Walleye as a management tool for controlling alewife populations: a study of Cayuta and Canadarago Lakes

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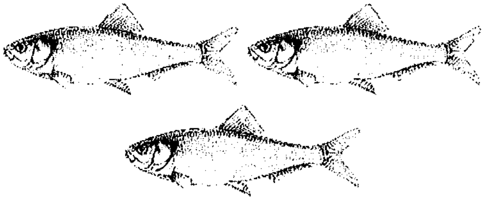

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Introduction

Alewife *Alosa pseudoharengus* is native to the North American Atlantic coast where it is either anadromous or forms landlocked populations. The species invaded upstate New York through the canal system in the second half of the 1800s (Smith 1985). When established, alewife populations are often abundant and represent a major prey fish for piscivores such as walleye *Sander vitreus*, black bass *Micropterus* spp. and salmonids (O'Gorman et al. 1987; Stewart and Ibarra 1991). Abundant alewife populations are also associated with often undesirable changes in lower trophic levels, such as declines of large zooplankton, increases in phytoplankton, and decreases in water clarity (Brooks and Dodson 1965; Wells 1970; Kohler and Ney 1981; Post et al. 2008). In New York State, large *Daphnia* and water clarity declined following the increase in alewife in Otsego Lake (Harman et al. 2002) and Onondaga Lake (Wang et al. 2010). Alewives can also affect fish community structure through predation on fish larvae (Brooking et al. 1998), by competing for zooplankton (Wells 1970), and by carrying high concentrations of thiaminase that break down the thiamine necessary for successful egg development in predators feeding on alewife (Fitzsimons et al. 1999). Alewives are therefore considered a risk to native fish populations in the Great Lakes basin (Madenjian et al. 2008).

Because both water clarity and recruitment of sport fish decline when alewives become established, there is an interest in developing management strategies for decreasing the abundance of land-locked alewife populations. Walleye can be effective predators on pelagic prey species (Forney 1977, Olson et al. 2001; Liao et al. 2004). Fingerling walleye have been introduced into several alewife lakes in New York with the objectives of establishing self-sustaining walleye populations and creating new fishing opportunities (Festa et al. 1987). If a sufficiently high walleye population can be built up through stocking, it may suppress an alewife population to levels that allow for survival of walleye fry – an example of predator "cultivation" of their prey resources (Walters and Kitchell 2001). Evaluation of the likelihood of success of such a strategy requires an understanding of the compensatory responses of the fish population being controlled.

Alewife populations may compensate for increased predation mortality by increased growth and condition, leading to higher fecundity, and decreased cannibalism. However, the degree to which alewife growth is density-dependent is not known, and Anderson and Neumann (2002) did not detect a density effect on growth of alewives when comparing a set of Connecticut lakes. Decreased abundance of adult alewives could also lead to decreased cannibalism and therefore increased survival of larvae, as observed in other fish species (Chevalier 1973; Parker-Stetter et al. 2007). Both the growth response and decreased cannibalism should result in alewife populations having a strong compensatory response to declining densities. Uncertainty related to the compensatory ability of alewives is a major gap in our understanding of the risks involved with various stocking levels of salmonids in the Great Lakes.

Given the limits to our understanding of both the response of alewife to increased predation mortality, and the ability to use walleye as a management tool for controlling alewife populations, New York State DEC funded two projects (Job 1-2 and 1-3 of the Federal Aid Project F-56-R) to study the alewife populations in Canadarago Lake (Job 1-2) and Cayuta Lake (Job 1-3). The goals of these two projects were to investigate the ecosystem and sportfish from increasing alewife populations, and the possibility of using walleye stocking as a management tool to control alewife in Cayuta Lake. To do this, we also needed to evaluate the use of hydroacoustics to measure alewife abundance in small lakes.

Study lakes and Methods.

Cayuta Lake is a shallow, eutrophic, 152 ha lake in central New York State (42°21.99 N, 76°44.10 W). The lake has a large littoral zone with dense submerged aquatic vegetation. The lake stratifies in the summer and oxygen depletion occurs below 4 m. Zebra mussels were first detected in the lake in 2005, but had not become abundant as of 2009, likely due to the limited hard substrate available in the lake. The dominant predators are walleye, largemouth bass *Micropterus salmoides* and chain pickerel *Esox niger*, with large populations of bluegill *Lepomis macrochirus*, pumpkinseed *Lepomis gibbosus*, and black crappie *Pomoxis nigromaculatus* present. Pond and fall fingerling walleye were stocked at a rate of 50 fish/ha in the lake from 1992 to 1996 for a total stocking of 76,000 fingerlings over 5 years (Olson et al. 2000). Between 2002 and 2006, NYSDEC stocked 350 walleye fall fingerlings/ha each year for a total stocking of 266,000 fish over 5 years. Walleyes were stocked from boats by NYSDEC Region 8 staff in open water outside the weed line in late August or early September, at an average size of 102-127 mm (depending on the year).

Canadarago Lake is a mesotrophic, 770 ha lake (42°49.05 N, 75°00.24 W) and one of the headwater lakes of the Susquehanna River. Stratification occurs each summer with a thermocline forming at 5-8 m, and the hypolimnion is generally anoxic for about 2 months. The lake supports a diverse fish community of at least 37 species. Walleye fingerling stocking in the 1980's established an abundant, self-sustaining walleye population and no additional stocking has occurred since then. Concomitant with increases in walleye abundance were decreases in walleye growth, increases in yellow perch growth, and decreases in yellow perch abundance. Predator populations are dominated by walleye, largemouth bass, smallmouth bass *Micropterus dolomieui*, and chain pickerel. Yellow perch, bluegill and pumpkinseed are the dominant forage species. Zebra mussels were first detected in 2002 and expanded rapidly to most hard bottom substrates in the lake. Canadarago Lake has been studied by New York DEC and Cornell University since the 1980s (Olson et al. 2001, Brooking et al. 2008).

In both lakes we used mark-recapture of walleye to estimate population size of age 3 and older fish, hydroacoustics to estimate abundance of alewife, age interpretation for growth rates, and diet analysis. We also conducted an angler diary program in Cayuta Lake. Details on the methods are in the two papers included with this report.

Results and Discussion

The results and discussion are presented in a publication (Brooking and Rudstam 2009, “Hydroacoustic target strength distributions of alewife in a net cage compared to field surveys: deciphering target strength distributions and effect on density estimates”. Trans.

"Analysis of compensatory responses in land-locked alewife: a tale of two lakes") that follow this introductory text. We refer the reader to those sections for details on methods and results, as well as a thorough discussion.

In the first paper, we improved on the acoustic techniques needed to assess alewife with downwards looking acoustics in inland lakes. We first established the expected target strength distribution of alewife using known length fish in a large net cage. This distribution was then used to identify which section of the target strength distribution could be considered alewife, and to develop a method for accounting for all alewife targets even when noise or invertebrates obscured part of the alewife target strength distribution. This work was necessary to allow us to measure alewife abundance in our lakes and to assess the response of alewife to the walleye management experiment in Cayuta Lake and to assess alewife population changes in Canadarago Lake.

In the second paper, we analyzed the data from Cayuta and Canadarago Lakes. Alewife have been present in Cayuta Lake since at least 1977 and the population ranged from 3,800 to 24,000 fish/ha from 1995 to 2009. Alewife were first observed in 1999 in Canadarago Lake and the population remained at low densities (<25 fish/ha) until reaching 370 fish/ha in 2006 and 1,000 fish/ha in 2009. Differences in lower trophic levels reflected higher planktivory rates in Cayuta than in Canadarago Lake. In Cayuta Lake, high stocking rates of fingerling walleye were maintained for five years (2002-2006) in an effort to build a walleye population that could decrease alewife abundance; however, density of adult walleye in Cayuta Lake (12-14 fish/ha) remained below the density in Canadarago Lake (21-24 fish/ha). Density explained 47 to 84% of the variation in alewife growth and condition (age 0- 2). Alewife in Canadarago Lake grew as fast as anadromous populations. Alewife recruitment (fall age0) was a non-linear function of spawner abundance (fall age 2 and older) and the number of recruit per spawner was higher in Canadarago Lake than in Cayuta Lake. Higher recruitment per spawner may be a response to higher egg production per individual when growth and condition increase, or decreased rates of cannibalism on larval alewife in Canadarago Lake.

The combined results from the two lakes allowed us to investigate the possible compensatory responses in land-locked alewife populations. The data was used to derive a Beverton-Holt stock-recruitment curve. This curve predicted that recruitment from alewife is at 50% its maximum already at densities as low as 400 adult spawners per ha. We did not detect a depressed recruitment rate at low densities. This indicates that alewife have strong compensatory responses to low density. An understanding of these responses is critical, not only for investigating the possibility of controlling alewife by stocking walleye, but also to understand the dynamics of newly invading alewife populations and to understand the risks to alewife populations of increased salmonid abundance in the Great Lakes associated with increased natural reproduction of Chinook salmon.

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[Article]

Hydroacoustic Target Strength Distributions of Alewives in a Net-Cage Compared with Field Surveys: Deciphering Target Strength Distributions and Effect on Density Estimates

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Abstract.—Acoustic estimation of fish abundance requires knowledge of the target strength (TS) distribution associated with the fish present. We measured the TS distribution at 70 kHz for five size-groups of alewives *Alosa pseudoharengus* (mean total length = 68–138 mm) swimming freely in a large net-cage. Although the mean and mode of the distributions were significantly related to fish length, the TS range obtained from each length-class was over 25 decibels (dB). The TS distributions were negatively skewed and had a tendency toward bimodality. The TS distributions at 70 and 123 kHz were similar for one alewife size-group that was measured with both frequencies. Small but inconsistent differences were found between day and night for the same groups of fish. Shapes of the TS distributions were similar when centered on the mode, and we derived a probability density function (PDF) for TS at 70 kHz as a function of fish length to describe these distributions. We used this PDF to predict TS distributions based on alewife gill-net catch from six lake surveys and compared predictions with in situ TS distributions from each acoustic survey. Observed and predicted distributions were similar for TS values greater than −50 dB, but the observed number of small TS values exceeded the predicted number for several of the surveys. Some of these smaller TS values were probably from invertebrates or smaller fish or were indicative of noise. Estimates of alewife density from lake surveys were highly affected by inclusion or exclusion of these smaller targets. We used the predicted TS distribution derived either from catch data or from the TS values greater than −50 dB to calculate the proportion of smaller TS values that were probably from alewives. Both methods resulted in similar abundance estimates, which were higher than estimates based on an existing TS–length regression for alewives.

Hydroacoustic surveys have been used for over three decades to estimate fish abundance (Love 1971; Ehrenberg 1972; Simmonds and MacLennan 2005). Acoustic backscattering is proportional to fish density, but the sometimes elusive goal of obtaining absolute fish density estimates requires that a fish's acoustic backscattering cross section (σ_{bs}; m^2/m^3) or the logarithm of σ_{bs}, target strength (TS; in decibels [dB]), is known. This property of the insonified fish is related to the fish's physical size and, in particular, swim bladder size (Love 1977; Foote 1985; Ona 1990). Target strength is further influenced by changes in swim bladder shape (due to water depth, degree of stomach fullness, and condition) and by the tilt angle of the fish relative to the sound beam (Ona 1990; Simmonds and MacLennan 2005). Even large fish can have small TS values at certain tilt angles (Horne and Jech 2005). Therefore, a fish of a certain size can give rise to a wide range of TS values, adding uncertainty to the in situ TS estimates. This is particularly problematic in freshwater applications, where in situ TS estimates are often used to scale acoustic backscattering and where there is often a mixture of species and size-groups present. Because of this variability, it can also be difficult to assign species or size-groups to modes in TS distributions (Parker-Stetter et al. 2006). We need to know the identity of measured in situ TS values for choosing correct thresholds in analyses and for using in situ TS distributions to separate acoustic densities into different fish size-groups. Further, if the expected TS distribution from each size-group can be estimated, we can then predict the full TS distribution expected from a fish population with known size structure.

