarithm of mean fall density, and t = the number of days between surveys (Quinn and Deriso 1999).

RESULTS

Climactic variables exhibited some degree of variability, but winter severity exhibited higher variability. The summer of 2002 had the highest level of cumulative heating degree days (hdd, Table 1). The lowest value for cumulative freezing degree days (hdd) occurred in the winter of 2001-2002, a year in which a large area of the lake remained ice-free all year (Figure 2). The highest value occurred in the winter of 2002-2003.

Alewife density was variable between fall and spring surveys and within seasons among years (Figure 3). Mean density in spring was significantly lower than in fall (ANOVA, $P<0.001$) in all years but one; mean density in spring 2002 was not significantly different from density in fall 2001 (ANOVA, $P>0.05$).

Acoustic estimates of daily instantaneous mortality (*Z*) also varied among years. The lowest acoustic value was observed in the winter of 2001-2002 ($Z = 0.0022$) and the highest value was observed in winter 2002-2003 ($Z = 0.0079$). These daily instantaneous mortality rates are equivalent to winter losses from the population of between 38 and 83% with a mean (±95% CI) of 62 ± 20%. If these daily rates were similar to rates throughout the remainder of the year, the annual percentage mortality for juvenile and adult alewives would have ranged from 56 to 94%, with a mean (±95% CI) of 75 ± 17 %.

Year	Hdd	Fdd	Z_d	$Z_{\%}$	Catch curve *Z*
1996-1997	339	416	0.0037	60	
1999-2000	302	553	0.0036	67	
2000-2001	274	599	0.0045	63	
2001-2002	322	269	0.0022	38	0.0016 (0-4)
2002-2003	363	773	0.0088	87	

Table 1. Cumulative heating degree days (Hdd, May-August), freezing degree days (Fdd, December-May), daily instantaneous overwinter mortality (Z_d), percent overwinter mortality ($Z_{\%}$), and daily instantaneous mortality from catch curve analysis from Otsego Lake and Otsego Lake alewives in the years shown. Values for hdd correspond to the summer of the first year shown in the pairs of years, fdd values correspond to the value for the winter ending in the second year of the pairs of years shown.

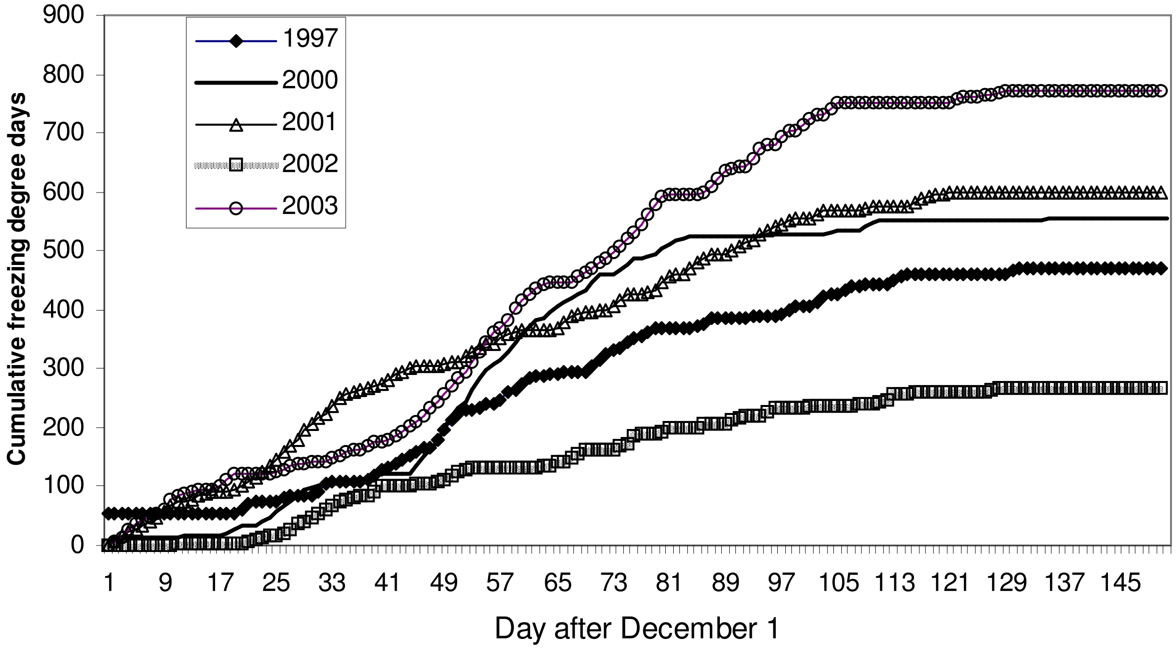

Figure 2. Cumulative freezing degree days versus day after December 1 as estimated from mean daily air temperature in the area of Otsego Lake, N.Y. in the years 1997, 2000-2003.