Although there is a considerable body of literature on TS values of marine fish species (see reviews by McClatchie et al. 1996; Simmonds and MacLennan 2005) and an increasing number of in situ TS measurements in freshwater fishes (Guillard and Gerdeaux 1993; Horppila et al. 1996; Appenzeller 1998; Kubecka and Duncan 1998; Crockett et al. 2006), there has been only limited attention given to

TABLE 1.—Number and size of age-0 and adult alewives measured for hydroacoustic target strength (TS; decibels [dB]) during daytime or nighttime in net-cage experiments and summary characteristics of the resulting TS distributions. A 70-kHz acoustic unit was used in all 2003 and 2004 experiments; 70- and 123-kHz units were used in 2005 experiments.

	Age 0, day		Age 0, night		Adult, day		Adult, night		Adult, day	
Variable	2003	2004	2003	2004	2003	2004	2003	2004	70 kHz	123 kHz
Number of fish in cage	7	4	7	4	10	4	10	4	7	7
Mean total length (mm)	74	62	74	62	138	124	138	124	131	131
Length range (mm)	73–77	58–69	73–77	58–69	119–159	120–127	119–159	116–130	125–134	125–134
Number of single targets	122	1,394	3,666	3,930	1,340	953	5,503	4,067	1,801	266
Number of fish tracks	9	75	124	150	64	70	116	74	144	65
Number of TS measures per track	13.6	18.6	29.6	26.2	20.9	13.6	47.4	55.0	12.5	4.1
Mean TS (dB)	−46.1	−47.4	−46.9	−48.0	−43.0	−45.2	−41.0	−45.7	−43.1	−41.6
TS mode (dB)	−45.0	−47.9	−45.7	−46.2	−39.9	−42.3	−38.6	−42.3	−41.5	−40.9
1st TS percentile (dB)	−60.3	−63.6	−63.3	−62.0	−61.2	−60.5	−58.6	−64.5	−62.3	−63.9
99th TS percentile (dB)	−41.6	−41.6	−41.9	−43.7	−37.4	−40.9	−36.8	−40.6	−35.6	−34.3

assemblages that included rainbow smelt *Osmerus mordax*, bloaters *Coregonus hoyi*, and alewives. Warner et al. (2002) used comparisons between in situ TS distributions and fish size distributions in lakes dominated by alewives to obtain a TS–length regression for alewives. However, Warner et al. (2002) assumed a unimodal normal distribution of alewife TS when conducting decomposition of the in situ TS distributions into different alewife size-groups. Recent results indicate that a unimodal normal TS distribution is not always a safe assumption (Ona 2003; Rudstam et al. 2003; Knudsen et al. 2004).

In this paper, we present TS measurements at 70 and 123 kHz for several size-groups of alewives swimming freely in a large net-cage (ex situ TS). Measurement of TS in net-cages has a long tradition in marine systems (e.g., Edwards and Armstrong 1983; Gauthier and Rose 2002; Ona 2003) but has been less common in freshwater. We describe the probability density function (PDF; e.g., Rudstam et al. 1987) of TS for the size range of alewives investigated, and we relate the mean, mode, and range of the TS distributions to fish size. These relationships are compared with the literature. We then use these results to predict the expected TS distribution from six alewife surveys in three New York lakes sampled with acoustics and small-mesh vertical gill nets, and we compare predicted TS distributions with observed in situ TS distributions from the same lakes. Finally, we compare fish density estimates using a number of possible assumptions to separate undesired targets from the observed TS distribution. We found that use of an expected TS distribution, rather than just expected mean TS, is important for deciphering the identity of observed potential uncertainty arising from unknown targets in acoustic surveys.

Methods

Cage data.—We measured the ex situ TS distribution of five size-groups of alewives from 59 to 159 mm total length during the summers of 2003–2005 (Table 1). Up to 10 fish of approximately the same length were held in a net-cage (3 m long × 3 m wide × 4 m deep; 3.2-mm Delta knotless nylon mesh) suspended at marinas adjacent to Oneida Lake, New York, with little or no current. The alewives used in 2003 and 2005 were held at the Cornell Biological Field Station (Bridgeport, New York) for several months before we took measurements. In 2004, alewives were obtained through seining in Cayuta Lake, New York, and were held for 2–7 d in tanks before being used in this experiment. Once placed in the cage, all fish were allowed to swim freely but were not fed; however, the cage mesh was large enough to allow plankton and possibly invertebrates to move through the cage. The acoustic transducer was suspended just under the surface in the middle of the net-cage. The cage was large enough that sound scattering from the side of the net was minimal. A standard calibration ball (32.1-mm-diameter copper sphere; TS = −39.2 dB) was suspended under the transducer just above the bottom of the cage (mean range from transducer = 3.5 m) to continuously monitor the performance of the unit. We collected data with a 70-kHz Simrad EY500 split-beam echo sounder in all years (0.2-ms pulse length; 11.4° for the 3-dB beam angle; 1.1 m for the 2× near field), and we used a 123-kHz Biosonics DTX digital split-beam echo sounder in 2005 only (0.4-ms pulse length;

Simrad unit does not use a lower data collection threshold. After 1 d and one night of data collection, the fish were removed from the cage and measured. At this time, we also confirmed that no wild fish had inadvertently entered the cage. No alewives were reused in any subsequent trials.

The acoustic data were analyzed using SonarData Echoview version 4.0. Tracks from single fish were identified by visual inspections of the echogram. We selected 150 fish tracks for the analysis; if fewer than 150 fish tracks were detected, all of the fish tracks were used (Table 1). All targets closer than 1.5 m from the transducer were removed from the analysis to avoid observing fish in the near field of the transducer. Target strength data for individual fish were analyzed. In Echoview, this can be done by creating a region bitmap mask to eliminate from analysis all data other than the selected fish tracks. For each group of fish (except in 2005), we calculated a calibration correction that was specific to that trial by exporting a large number (>5,000) of the single targets from the calibration ball on the echogram and comparing the measured mean TS of the ball (−40.3 ± 1.0 dB [mean ± SD]; $n = 64{,}065$) with its known mean TS (−39.2 dB at 25°C). In 2005, we calibrated both units before the measurements were taken. Sound speed and absorption coefficient were set according to temperatures present during the experiment (23–26°C). Single-fish criteria were (1) TS greater than −75 dB, (2) maximum two-way beam compensation of 12 dB, (3) pulse duration between 0.6 and 1.5 times the pulse length at −6 dB of the peak value, and (4) a 0.6° standard deviation of the major and minor axis angles. These single-fish criteria were the same for 70- and 123-kHz data. The choice of compensation model was set to Simrad (Soule et al. 1997) for the 70-kHz Simrad data and Biosonics (proprietary compensation model) for the 123-kHz Biosonics data. We exported each TS greater than −75 dB and the associated angular and depth information.

We calculated three measures of the combined TS distribution for each group of fish: (1) the range of measured TS values (dB), (2) the mode of the TS distribution, and (3) the mean TS obtained by back-transformation of mean σ_{bs}. We used linear regression to correlate mean and mode of the TS distribution to the logarithm of average fish length used in each trial (70-kHz data only). We used the 123-kHz data in 2005 for direct comparison with the 70-kHz data collected on the same group of alewives.

The measured echo strength (often referred to as for an effect of target depth (continuous variable), beam compensation (continuous variable; a proxy for distance from the center of the beam), and quadrant (categorical variable) on TS using a general linear model (JMP version 4.0). We also included day–night as a categorical variable in these analyses. These analyses were done for each fish length-group.

Because the shapes of the TS distributions from different fish sizes were relatively similar (see Results), it is possible to predict an expected TS distribution for alewives of any size within the size range investigated using a standard TS curve. The sum of such standard curves weighted for the relative proportion of different length-groups in the catch would be the expected TS distribution for the length distribution of alewives obtained in the field. We developed such a TS curve for alewives by aligning the mode of all ex situ TS distributions normalized to sum to 1.0 (equivalent to a PDF for each distribution) and then averaging these PDFs to obtain a PDF for any TS mode. We used TS mode rather than TS mean to align the curves because the TS mean was more sensitive to the variable degree of bimodality in the data. This PDF can be used to calculate the expected TS from the alewife population present in a lake. Of course, this method should only be applied to alewife sizes similar to the ones used in the ex situ TS measurements (range = 58–159 mm). Smaller fish may have more unimodal distributions (Rudstam et al. 2002; Frouzova and Kubecka 2004).

Field collections.—We used acoustic data combined with small-mesh gill-net samples from six surveys in three New York lakes. Cayuta Lake (42°22′ 00″N, 76°44′ 04″W) is a shallow, productive, 152-ha lake with a mean depth of 4.8 m and a maximum depth of 8 m. Otsego Lake (42°45′ 36″N, 74°53′ 31″W) is a 1,651-ha, steep-sided, oligotrophic lake with a maximum depth of 50.6 m and mean depth of 24.9 m. Onondaga Lake (43°05′ 40″N, 76°12′ 60″W) is a eutrophic, 1,191-ha lake with a maximum depth of 19 m; alewives recently experienced a large population increase in this lake. Alewives were the dominant pelagic fish species in all three lakes and typically contributed close to 100% of the total catch in small-mesh gill nets.

During all surveys, we used pelagic small-mesh gill nets (square mesh sizes = 6.25, 8.00, 10.00, 12.50, 15.00, 18.75, and 25.00 mm). Nets were suspended from the surface to a depth of 6 m in Cayuta and Onondaga lakes and were fished on the surface and bottom to cover all depths down to 12 m in Otsego lakes and up to 12 h in Otsego Lake. Length frequency distributions were adjusted to account for alewives that were counted but not measured; these distributions were then corrected for size selectivity of the nets (selectivity curves presented by Warner et al. 2002). We used this corrected length frequency to predict the acoustic TS distribution given the ex situ TS distribution from the net-cage. The expected TS distributions from each 5-mm length-group were summed to obtain a predicted TS distribution for comparison with the observed TS distribution from the acoustic survey.

Acoustic data in the lakes were collected after dark using the same echo sounders used for the cage data. Six surveys are presented: three conducted with the 70-kHz unit, two performed with the 123-kHz unit, and one conducted using both units towed simultaneously from the same boat. Surveys were done in 6–10 transects throughout the entirety of each lake, and the transducer was towed at a depth of approximately 0.5 m. The systems were calibrated with a standard 32.1-mm copper sphere either immediately before or within a few days of the survey. Pulse length used was 0.2 ms for all 70-kHz surveys and either 0.2 ms (Cayuta Lake) or 0.4 ms (Otsego Lake) for the 123-kHz surveys. Sound speed and absorption coefficient were set according to temperatures during sampling. Single-target detection settings were the same as for the cage data.

For the six surveys, density of alewives between 2 m from the surface (1.5 m from the transducer) and the bottom was calculated using several different methods to illustrate the effects each would have on the density estimate. These numbers do not represent whole-lake densities of alewives; no corrections were made for fish in the top 2 m of the lake. Density was first estimated using the in situ mean TS of all targets greater than −75 dB and a depth-varying echo integration threshold that included only volume backscattering from targets larger than −75 dB at the edge of the beam (at the 3-dB beam angle). This excludes contributions from targets smaller than −75 dB (ParkerStetter et al. 2009). We expected this to give a high density estimate because many of the smaller targets (even those above −75 dB) are likely to be invertebrates and smaller fish (Gal et al. 1999; Rudstam et al. 2002). Second, we calculated density based on all targets greater than −61 dB (and echo integration thresholds relevant to a −61-dB target). A TS threshold of −61 or −60 dB is common in Great Lakes alewife surveys (Argyle 1992; alewives. Third, we estimated the proportion of targets greater than −61 dB that were also greater than −50 dB (TS values greater than −50 dB are unlikely to include nonfish targets) and we used the predicted TS distribution from the gill-net catch to estimate the proportion of targets smaller than −50 dB that should be from alewives. The fourth method was similar except that the predicted number of targets smaller than −50 dB was calculated from the best fit of the combined TS distributions for age-0 alewives and age-1 and older alewives to the in situ TS data over −50 dB. This is similar to a method suggested by Parker-Stetter et al. (2006) for rainbow smelt. The difference between the previous two methods is that the proportions of age-0 fish and age-1 and older fish were determined by the gill-net catches in the third method and by the in situ TS distribution in the fourth method. The fourth method also allowed us to compare an estimate of the proportion of age-0 alewives in the population derived from the in situ TS distributions with the proportion of age-0 fish caught in the gill nets corrected for gill-net selectivity. Lastly, we estimated density using the mean TS predicted from the gill-net catch (using the TS–length regression equation of Warner et al. 2002) rather than the in situ mean TS measured in the acoustic analysis. This method is commonly used in marine surveys (Ona 2003; Hjellvik et al. 2004), where dense fish schools are common and individual fish are difficult to separate.

Results

Ex Situ Target Strength from Caged Alewives

Target strength distributions from the caged alewives were wide for all length-groups, ranging from −34.3 to −64.5 dB (Table 1), and 99% of the TS measurements were between −61 and −37 dB (range = 25 dB). Both mean TS and the mode of the TS distribution increased with fish length. Mean TS ranged from −41.0 to −48.0 dB, and TS modes ranged from −38.6 to −47.9 dB (Table 1). The TS distributions were highly negatively skewed (Figure 1). Similar but not identical distributions were found in the 2005 comparison (Figure 2) for TS with the 70-kHz (TS = −43.1 ± 5.9 dB [mean ± SD], $n = 1{,}801$) and 123-kHz units (−41.6 ± 5.7 dB, $n = 266$); a significantly higher TS mean (+1.5 dB) was observed for the 123-kHz data ($t = -4.58$, $P < 0.001$).

Several variables were included in a general linear model to investigate the effects of location in the beam and day–night on ex situ TS. We found weak but often

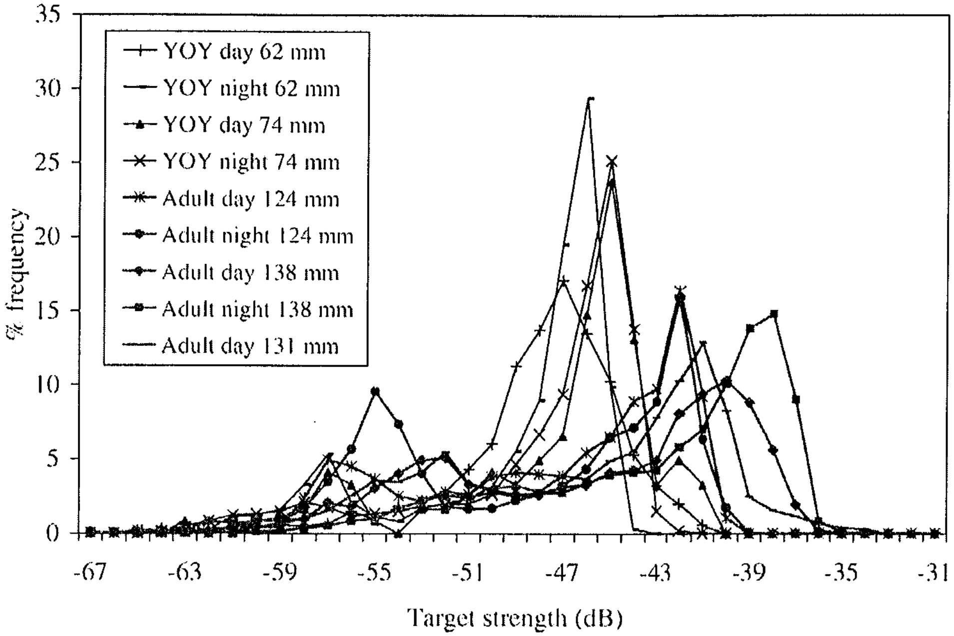

FIGURE 1.—Distribution curves (percent frequency) describing the hydroacoustic target strengths (decibels [dB]) of alewives in net-cage experiments conducted during day and night with fish of various sizes (black lines and symbols = age-0 fish; gray lines and symbols = age-1 and older fish).

(Table 2; general linear model for each group of alewives). We conclude that either (1) the beam compensation algorithm does not perfectly reflect the actual beam patterns of our transducers or (2) there is some error in the angular data and therefore in the determination of fish location in the beam. We cannot separate those two possibilities, and both are probably contributing to the observed statistically significant effect of beam location on TS measurements. However, these errors associated with the split-beam function of the transducers only explained about 5% of the total variance in measured TS. The shape of the TS

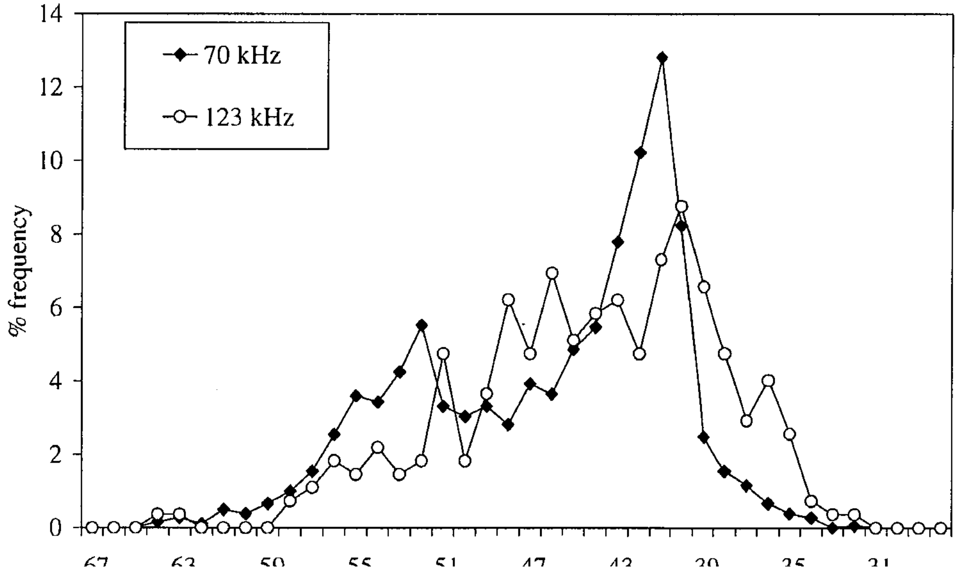

TABLE 2.—Differences in measured mean hydroacoustic target strength (ΔTS; decibels [dB]), illustrating the effects of daytime versus nighttime survey period, target range (m) from the transducer, measured distance of the target from the center of the beam, and target location in individual beam quadrants (Q1–Q4) on observed TS of age-0 and adult alewives used in net-cage trials (na = data not available). Results (*P*-values) are from a general linear model (distance from center and range = continuous variables; day–night and quadrant = categorical variables). A 70-kHz acoustic unit was used in all 2003 and 2004 experiments; 70- and 123-kHz units were used in 2005 experiments.

	Age 0		Adult		Adult, 2005	
Variable or statistic	2003	2004	2003	2004	70 kHz	123 kHz
Length-group (mm)	74	62	138	124	131	131
Adjusted r^2	0.05	0.04	0.06	0.04	0.12	0.06
Whole model (*n*)	3,788	5,324	6,843	5,020	1,801	266
Diel effect: *P* (df = 1)	0.08	0.62	<0.01	<0.01	na	na
ΔTS (day – night)	0.76	0.63	−1.96	0.51	na	na
Range effect: *P* (df = 1)	0.28	<0.01	<0.01	<0.01	<0.01	<0.01
ΔTS (1.5 – 3.0 m)	0.53	1.27	−5.30	0.11	−5.60	−4.72
Distance from center: *P* (df = 1)	0.01	<0.01	0.39	0.80	<0.01	0.41
ΔTS (12 dB – center)	2.57	1.74	−0.34	0.32	2.50	1.48
Quadrant effect: *P* (df = 3)	<0.01	<0.01	<0.01	<0.01	<0.01	0.83
ΔTS (Q2 – Q1)	−0.78	0.58	0.42	0.44	−0.27	−2.62
ΔTS (Q3 – Q1)	−0.72	0.84	0.61	0.97	−0.95	−3.55
ΔTS (Q4 – Q1)	−0.87	−0.10	0.80	0.24	−1.26	−3.00

distribution was similar for targets in the center versus outer portion of the beam, targets close to versus farther from the transducer, and targets in different quadrants of the beam (Figure 3). Therefore, we conclude that none of these factors are responsible for the wide distribution and bimodality of TS measured from fish targets in the cage.

Significant differences in mean TS between day and night did occur, but the directional change was not consistent among trials (Table 2). The differences were less than 1 dB in all cases except for adult alewives in 2003 (difference = 2.0 dB). Differences may be due to fish behavior. In all 70-kHz trials during 2003 and 2004, more measures per fish track were found at night (39.5 ± 6.94 [mean ± SE], $n = 4$) than during the day (16.7 ± 1.85, $n = 4$; $t = -3.14$, $P < 0.03$); this result was probably due to slower swimming speed during the night (Arrhenius et al. 2000). Fish in those years also spent more time near the surface during the day than during the night. The opposite was found in 2005; a different marina was used in 2005, and a streetlight was close to the cage setup. At this location, alewives moved towards the surface during dusk probably because they were attracted to the light, and very few targets were detected in the acoustic beam below 1.5 m at night.

Both the mean and mode of TS were highly correlated with the logarithm of fish total length. Fish length alone explained 90% of the variance in TS mode in the trials

$$\mathrm{TS}_{\mathrm{mode}}(\mathrm{dB}) = (19.1 \pm 2.4) \times [\log_{10}(\text{fish length, cm}) - (62.2 \pm 2.4)],$$

and the equation for the TS mean was

$$\mathrm{TS}_{\mathrm{mean}}(\mathrm{dB}) = (13.1 \pm 2.9) \times [\log_{10}(\text{fish length, cm}) - (58.2 \pm 2.9)].$$

For comparison with other studies, we also calculated the intercept for an equation with a slope of 20 (intercept denoted as b_{20}; a standard for TS–length regressions; Simmonds and MacLennan 2005). The b_{20} was −63.1 ± 0.33 dB (mean ± SE) for the TS mode and −64.9 ± 0.53 dB for the TS mean. Applying the slope of 20.54 from Warner et al. (2002) resulted in an intercept of −63.6 ± 0.18 dB.

The TS distributions from different fish length-groups were similar when the distributions were aligned by the TS mode (Figure 5). We used the average of these curves at 1-dB intervals from the TS mode to predict the TS distribution resulting from a target with a given mode. To facilitate the use of our approach to other alewife populations, we also fitted a PDF that is the sum of a skewed normal distribution and a normal distribution to these averages. This PDF describes the TS distribution in terms of deviations from the TS mode:

$$f(\mathrm{TS} - \mathrm{TS}_{\mathrm{mode}}) = 0.183\left\{P_1 e^{-0.5K_1^2} + (1 - P_1) e^{-0.5K_2^2}\right.$$

and

$$K_2 = [(\text{TS} - \text{TS}_{\text{mode}}) - \mu_2]/s_2$$

and the fitted parameters are $P_1 = 0.176$ (the proportion of the first curve), $K_1 = 3.31$ (skewness constant for curve 1), $\mu_1 = -11.27$ (mean of curve 1), $s_1 = 3.46$ (SD of curve 1), $\mu_2 = -0.89$ (mean of curve 2), $s_2 = 1.88$ (SD of curve 2), $K_2 = 0.57$ (skewness constant for curve 2), and 0.183 is a constant used to normalize this function to a sum of 1.0 (i.e., the function becomes a PDF). Because TS mode is strongly related to fish length (Figure 4), this curve can be used to calculate the expected TS distribution at 70 kHz for any alewife length within the range of fish lengths investigated (58–159 mm); the sum of such curves weighted by the proportion of the alewife population in different length-groups is the PDF of TS for the alewife population.