Daily instantaneous winter mortality rate was significantly positively correlated with cumulative freezing degree-days (r^2 =0.84, p =0.029, SE of estimate = 0.009, N =5, Figure 3). The catch curve estimate of daily instantaneous mortality for all age groups was from fish captured in August and October 2002, with the mortality estimate for yearling and older fish corresponding to the year from 2001 to 2002. The relationship between *LN*(catch) and age was significant (r^2 = 0.76, p = 0.001, N = 10). The slope (±95% CI) for the regression of *LN*(catch) vs. age was –0.59 (±0.26), corresponding to a daily instantaneous mortality rate of 0.0016.

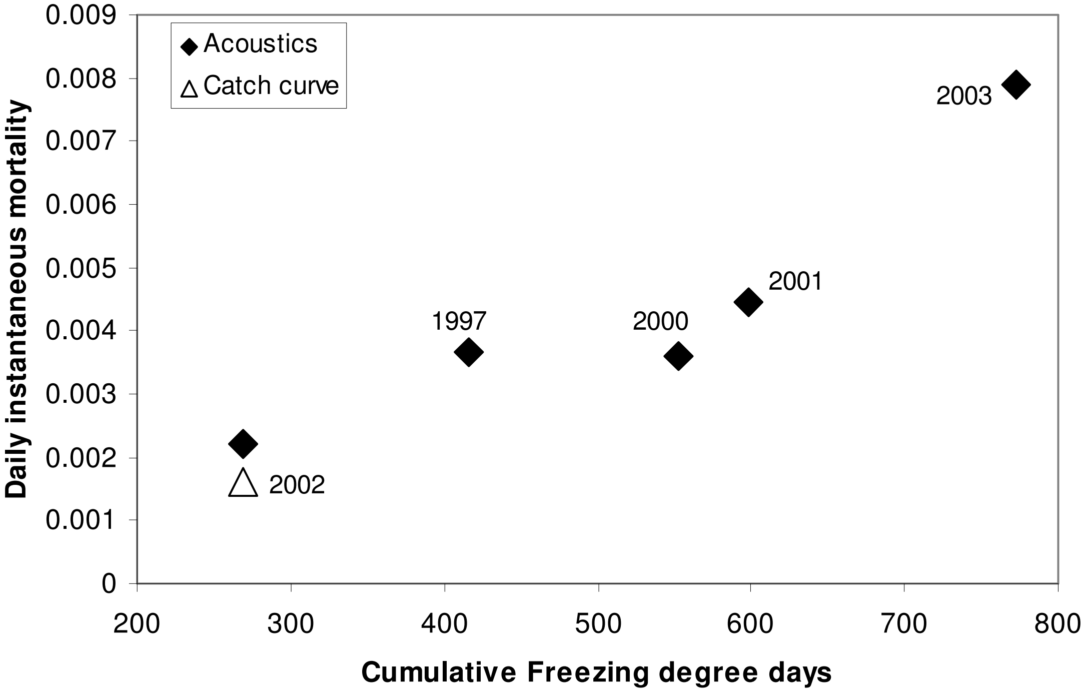

Figure 3. Relationship between cumulative overwinter instantaneous mortality rates and cumulative freezing degree days between December and May. Also shown is the estimate of daily instantaneous mortality from catch curve data for the year 2001-2002.

DISCUSSION

Hydroacoustic surveys offer a number of advantages over other methods used to assess pelagic prey fish populations and their vital rates. Acoustic gear allows sampling of a much larger volume of water, provides a much higher degree of spatial coverage, and may not be as severely influenced by size selectivity common to other gears. In this study we demonstrated that acoustic surveys in fall and winter provided an opportunity to examine one period (winter) of potentially high alewife mortality. We have shown that overwinter mortality in five winters was variable, and that a significant portion of this variability was explained by an index of winter severity. Furthermore, our results suggest that even in mild winters, a significant portion of annual mortality occurs during winter.