Field Data: Predicted versus Observed Target Strength Distributions

Alewives dominated the gill-net catch in all surveys, and catches of alewives ranged from 122 (Otsego Lake, 2005) to 787 (Cayuta Lake, 2006). Mean size of age-0 alewives ranged from 73 to 116 mm, and mean size of adults ranged from 133 to 151 mm (Table 3). Overall size range of alewives was 51–213 mm. The 2005 survey in Otsego Lake was the only survey where alewives constituted less than 98% of the total catch (73.5%). In that survey, the emerald shiner *Notropis atherinoides* was the next most abundant species, and adult yellow perch *Perca flavescens*, walleyes *Sander vitreus*, and several other species were also present. In the past, over 90% of the catch in Otsego Lake has consisted of alewives, and this was also the case in 2006 and 2007 (M. Cornwell, State University of New York [SUNY] at Cobleskill, unpublished data).

We predicted TS distributions in each lake based on the average of the ex situ TS distributions weighted by the proportion of different length-groups caught in the small-mesh gill nets. These predicted TS distributions were compared with the actual in situ TS distributions from the six acoustic surveys (Figure 6). For targets greater than −61 dB, the TS modes in the predicted distributions were within 2 dB of the observed mode. For example, the Otsego Lake 2005 survey yielded almost identical distributions for observed TS at 70 and 123 kHz and the predicted TS distribution using the net catches. In other surveys, there was a greater number of smaller targets in the observed data than would be

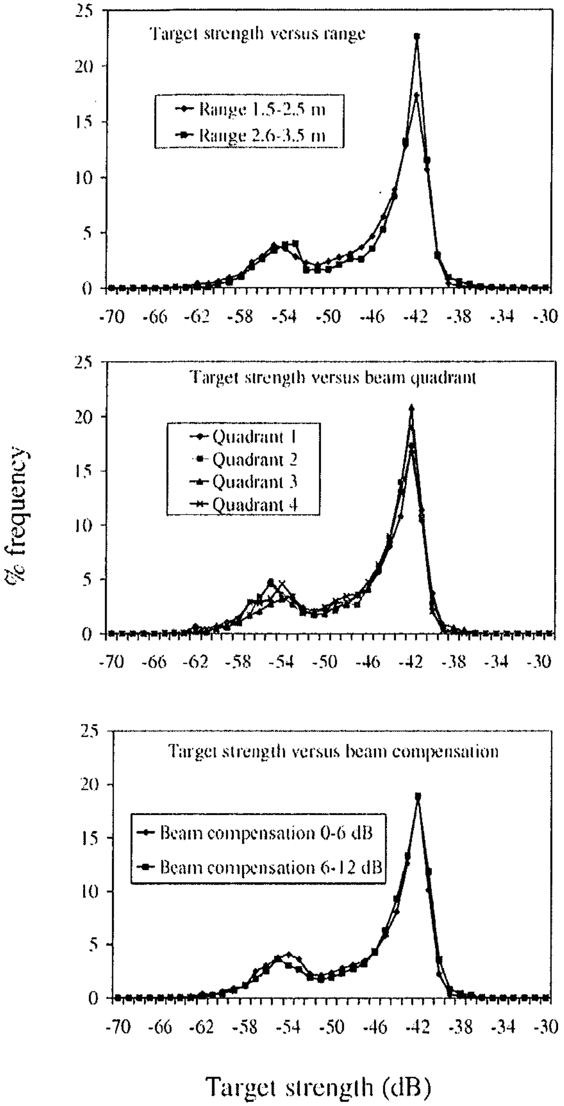

FIGURE 3.—Distributions (percent frequency) describing the hydroacoustic target strengths (decibels [dB]; adjusted to compensate for fish length) of alewives detected with a 70-kHz acoustic unit during a net-cage study; distributions are shown for targets at different ranges from the transducer, in different beam quadrants, and at different beam compensation levels. Beam compensation is used to indicate distance from the center of the beam (0 dB when on axis; 6 dB when located at the half-power beam angle).

values, probably from larval phantom midges *Chaoborus* spp. that are abundant in this lake (authors' personal observations).

Field Data: Effect of Lower Threshold on Density

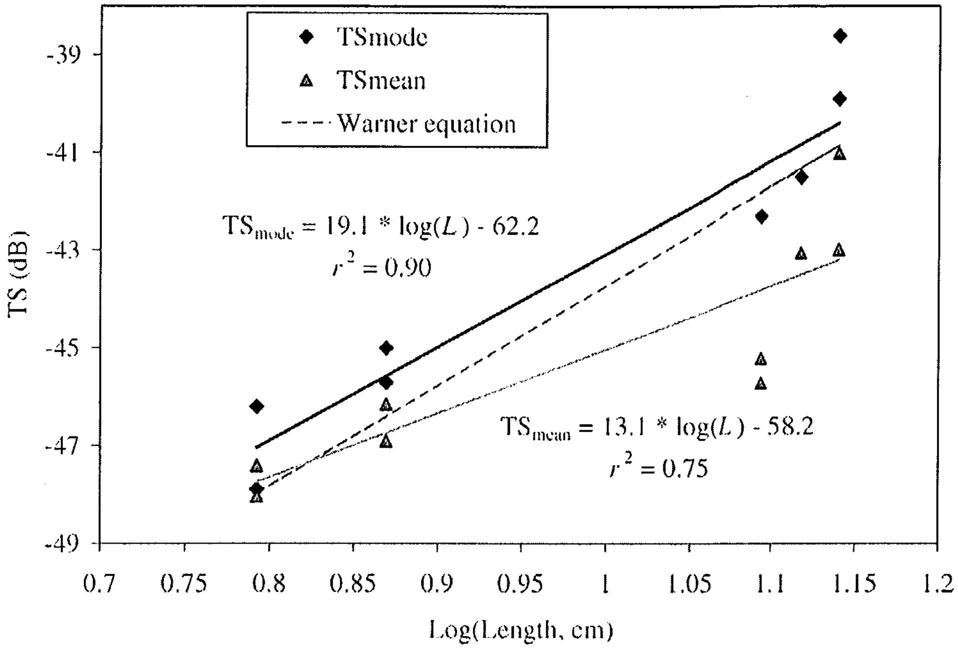

FIGURE 4.—Relationship between log-transformed mean total length (*L*; cm) of alewife groups used in net-cage experiments and the mean or mode of hydroacoustic target strength (TS; decibels [dB]). Dashed line represents the TS–length equation of Warner et al. (2002).

nonfish targets and resulted in high density estimates, ranging from 2,428 to 26,191 targets/ha. The density using a TS threshold of −61 dB (1,736–7,636 targets/ha) should be more representative of the actual fish density. However, in some surveys, there were higher numbers of in situ TS values in the range of −61 to −50 dB than would be expected from our ex situ predictions (Figure 6), and these density estimates probably

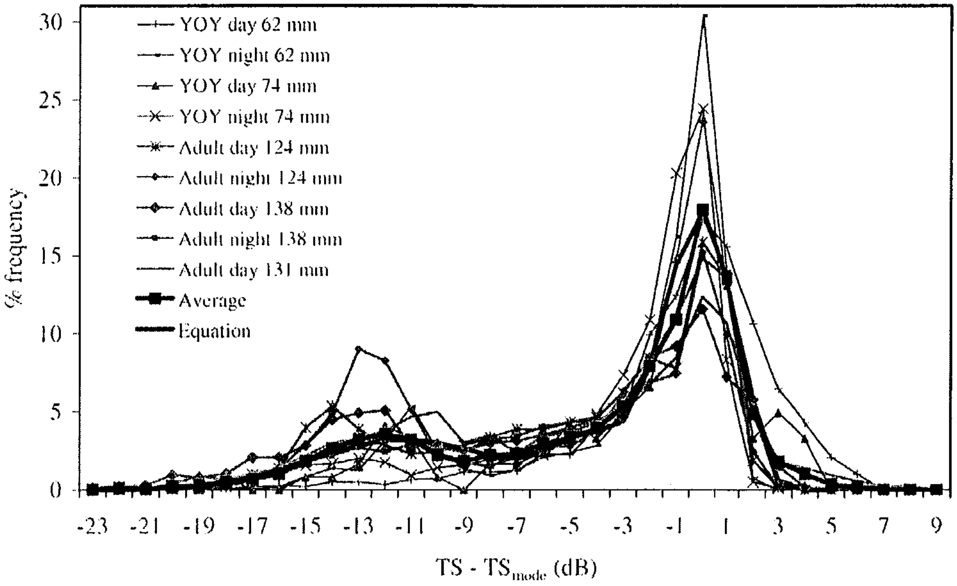

TABLE 3.—Average total length (TL) and proportion of age-0 and adult alewives in the small-mesh gill-net catch from six field surveys performed in conjunction with acoustic surveys in Cayuta, Otsego, and Onondaga lakes, New York.

	Lake and date					
Group and variable	Cayuta 6 Oct 03	Cayuta 5 Oct 04	Cayuta 4 Nov 05	Cayuta 9 Oct 06	Otsego 5 Oct 05	Onondaga 17 May 05
Age-0 alewives						
Mean percentage of gill-net catch	60	27	46	40	61	4[a]
Range in percent catch	57–64	16–34	14–67	34–45	46–64	0–17[a]
Mean TL (mm)	80	87	101	88	73	116[a]
Size range (mm)	74–88	71–103	72–112	75–105	51–93	108–123[a]
Adult alewives						
Mean percentage of gill-net catch	40	73	52	59	12	96
Range in percent catch	36–43	66–84	33–80	54–65	11–19	83–100
Mean TL (mm)	144	132	146	150	141	151
Size range (mm)	123–193	114–164	125–213	120–180	124–175	131–164
Other species						
Mean percentage of gill-net catch	<1	0	2	1	27	<1
Range in percent catch	0–1	0	0–5	0–1	25–35	0–1

[a] For Onondaga Lake in spring 2005, yearling alewives were combined with age 0 for the closest comparison with fall age-0 fish from other lakes.

included some invertebrate or non-alewife targets. Therefore, we also estimated density using the proportion of targets above −50 dB and calculated the number of targets expected in the range of −61 to −50 dB from the predicted TS distributions using the gill-net catches. This method reduced densities by 10–52% depending on the proportion of targets between −61 and −50 dB. Using the in situ TS distribution to predict the proportion of age-0 and older fish gave similar results. Lastly, use of the TS mean estimated from the length distribution in the gill-net catch instead of the in situ TS mean from the survey resulted in densities that were 38–68% lower than those obtained by simply using the −61-dB cutoff and 6–46% lower than those obtained by the two methods using the −50-dB cutoff with correction for smaller targets.

The density estimation method of varying the percentage of age-0 fish versus adult fish to get the best fit to the observed TS distribution also gave us an independent estimation of the percentage of age-0 fish in each survey (Figure 8). The proportions of age-0 fish from acoustic surveys and gill-net surveys were correlated ($r^2 = 0.80$, $P < 0.01$); however, the age-0 fish percentages derived from the in situ TS distributions were almost always higher than the percentages derived from the gill-net catches even after accounting for gill-net selectivity. This may be a reflection of (1) the presence of smaller targets influencing the predicted age-0 fish percentages or (2) a bias in the gill-net catches against small fish.

timing of the survey is selected to coincide with times of year when a target species aggregates in specific areas (e.g., spawning aggregations of Atlantic herring *Clupea harengus* in the Gulf of Maine; Overholtz et al. 2006). On the other hand, the smaller size of lakes allows for surveys to be conducted entirely during the night, when the fish are dispersed. In such conditions, in situ TS distributions can be used routinely to translate echo integration into absolute fish density and to give information on the size structure of the fish present (Warner et al. 2002; Simmonds and MacLennan 2005; Parker-Stetter et al. 2006). However, the assumption that each mode in a TS distribution is from a specific size- or age-group is not always valid (Williamson and Traynor 1984; Rudstam et al. 2003), and even large fish can give rise to small echoes at certain tilt angles (Horne and Jech 2005).

Our results from the cage experiments show that the TS distributions for all size-groups of alewives tested had a large range of around 25 dB, were negatively skewed with a pronounced peak, and were only slightly bimodal. Ona (2003) noted a strikingly similar range and a sometimes bimodal shape of the TS distribution for Atlantic herring in large net-pens. We determined that our large range in TS distributions was not due to location in the beam, as this only accounted for 4–12% of the total variance in TS. Also, the presence of small TS values was not due to inclusion of nonfish targets because only TS measures within identifiable fish traces were included and because large and small TS values were sometimes measured as consecutive

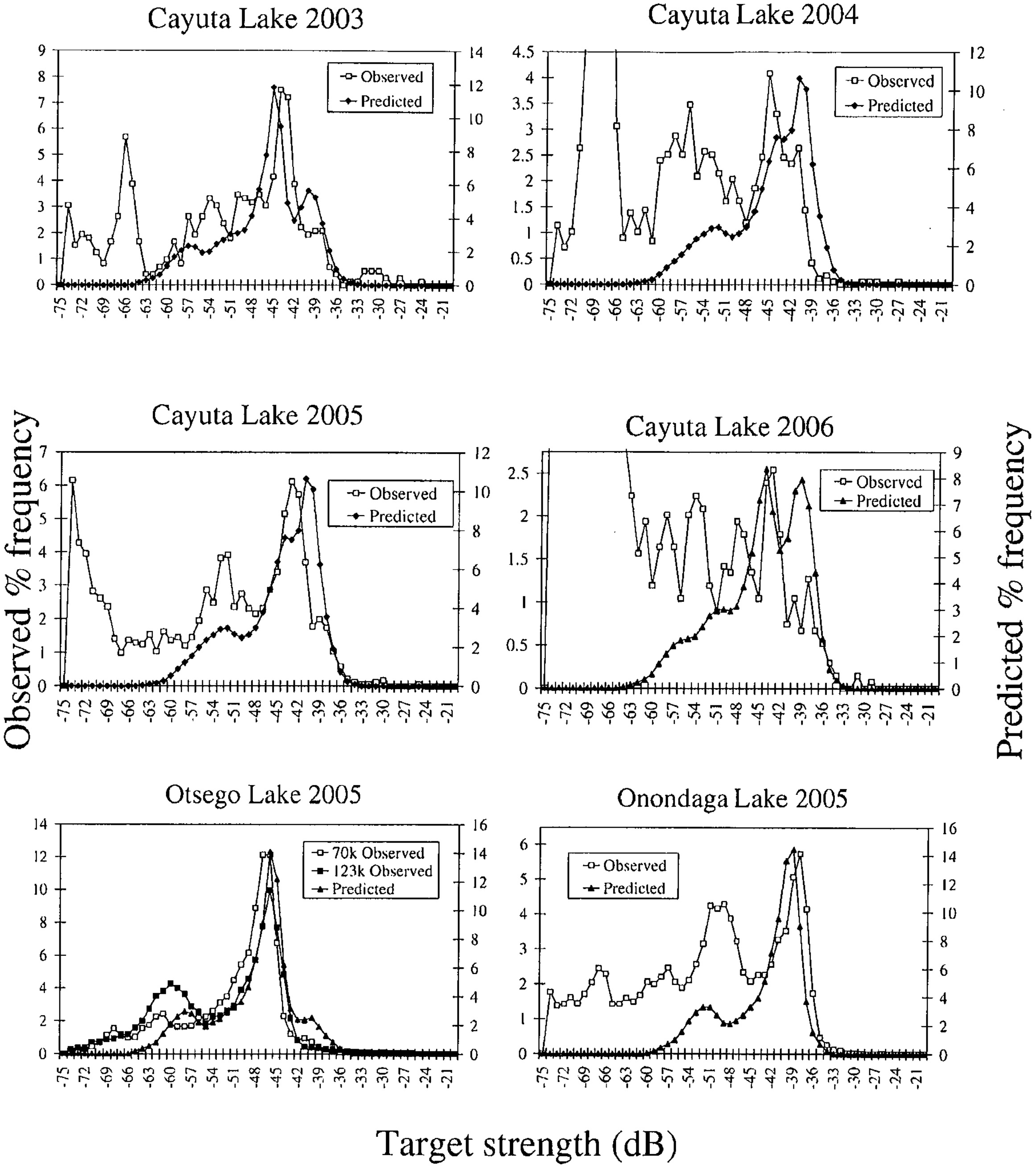

FIGURE 6.—Distributions (percent frequency) of hydroacoustic target strengths (decibels [dB]) observed during acoustic surveys in Cayuta, Otsego, and Onondaga lakes, New York, compared with predicted target strengths based on alewife total length distributions from gill-net surveys.

similar when centered on the TS mode (Figures 3, 5). Because the TS mode was highly correlated with fish length (Figure 4), this relationship can be used for

The main mode in the ex situ TS distribution contributed most of the observed echoes. Of all targets attributed to alewives, only 12–39% were below −50

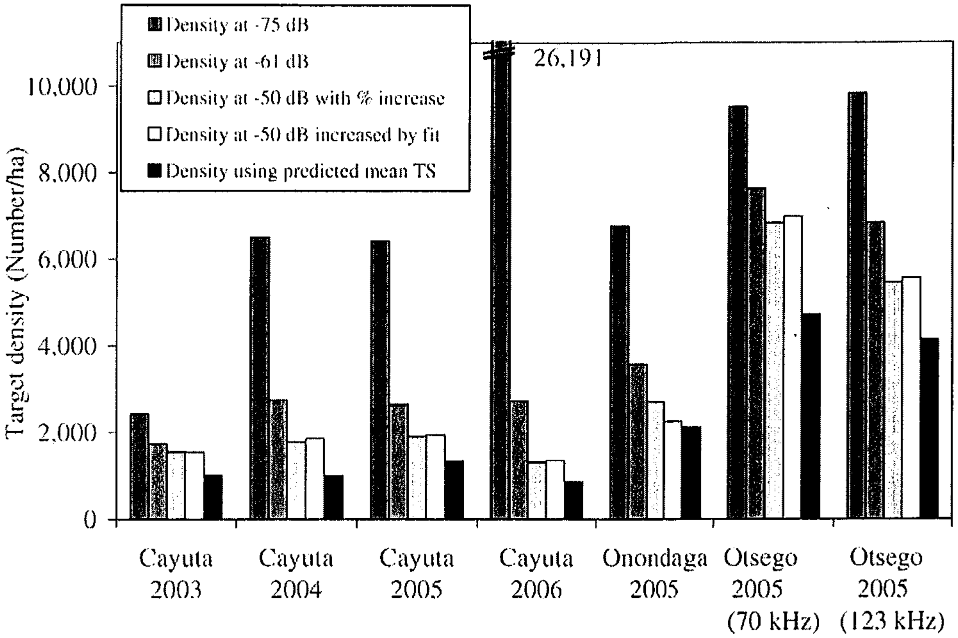

FIGURE 7.—Changes in estimates of fish density based on different minimum target strength (TS; decibels [dB]) thresholds in surveys of Cayuta, Otsego, and Onondaga lakes, New York. Densities represent the number of targets per hectare from 2 m to the bottom without adjustment for fish closer to the surface. Otsego Lake was surveyed with 70- and 123-kHz acoustic units. The 70-kHz acoustic unit was used for the Cayuta 2003, Cayuta 2004, and Onondaga 2005 surveys. The 123-kHz acoustic unit was used for the Cayuta 2005 and Cayuta 2006 surveys.

2004). European whitefish *Coregonus lavaretus* (Appenzeller 1998), and rainbow smelt (Rudstam et al. 2003; Parker-Stetter et al. 2006). However, alewives appear to have a more consistent main mode in their TS distribution, at least according to our ex situ measurements; this consistency was also observed by Ona (2003) in a study of Atlantic herring. Although theoretical models (Horne and Jech 2005) and observations in small enclosures show that alewives can give rise to small echoes and multimodal TS distributions (L.G.R., personal observation), the resulting distributions measured in lake surveys are often not bimodal. Warner et al. (2002) also observed mostly unimodal distributions from alewives when tracking single fish.

Differences in TS between day and night due to diel patterns in vertical migration, schooling behavior, and tilt angles have been observed in some studies (Appenzeller and Leggett 1992; Luecke and Wurtsbaugh 1993; Hjellvik et al. 2004; Jurvelius and Marjomaki 2008). Diel behavior differences were observed in our cage studies; however, the day–night differences in TS were not consistent among alewife between day and night. Luecke and Wurtsbaugh (1993) observed lower densities of kokanee *Oncorhynchus nerka* (lacustrine sockeye salmon) during moonlit nights than on dark nights in a western reservoir.

In the 2005 cage study and 2005 Otsego Lake survey, we found little difference in TS distributions between the 70- and 123-kHz acoustic units. Both 70- and 120-kHz frequencies are used in the Great Lakes

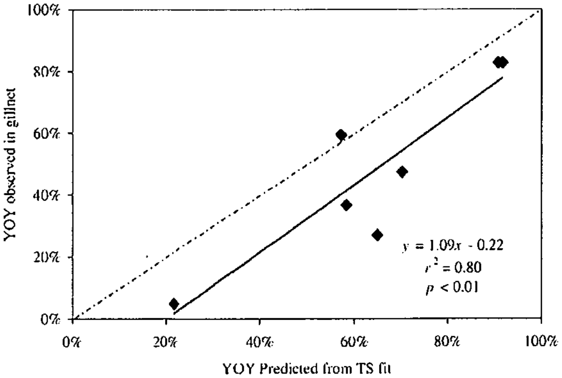

FIGURE 8.—Comparison of the percentage of age-0 alewives

for alewife surveys. Fish TS is more variable at higher frequencies because TS is more sensitive to tilt angle at higher frequencies (Dawson and Karp 1990; Horne and Jech 2005). However, the differences between 70 and 120 kHz may not be sufficient to appreciably affect the TS distribution and average in situ TS for most fish groups in the Great lakes (Rudstam et al. 1999; Guillard et al. 2004; Jurvelius et al. 2008; this study); however, fish TS can be strongly frequency dependent for species without swim bladders (Fernandes et al. 2006) and for small fish at low frequencies (Fässler et al. 2007). We applied the ex situ TS distribution to field data collected at both 70 and 123 kHz and found good agreement between predicted and observed TS distributions (see below).

Fish size affects TS (Love 1971; Simmonds and MacLennan 2005), and our results showed a strong correlation between alewife length and the resulting TS. However, our results indicate that the TS mode is a better predictor of fish length than the TS mean because of the highly skewed and sometimes bimodal nature of the TS distribution (similar to Atlantic herring; Ona 2003). A distribution of TS should be expected from fish of a given size (as was observed here; see also Medwin and Clay 1998; Horne and Jech 2005). Also, scaling of volume backscattering used in echo integration is done with the average σ_{bs} (TS = 10 × $\log_{10}\sigma_{bs}$), and this value should be calculated by converting all TS values to σ_{bs} values before calculating the average (Simmonds and MacLennan 2005; Rudstam et al., in press). The TS mode is not an appropriate value with which to scale volume backscattering. However, TS modes may be useful for identifying fish length-groups from TS distributions.