Although acoustic surveys offer some advantages over traditional sampling gears, as with other gears, there are inherent assumptions and sources of uncertainty/error that may be important. For this study, we had to assume that the acoustic targets were actually members of the population of interest (alewives). Strong evidence in support of this assumption was observed in this study and in a previous study (Warner et al. 2002); in both studies, alewives comprised 90-100% of the gill net catch. Further support exists from other gears (larval and midwater trawls, M. Cornwell, unpublished data). Second, we had to assume that our interpretation of alewife acoustic size and the target strength range assumed to be alewives were appropriate. Because we used an in situ TS-length equation (Warner et al. 2002) developed from data collected in this lake, we feel that our understanding of alewife acoustic size supported our choice of the TS range to include in the analyses. More recent research on the TS of caged alewives 7-15 cm total length indicates that the TS-length equation used to interpret acoustic data was appropriate, with ~99% of TS values >-61 dB (D. M. Warner, unpublished data). The acoustic size range of alewives <7 cm is less clear, but there are few organisms present in the lake that are likely to have TS values in the range included in our analyses, and it is likely that invertebrate targets (zooplankton or insect larvae) would have to have been detected in clumps to have TS within the range we included.

The literature on alewife population dynamics does not include estimates of overwinter mortality, and with the exception of work in O'Gorman et al. (in press), estimates of annual mortality are rare and dated. The magnitude of overwinter mortality rates observed in this study was similar to annual mortality rates of 40-89% of Lake Michigan alewives in the late 1960s (Brown 1972), and the daily instantaneous mortality estimates were similar to those of Pacific herring observed by Stokesbury et al. (2002). The acoustic mortality estimate for the winter of 2002 was similar to but higher than the catch curve estimate for the year from 2001-2002. This difference may have been caused by a number of factors, including the possibility that YOY alewives were not fully recruited to the gill nets but were detected acoustically. If these fish were not caught in representative numbers, their contribution to catch curve mortality estimates would be underestimated. Interestingly, the lowest overwinter instantaneous mortality rate occurred during a winter in which the lake did not freeze. During this winter, water temperatures were <2 degrees C°, the lowest during the study period. It may be that air temperature is not the most appropriate indicator of winter severity, and future efforts will include winter water temperatures, perhaps from the Cooperstown Village water intake.

REFERENCES

Bergstedt, R. A. and R. O'Gorman 1989. Distribution of alewives in southeastern Lake Ontario in autumn and winter: a clue to winter mortalities. Transactions of the American Fisheries Society 118: 687-692.

Brown, E. H. 1972. Population biology of alewives, *Alosa pseudoharengus*, in Lake Michigan, 1949-1970. Journal of the Fisheries Research Board of Canada **29**: 477-500.

Colby, P. J. 1973. Response of the alewives, *Alosa pseudoharengus*, to environmental change. Pages 163-199 *in* W. Chavin, editor. Responses of fish to environmental changes. Charles C. Thomas, Springfield, Illinois.

Eck, G. W., and E. H. Brown Jr. 1985.. Lake Michigan's capacity to support lake trout (*Salvelinus namaycush*) and other salmonines: an estimate based on the status of prey populations in the 1970s. Canadian Journal of Fisheries and Aquatic Sciences. 42: 449-454.

Harman, W. N., Albright, M. F., and D. M. Warner 2002. Trophic changes in Otsego Lake, NY following the introduction of the alewife (Alosa psuedoharengus). Lake and Reservoir Management 18(3): 215-226.

Madenjian, C. P., T. O. Hook, E. S. Rutherford, D. M. Mason, T. E. Croley II, E. B. Szalai, and J. R. Bence. 2004a. Recruitment variability of alewives in Lake Michigan. Transactions of the American Fisheries Society 133: in review.

O'Gorman, R., and B. F. Lantry. In press. Effect of Stock Size, Climate, Predation, and Trophic Status on Recruitment of Alewives in Lake Ontario, 1978-2000. Transactions of the American Fisheries Society.

Quinn, T. J. I., and R. B. Deriso 1999. *Quantitative Fish Dynamics*, Oxford University Press. New York.

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. Hansson, T. Lindem, and D. W. Einhouse. 1999. Comparison of target strength distributions and fish densities obtained with split and single beam echo sounders. Fisheries Research 898:1-8

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

Stokesbury, K. D. E., J. Kirsch, et al. 2002. Natural mortality estimates of juvenile Pacific herring (*Clupea pallasi*) in Prince William Sound, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 59(3): 416-423.

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.