Our TS mean equation was similar to but slightly lower than the Warner et al. (2002) equation (Figure 4). The difference was largest for adult alewives in 2004; this data set had the largest proportion of small targets and was the most bimodal. Warner et al. (2002) assumed that a given size-class of fish has a unimodal and approximately normal TS distribution; this was supported with in situ data from Lake Ontario and Otsego Lake on individual fish tracks. Thus, their analysis did not include the smaller TS values observed in this study, and we would therefore expect a lower mean TS in our study as well as in the field. For comparisons, it is common practice to calculate the b_{20} (Simmonds and MacLennan 2005). The b_{20} (mean ± SE) in our study was −63.1 ± 0.33 dB for TS mode and −64.9 ± 0.53 dB for TS mean. The equation of marine equation for clupeids (Foote 1987: $b_{20} = -71.9$ dB). This may not be only an effect of salinity, however, as more recent investigations have found that clupeids from both brackish and marine areas have higher TS than predicted from this standard equation (Ona 2003: $b_{20} = -67.3$ dB at 38 kHz; Didrikas and Hansson 2004: $b_{20} = -67.8$ dB at 38 and 70 kHz; Peltonen and Balk 2005: $b_{20} = -63.9$ dB at 38 kHz). Warner et al. (2002) reviewed TS–length equations for other species similar to alewives (also available from www.acousticsunpacked.org).

Effects on Density Estimation

Acoustic fish density is obtained by dividing the acoustic backscattering coefficient by the average σ_{bs} (Simmonds and MacLennan 2005). In situ σ_{bs} has the advantage of measuring the σ_{bs} of the fish during particular survey conditions and therefore includes effects of changes in behavior, tilt angle, and pressure on σ_{bs}. However, to do this, it is necessary to decide which TS range will be included in the calculations of average σ_{bs}. All density estimates using in situ TS apply a minimum threshold for the targets to be designated as fish to remove the contribution from invertebrates, bubbles, and electric and acoustic noise. This threshold is often between −65 and −50 dB, but some researchers interested in larval fish have used thresholds as low as −76 dB (Rudstam et al. 2002; Parker-Stetter et al. 2006). In lakes with large numbers of small targets, the choice of lower threshold can significantly affect density estimates. The selection of an appropriate TS range requires an understanding of the expected TS distribution from each species and size-group present; understanding the identity of smaller targets is particularly important. We believe our ex situ TS distribution provides that information for alewives.

We calculated fish density using five possible assumptions for identifying the proportion of smaller echoes that were probably from alewives. Density of all targets larger than −75 dB gave very high estimates that were probably due to the inclusion of small, non-alewife targets. We do not expect more than 1.4% of alewife TS measures to be below −61 dB based on our ex situ TS distributions. These small targets could be from phantom midge larvae and other invertebrates; gas bubbles due to anoxic conditions; or small, nontarget fish species that are invulnerable to the sampling gear used (Rudstam et al. 2002; Knudsen et al. 2004; Holbrook et al. 2006; Jurvelius et al. 2008).

may also include some non-alewife targets. Densities obtained by use of a −61-dB minimum threshold averaged 47% lower than those obtained using the −75-dB threshold (range = 20–90% depending on the number of small targets present; see Figure 6).

As an alternative method, we used the ex situ TS relationship to predict the TS distribution that would be expected based on the gill-net catch. This was similar to the observed TS distribution for two surveys (Cayuta Lake in 2003 and Otsego Lake in 2005; Figure 6). For those lakes, a −61-dB threshold should work well. However, in the other lakes, the number of small targets observed was substantially larger than the number predicted; this result was probably due to the presence of small, nonfish targets or smaller fish larvae (e.g., Cayuta Lake in 2004 and 2006; Figure 6). When this is the case, an acoustics estimate based on a −61-dB threshold may substantially overestimate the number of alewives present. However, the shape of the distribution for TS values greater than −50 dB was similar to our predicted TS, even in lakes with numerous smaller targets. In lakes with a high number of small targets, density estimates derived either from the gill-net size structure or from the fit to the in situ TS distribution for targets greater than −50 dB probably give more accurate estimates of the true fish density. These two density estimates were similar because the proportions of age-0 and age-1 and older alewives obtained in gill nets and the proportions derived from the fit to in situ TS were similar. The final comparison, in which σ_{bs} was calculated from our gill-net catches using the Warner et al. (2002) equation and the echo integration data, resulted in lower density estimates than were obtained from all the other methods because the equation was derived using a normal distribution of expected targets from a given fish size and therefore excluded small TS values (i.e., tail of the TS distribution) from the mean σ_{bs} calculations. The densities calculated using the cage-derived TS distribution were between 3.8% and 18.4% higher than densities obtained using the Warner et al. (2002) equation.

The correspondence between our ex situ predicted TS distribution from gill-net catches and the in situ distributions for TS greater than −50 dB is encouraging. This suggests that we are getting comparable results from net-cages and lakes and that the TS distributions can be used to estimate the proportion of age-0 and older alewives present. It also suggests that the proportion of smaller targets that are probably

Bimodality and shape of the TS curves probably change under different alewife activity levels, which are likely to vary from survey to survey depending on temperature, feeding activities, and time of year. It is possible that even small changes in conditions (e.g., light levels during a full moon versus a cloudy night; windy versus calm nights) could influence activity and therefore TS. However, using a threshold or a standard equation for calculations of in situ TS does not eliminate these biases. Clearly, it is important to understand the identity of the measured smaller targets, and this may require directed sampling with sampling gear different from traditional trawls or gill nets.

Our method can also be biased by selectivity of the fish sampling gear. Based on sampling in previous years with both midwater trawls and the gill nets used here, we know that there were few if any smaller alewives present in these lakes (L.G.R., unpublished data). However, the proportion of age-0 alewives in the trawls is higher than that in the gill nets. A higher proportion of age-0 fish in trawls than in gill nets was also suggested by the fit to the acoustics data. It is likely that gill nets have higher selectivity for larger fish than is accounted for by the gill-net selectivity curves, which do not reflect decreased visibility of larger mesh nets or increased activity and swimming speed of larger fish. Both mechanisms will increase the gill-net catchability of larger fish (Hamley 1975; Rudstam et al. 1984; Anderson 1998).

We have presented a PDF for expected alewife TS in lakes; this PDF can be used to predict the resulting TS distribution from the sampled fish. This allows the investigator deciphering the identity of targets in the TS distribution to arrive at less-biased density estimates. Although our results are encouraging, our lakes were dominated by alewives; therefore, this process will be more difficult in mixed-species assemblages. Also, the ability to calculate densities of age-0 fish and age-1 and older fish directly from the acoustics data requires at least an unbiased sample of the length distribution of each fish group as well as a sufficient separation of the length modes of the two age-groups. In our experience, it is difficult to visually identify two size-groups in the TS distributions if the difference in mean length is less than 30 mm. If one of the groups is more abundant than the other, visual separation may require a larger length difference.

Our comparison between ex situ TS from cages and in situ TS from the lakes points out the need for researchers to more carefully sample potential targets dB at 70 kHz (Rudstam et al. 2002) and between −63 and −56 dB at 120 kHz (Frouzova and Kubecka 2004). An investigator seldom knows whether these small targets are present until after the acoustic data are obtained and processed, even on lakes and at times of year that have been sampled successfully in the past. Identification of the source of these smaller targets will require use of multiple sampling gears (including ones that sample nonfish targets) across a broad range of size selectivity and in a sufficiently stratified number of sites. Target strength must be thought of as a wide distribution (sometimes bimodal) rather than a single mean value when interpreting TS distributions observed from field data. Application of controlled TS studies like ours to other species and age-groups will better allow researchers to decipher TS distributions from acoustic surveys in lakes where potential targets belong to mixed-species and mixed-age assemblages.

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Paper 2. Rudstam, L.G., T. E. Brooking, S. D. Krueger, and J. R. Jackson: Analysis of compensatory responses in land-locked alewife to walleye predation: a tale of two lakes.

Analysis of compensatory responses in land-locked alewife to walleye predation: a tale of two lakes.

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Abstract

We compared one established and one expanding land-locked alewife population (Cayuta and Canadarago Lakes) to evaluate compensatory responses in alewife to walleye predation. Alewives have been present in Cayuta Lake since at least 1977 and the population ranged from 3,840 to 24,470 fish/ha from 1995 to 2009. Alewives were first observed in 1999 in Canadarago Lake and the population remained at low densities (<25 fish/ha) until reaching 370 fish/ha in 2006 and 1,050 fish/ha in 2009. Differences in zooplankton reflected higher planktivory rates in Cayuta than in Canadarago Lake and the changes in alewife over time in Canadarago Lake. In Cayuta Lake, high stocking rates of fingerling walleye were maintained for five years (2002-2006) in an effort to build a walleye population that could decrease alewife; however, density of adult walleye in Cayuta Lake (age 3+, 12-14 fish/ha in 2002, 2006 and 2009) remained below the density in Canadarago Lake (age 3+, 21-24 fish/ha in 2004 and 2008). Alewife density explained 77 to 84% of the variation in alewife length-at-age and 48 – 84% of the variation in condition (age 0, age 1 and age 2) among years and lakes. Length of alewife in Canadarago Lake at low density was similar to observations in anadromous populations. Alewife recruitment (measured as the number of fall age 0 per spawner) was higher in Canadarago Lake than in Cayuta Lake. The combined data from both lakes yield a Beverton-Holt stock-recruitment curve that rises rapidly at low alewife densities with 50% of the maximum recruitment predicted already at densities of 391 spawners/ha. Compensatory responses in alewife likely includes both higher fecundity per individual and decreased cannibalism at low densities and need to be considered when evaluating piscivore levels needed to control alewife populations, or conversely, when evaluating the risk of alewife population collapse as a response to increased predation rates. Although alewife abundance did decline in response to walleye stocking in Cayuta Lake, we were unable to increase the adult walleye population to levels needed to decrease alewife recruitment.

Introduction

Alewife *Alosa pseudoharengus* is native to the North American Atlantic coast where it is either anadromous or forms landlocked populations (Smith 1985). In upstate New York, the species was noted in the larger of the Finger Lakes in 1868 and in Lake Ontario in 1873, probably spreading to these lakes through the canal system (Smith 1985). When established, alewife populations are often abundant and represent a major prey fish for piscivores such as walleye *Sander vitreus*, black bass *Micropterus* spp. and salmonids (Odell 1934; O'Gorman et al. 1987; Stewart and Ibarra 1991; Anderson and Neumann 2002). Abundant alewife populations are also associated with often undesirable changes in lower trophic levels, such as declines of large zooplankton, increases in phytoplankton, and decreases in water clarity (Brooks and Dodson 1965; Wells 1970; Kohler and Ney 1981; Post et al. 2008). In New York State, large *Daphnia* and water clarity declined following the increase in alewife in Otsego Lake (Harman et al. 2002) and Onondaga Lake (Wang et al. 2010).

Alewives can affect fish community structure through predation on fish larvae (Crowder 1980; Kohler and Ney 1980; Brooking et al. 1998), by competing for zooplankton (Wells 1970; Peterson et al. 2006), and by carrying high concentrations of thiaminase that break down the thiamine necessary for successful egg development in predators feeding on alewife (McDonald et al. 1998; Fitzsimons et al. 1999). Alewife predation on fish larvae has been shown to decrease recruitment success of percids (Mason and Brandt 1996; Fielder et al. 2007) and lake trout *Salvelinus namaycush* (Krueger et al. 1996). Alewives are therefore considered a risk to native fish populations in the Great Lakes basin (Madenjian et al. 2008).

Because both water clarity and recruitment of sport fish decline when alewives become established, there is an interest in developing management strategies for decreasing the abundance of land-locked alewife populations. Both models and empirical data from the Great Lakes suggest that salmonid stocking can depress alewife populations (Jones et al. 1993; Kitchell et al. 1994). However, walleye can also be effective predators on pelagic prey species (Forney 1977; Johnson et al. 1992; Olson et al. 2001; Liao et al. 2004). Fingerling walleye have been introduced into several alewife lakes in New York with the objectives of establishing self-sustaining walleye populations and creating new fishing opportunities (Festa et al. 1987; Olson et al. 2000). If a sufficiently high walleye population can be built up through stocking, it may suppress an alewife population to levels that allow for survival of walleye fry – an example of predator "cultivation" of their prey resources (Walters and Kitchell 2001). Evaluation of the likelihood of success of such a strategy requires an understanding of the compensatory responses of the fish population being controlled (Myers 2001; DeRoos et al. 2007, Zipkin et al. 2008).

Alewife populations may compensate for increased predation mortality by increased growth and condition, leading to higher fecundity, and decreased cannibalism. Most land-locked alewife populations grow slowly compared to anadromous populations (Graham 1954; Smith 1985; Post et al. 2008). Land-locked alewives can mature at age 2 or 3 at a total length of 120-150 mm and produce between 11,000 and 22,000 eggs (Norden 1967) whereas anadromous populations typically mature later, at age-4 to 5, at lengths of 240-280 mm and produce 100,000-200,000 eggs (Jessop 1993, 2003), although fecundity of over 450,000 eggs has been reported (Loesch 1987). Slower growth of land-locked populations could be a physiological effect of living in freshwater – clupeids in the brackish Baltic Sea grow slower the possibility of building walleye populations high enough to control alewife in productive inland lakes.

Methods

Study Areas

Cayuta Lake is a shallow, relatively small lake in central New York State (Table 1). The lake is eutrophic and spring total phosphorus concentrations can be high (over 100 µg/L in some years). A tributary stream at the north end of the lake allows for potential walleye spawning and concentrates walleye during the spawning run. The lake has a large littoral zone with dense submerged aquatic vegetation. The lake stratifies in the summer and oxygen depletion occurs below 4 m. Zebra mussels were first detected in the lake in 2005, but had not become abundant as of 2009, likely due to the limited hard substrate available in the lake. The dominant predators are walleye, largemouth bass *Micropterus salmoides* and chain pickerel *Esox niger*, with large populations of bluegill *Lepomis macrochirus*, pumpkinseed *Lepomis gibbosus*, and black crappie *Pomoxis nigromaculatus* present. Alewives were first detected in 1977, and had established an abundant population prior to the mid 1990s (Olson et al. 2000). Pond and fall fingerling walleye were stocked at a rate of 50 fish/ha in the lake from 1992 to 1996 for a total stocking of 76,000 fingerlings over 5 years (Olson et al. 2000). Between 2002 and 2006, NYSDEC stocked 350 walleye fall fingerlings/ha each year for a total stocking of 266,000 fish over 5 years. Walleyes were stocked from boats by NYSDEC Region 8 staff in open water outside the weed line in late August or early September, at an average size of 102-127 mm (depending on the year).

Canadarago Lake is a mesotrophic lake located in central New York and one of the headwater lakes of the Susquehanna River (Table 1, Harr et al. 1980). This lake is about 5 times larger than and twice as deep as Cayuta Lake and has been studied since the 1970s by Cornell University and NYSDEC (Green 1986; Rudstam et al. 1996b; Olson et al. 2001; Brooking et al. 2008). Stratification occurs each summer with a thermocline forming at 5-8 m, and the hypolimnion is generally anoxic for about 2 months. The lake supports a diverse fish community of at least 37 species. Walleye fingerling stocking in the 1980's established an abundant, self-sustaining walleye population and no additional stocking has occurred since then. Concomitant with increases in walleye abundance were decreases in walleye growth, increases in yellow perch growth, and decreases in yellow perch abundance. Predator populations are dominated by walleye, largemouth bass, smallmouth bass *Micropterus dolomieu*, and chain pickerel. Yellow perch, bluegill and pumpkinseed are the dominant forage species. Alewives were first detected in the lake in 1999 when two fish were caught in NYSDEC standard gillnetting. Zebra mussels were first detected in 2002 and expanded rapidly to most hard bottom substrates in the lake.

Limnology

At Cayuta Lake, bi-weekly or monthly measures of water temperature, dissolved oxygen, total phosphorus, and water clarity (Secchi disk depth) were collected by the Schuyler County Soil and Water Conservation District (SWCD) from 1988 to 2008 and made available to us by Lloyd Wetherbee (SWCD). Funding for the SWCD sampling program was discontinued in 2009, so data were not collected in that year. We also collected zooplankton

However, it could also be a response to the high densities typically found in land-locked populations. If density is important, the size and fecundity of anadromous alewives indicate that growth, condition, and fecundity could increase substantially at low densities. However, the degree to which alewife growth is density-dependent is not known, and Anderson and Neumann (2002) did not detect a density effect on growth of alewives when comparing a set of Connecticut lakes. Decreased abundance of adult alewives could also lead to decreased cannibalism and therefore increased survival of larvae, as observed in other fish species (Chevalier 1973; Dong and DeAngelis 1998, Parker-Stetter et al. 2007). Both the growth response and decreased cannibalism should result in alewife populations having a strong compensatory response to declining densities.

Evidence for strong compensatory responses in land-locked alewife populations comes mainly from the Great Lakes. In Lake Ontario, one of the largest year classes of alewives was formed the year after large winter die-offs in 1977 and 1978 (O'Gorman and Schneider 1986; Ridgway et al. 1990) and the stock-recruitment curve for alewives in Lake Ontario increases steeply at low alewife abundances (O'Gorman et al. 2004). Similarly, in Lake Huron, the 2003 alewife year class was very abundant in the fall of 2003 even though the adult alewife population was low that year (Schaeffer and Warner 2007; Riley et al. 2008). The Lake Huron alewife population subsequently crashed because of high mortality of the 2003 year class during the winter of 2003-2004 and there was a resurgence of native species following that decline (Fielder et al. 2007; Schaeffer et al. 2008). Uncertainty related to the compensatory ability of alewives was identified as a major gap in our understanding of the risks involved with various stocking levels of salmonids in Lake Ontario by a technical panel in 1996 (Rudstam et al. 1996a).

In this paper, we use data from two lakes in central New York with land-locked alewife populations to explore the range of compensatory responses in the presence of high predator densities. Both lakes are productive and have relatively high abundances of piscivores, primarily walleye. Cayuta Lake had abundant alewives and a high walleye biomass established by previous stocking (Olson et al. 2000). In this lake, the New York State Department of Environmental Conservation (NYSDEC) increased walleye stocking rates to 350 fingerlings/ha from 2002-2006 as a management experiment with the goal of increasing the walleye population and reducing alewife density. Canadarago Lake had a newly established and increasing alewife population, and a naturally reproducing and abundant walleye population. Thus, we expected to observe alewife responses to decreased density if predation rates on alewife increased in Cayuta Lake and to observe responses to increased density if the alewife population increased in Canadarago Lake. The contrast between these two alewife populations should reveal the range of compensatory responses possible in land-locked alewife populations. We investigated the effect of density on length-at-age and condition of age-0, age-1, and age-2 alewives measured in the fall, and the effect of spawner abundance on recruitment. In both lakes, we estimated walleye populations using mark-recapture, zooplankton abundance with vertical net tows, and alewife populations using hydroacoustics and small-mesh gill nets. Winter temperatures were also measured, as temperature can affect overwinter mortality (Ridgway et al. 1990; Snyder and Hennessey 2003). Finally, we used angler diaries in Cayuta Lake to measure the possible response of decreased alewife abundance on walleye catch rates. We expected catch rates to increase when prey fish abundance declined (VanDeValk et al. 2005). We end with a discussion on vertical tows from the bottom to the surface with a 0.5 m diameter, 153 µm zooplankton net. Although the number of occasions zooplankton were collected varied among years, we consistently collected zooplankton in September-October in conjunction with the fall alewife survey.

At Canadarago Lake, limnological data were collected monthly from May to October from 1990 - 2009 at one standard, center-lake station (Brooking et al. 2008). Temperature and oxygen were measured at 1 m depth intervals using a YSI meter, and Secchi disk depth recorded. A water sample was also collected just under the surface for total phosphorus, nitrate, and chlorophyll-*a* and analyzed following standard techniques (see Idrisi et al. 2001). A vertical zooplankton tow was taken from bottom to top in about 12 m (40 ft) of water using the same style net used Cayuta Lake. In both lakes, we moored a winter temperature recorder under the ice, floating 1 m off bottom in the deep section of the lake (about 7 m in Cayuta Lake and 12 m in Canadarago Lake).

In the laboratory, crustacean zooplankton were identified to species, counted and measured using a microscope and digital tablet. Lengths were converted to dry weight using length-weight regressions used for Oneida Lake, New York. Details on counting techniques can be found in Rudstam and Mills (2008).

Walleye abundance estimates

Population size of adult (age 3 and older) walleye was estimated with mark-recapture during three years in Cayuta Lake (2002, 2006, 2009) and 2 years in Canadarago Lake (2004 and 2008). Oneida style trapnets (Forney et al. 1994) were set in and around spawning tributaries (up to 6 sites per lake) as soon as the lakes were ice-free, either the last week in March or the first week in April. Nets were emptied every 1-2 days. All walleye were counted, sexed, and fin clipped before release. Approximately 25% of the marked walleyes were measured and scales collected for aging. We pulled all nets at the end of the spawning run when catches declined and water temperatures reached 12-14°C.

Recapture samples were conducted with electrofishing and gill nets in both lakes. We used a pontoon electrofishing boat either in the spring or fall of each marking year, allowing at least 30 days post-marking for the fish to leave the spawning streams and return to the main body of the lakes. Each lake was divided into 4 sections and approximately equal recapture effort was conducted in each section. Collected walleyes were checked for fin clips, and a subsample was measured, weighed, and scales collected for aging. All walleye collected during recapture sampling were released. Gill nets were set in Cayuta Lake in October, 1996, 2000, 2002-2006 and 2008-2009 (3-6 nets per year) and in Canadarago Lake bi-annually from June to September (8 nets per year as part of a standard monitoring program, Brooking et al. 2008). Each monofilament gill net was 45.7 m (150 ft) long, with six 7.6 m (25 ft) panels. We used two different nets in Cayuta Lake; one with mesh sizes from 38 mm to 102 mm (1.5" to 4") stretch mesh and the other with mesh sizes from 89 to 152 mm (3.5 – 6"). The smaller mesh nets were used in 1996, 2000, and 2006, the larger mesh nets in 2002-2003, and both nets in other years. Only the smaller mesh nets were used in Canadarago Lake. Nets were set overnight in Canadarago Lake for a total soak time of 18 hours, and set at dusk in Cayuta Lake and retrieved 3-12 hours later. All fish captured were identified by species, counted, measured, weighed, and checked for fin clips. Scales and otoliths were collected from walleye for age determination, and stomachs removed for diet

In the laboratory, we identified and measured all identifiable prey fish in the diet of walleyes from Cayuta Lake. Impressions of walleye scales from the spring trap netting and the fall gillnetting were made on acetate slides and projected onto a screen for age interpretation. Otoliths from the fall gillnet sample of walleye in Cayuta Lake were mounted in clear resin and cross-sectioned using a thin-sectioning diamond blade saw to determine age and growth rate. Walleye condition was assessed using the relative weight index (Murphy et al. 1991).

The total age-3 and older walleye population was estimated using the Chapman modification of the Petersen mark-recapture estimate and the associated variance estimator (Hayes et al. 2007). Because the number of recaptures was over 35 in each lake and year, we calculated confidence limits using a normal approximation. Abundance estimates refer to abundance at the time of marking (early spring). Total walleye biomass (kg/ha) was estimated by multiplying the number of walleye by the average weight of the marked fish calculated from measured spring lengths and lake-specific length-weight regressions (derived from fish caught in the fall of 1995 to 2008):

Cayuta Lake:
$\log_e(W, \text{g}) = -14.12 + 3.44 \log_e(L, \text{mm})$, $r^2 = 0.998$, $P<0.001$, df = 253, range 136 – 699 mm

Canadarago Lake:
$\log_e(W, \text{g}) = -13.65 + 3.33 \log_e(L, \text{mm})$, $r^2 = 0.985$, $P<0.001$, df=397, range 156-603 mm

Alewife sampling

Alewife populations were assessed using hydroacoustics and small-mesh gillnets in the fall. Each net was 21 m long by 6 m deep and consisted of seven 3 m wide panels of different mesh sizes (6.2, 8, 10, 12.5, 15, 18.7 and 25 mm bar mesh). These mesh sizes are effective for catching alewives 50 to 250 mm length (Warner et al. 2002). Most age-0 alewives should be larger than 50 mm by September as less than 1 % of alewives caught in Cayuta Lake with a small-mesh, 2 by 2 m frame mid-water trawl were smaller than 50 mm in sampling concurrent with gill net samples during 2000 and 2002 and in November of 2005. This trawl was designed to capture larval and juvenile fish (first 2 m of the trawl with a mesh size of 12.7 mm stretch mesh, the next 2 m with 6.4 mm stretch mesh, and the cod end of the net consists of a 0.5 m plankton net and bucket with 1 mm mesh). Further, average lengths of age-0 alewife (mean (SD)) in the trawl and in the gill nets were similar (although significantly different in 2000 and 2002 but not in 2005, 72.3 (6.5) mm (trawl), 76.6 (8.7) mm (nets) in 2000, 90.2 (6.8) mm (trawl) and 95.1 (7.3) mm (nets) in 2002, 99.8 (8.2) mm (trawl), 101.3 (8.3) mm (nets) in 2005). Gill nets were set in approximately 6 m of water in Cayuta Lake and therefore sampled water from the surface to the bottom. In Canadarago Lake, we set these nets both from the surface to 6 m depth and between 6 m depth and the bottom at 12 m. At the 12 m deep sites, catches in the 0-6 m and 6-12 m nets were combined.

All alewife from both lakes were counted, and a sample measured and weighed. Otoliths were dissected from a subsample of approximately 40 alewives and aged using a dissecting microscope (LaBay and Lauer 2006). Approximately 40 alewives from each year were dried for 5-7 days in a drying oven at 70° C to measure dry to wet weight ratio. This and Brandt 1995). Data were not available from year 2006 in Canadarago Lake because aging samples were lost Catches were calculated by net hour and proportions of age-0 fish calculated based on length distribution of all fish caught and the lengths of the aged fish. Proportion of age-1 fish was calculated from the proportion of adult alewife aged as age 1. For the year with missing age sample (2006 in Canadarago Lake), we estimated the age structure from the length distribution and the size of aged fish from 2005 and 2007.

Hydroacoustic surveys were conducted in the fall to estimate the abundance of alewife in both lakes (between September 18 and October 27 in 1995, 2000 and 2002-2009 in Cayuta Lake and between October 16 and November 11 in 2003-2009 in Canadarago Lake). Surveys were conducted along transects that traversed the long axis of the lake in a zigzag pattern, or along several parallel transects. We used a 70 kHz, split-beam Simrad EY500 echo sounder from 1995 to 2004 (pulse length 0.2 ms, 11.4° beam width) and a Biosonics DtX 123 kHz echo sounder from 2005 to 2009 (beam width 7.8° in 2005-2007, 7.5° in 2008, 6.8° in 2009, pulse length 0.2 or 0.4 ms). Each unit was calibrated with standard targets within a month of the surveys. The transducer was mounted on a boom at a depth of 0.5 m. Acoustic data were analyzed with EchoView v4.80 (Myriax Ltd.). Echograms were checked to remove the lake bottom, bubbles from waves, echoes from macrophytes, and other non-fish echoes. Questionable areas were not included in the analyses. We attempted to sample as close to the bottom as possible by re-defining the bottom exclusion zone at high magnification; in most cases this was no more than 0.5 m off the bottom. All densities were calculated from average in-situ backscattering cross section and echo integration within each transect with single fish detection settings and thresholds following the standard operating procedure for Great Lakes acoustics (Parker-Stetter et al. 2009). The smallest target of interest was set to -61 dB based on expected target strength (TS) from alewife of the size range caught in gill nets (Brooking and Rudstam 2009) and the shape of the in situ TS distributions. The signal to noise ratio was above 10 dB throughout the water column for a -61 dB target in both lakes and all units. In some surveys, the number of targets between -61 and -50 dB were higher than expected from alewife and likely represent bubbles or invertebrates (examples in Brooking and Rudstam 2009). For these surveys, we calculated target density based on a higher threshold (up to -50 dB) and multiplied these densities by a correction factor to account for targets between -61 dB and the higher threshold that should be alewife given the size structure of the alewife caught in the vertical gill nets (calculated from equations in Brooking and Rudstam 2009). Analyses were conducted using each transect as an elementary sampling unit and using one depth layer from 2 m depth to the bottom. Data observed closer than 1.5 m from the transducer are not usable due to near-field dynamics of these transducers (Parker-Stetter et al. 2009), which limits the survey to water depth of 2 m and deeper.

In some surveys a large portion of the alewife population was caught between the surface and 2 m depth in the vertical gill nets; depths that were not surveyed with acoustics. To account for these fish, we assumed that catchability per unit area of netting was the same in water 0-2 m as in 2-6 m (and 2-12 m at the deeper sites in Canadarago Lake). Areal fish density ($FD_{0\text{-}2m}$ in fish/ha) in the top layer can then be calculated from the ratio of the total catch in the gill nets in 0 – 2 m deep water ($C_{0\text{-}2m}$) and in 2 m to the bottom ($C_{2m\text{-}Bot}$) as

$$FD_{TOT} = FD_{0\text{-}2m} + FD_{2m\text{-}Bot} = FD_{2m\text{-}Bot}\,(1 + C_{0\text{-}2m}/C_{2m\text{-}Bot})$$

We calculated the correction factor CF=$[1+C_{0\text{-}2m}/C_{2m\text{-}Bot}]$ for each net with more than 10 alewife caught, and then calculated the average of the replicate net sets. Variance of the combined estimate of alewife is obtained from standard formulas for the variance of a product (CF × $FD_{2m\text{-}Bot}$). Alewife mortality was calculated from the decline in abundance of a cohort from one year to the next (from age 0 to age 1, and for adults from age 1 and older to age 2 and older).

Angler Catch Rates

To determine whether walleye catch rates increased as alewife abundance decreased, we implemented an angler diary program in Cayuta Lake from 2004-2009. Volunteer anglers recorded date, start time, stop time, number of people fishing, and number caught by species for each individual trip in fishing diaries provided by Cornell University. Anglers were also asked to measure any walleye they caught. At the end of each fishing season, anglers were sent postage-paid envelopes to return diaries. After data entry, diaries were returned to anglers with a summary of their individual catch and summary of the overall catch.

Results

Limnology

Cayuta Lake: -Spring (May-June) total phosphorus (TP) ranged from 5 to 320 µg/L in Cayuta Lake, consistent with its eutrophic classification (average 64 µg/L, Table 1). Annual average Secchi disk depths in Cayuta Lake (May –September) were consistently low and ranged from 0.9 to 1.4 m from 1988 to 2008 (average 1.2 m, Table 1). Maximum recorded Secchi depth for any time period was 2.4 m (May 1994). There were no significant changes in spring TP or Secchi disk depth with time (TP: r^2=0.01, df=20, P=0.74 ; Secchi depth: r^2=0.05, df=17, P=0.36).

Because fall (September-October) zooplankton samples were consistently available from Cayuta lake for 11 years (1992-1996 and 2004-2009), we only used these samples for comparisons between lakes and over time. In years when spring and summer samples were taken, the zooplankton assemblage was similar to the fall assemblage. Samples consisted mainly of the small cladocerans (*Bosmina longirostris, Ceriodaphnia quadrangular* and *Chydorus sphaericus* and cyclopoid copepods). Calanoid copepods were rare and *Daphnia* was not present in any sample. Average zooplankton body size never exceeded 0.4 mm (Table 1), and there was no detectable time trend (r^2=0.08, df=9, P=0.40). Density (mean 116 #/L) and biomass (mean 144 µg/L) of zooplankton in fall samples were variable with no significant time trends (Density: r^2=0.04, df=9, P=0.53, Biomass: r^2=0.23, df=9, P=0.13, Table 1, Figure 1). Water temperature during the winters of 2003 to 2007 were above 2°C for most of the winter ice cover period with no days below 1°C (Table 1).

Canadarago Lake - In Canadarago Lake, average spring TP (1994-2008) was 9.6 µg/L (range 6.1 to 18.3 µg/L) with no significant time trend (r^2=0.10, df=13, P=0.25, Table 1). The increase in zebra mussels after 2002 coincided with a significant increase in water clarity

(P=0.002, t-test, $N_1 = 9$, $N_2=6$), and a marginally significant decrease in chlorophyll-a levels from 4.5 to 3.3 µg/L (P=0.098, t-test, $N_1 = 9$, $N_2=5$, Figure 1). As in typical temperate lakes (Sommer et al. 1986; Mills and Forney 1988), an early spring clear water phase was followed by late summer decreases in water clarity associated with declines in *Daphnia* populations, presumably the result of predation by planktivorous fish (primarily age-0 yellow perch in Canadarago Lake, Olson et al. 2001). The zooplankton assemblage included the small cladocerans and copepods present in Cayuta Lake, but biomass was dominated by *Daphnia* and larger calanoid copepods. For comparisons with Cayuta Lake, where we only have consistent zooplankton data from September-October each year, we present zooplankton mean size, density and biomass as the average of samples collected from September through November in Canadarago Lake. Zooplankton density and biomass from 1990 to 2008 varied between years, but without a time trend (Density: 18 to 89 #/L, $r^2=0.05$, df=17, $P=0.35$; Biomass: 119 to 452 µg/L, $r^2=0.007$, df=17, $P=0.72$). However, the last year in the time series (2009) had the second highest zooplankton densities and the lowest biomass of any other year between 1990 and 2008 (81 #/L, 116 µg/L, Figure 1). Zooplankton mean size ranged from 0.59 to 1.35 mm from 1992-2008 (no time trend, $r^2=0.10$, df=17, $P=0.19$), with a large decrease to 0.37 mm in 2009 (September 24 and October 14 2009, Figure 1). The declines in biomass and mean size in 2009 were associated with the disappearance of large *Daphnia* and a decline in calanoid copepods between August and October 2009. In previous years, *Daphnia pulicaria* was the dominant species and present in most fall samples, although the smaller *Daphnia mendotae* dominated from August 2008 to August 2009. *Daphnia* were no longer present in October 2009. Winter water temperatures were below 2°C for extended periods of time but rarely below 1°C (Table 1).

Walleye

Cayuta Lake. Trap netting during the spawning run in Cayuta Lake resulted in the marking of 461 to 760 walleye in 2002, 2005 and 2008. Effort varied from 28-117 net-nights, and declined over time as we became more efficient at targeting the walleye spawning run. By-catch was considerable and consisted mostly of chain pickerel, white suckers *Catostomus commersoni*, bullhead (*Ameiurus natalis* and *A. nebulosus*), black crappie, yellow perch, bluegill and pumpkinseed (Table 2). In the combined electrofishing and gillnetting samples, the recapture ratio of marked walleye ranged from 0.26-0.36 over the three estimates, resulting in an estimated population of 11.6-13.8 age-3 and older walleye/ha and a biomass of 20.1-24.2 kg/ha (Table 2). The coefficient of variation ranged from 11 to 12 %. Despite the high stocking rates in Cayuta Lake, the adult walleye population only increased by about 20% from 2002 to 2009 as the increase from stocking in 2002-2006 was compensated by mortality of the 1992-1996 year classes. The abundance of walleye from the 1992-1996 stocking decreased from 11.6 fish/ha in 2002, to 8.1 fish/ha in 2006 and 5.4 fish/ha in 2009 (based on identification of the 1992-1996 year classes from the length distribution). At the same time, abundance of age 3 and older fish originating from the 2002 to 2006 stockings increased to 5.1 fish/ha in 2006 and to 8.4 fish/ha by 2009 when all stocked year classes contributed to the adult population. Annual mortality calculated from these data for the 1992-96 stocking were 9.5% for 2002-2006 (age 6-10 to age 10-14)and 12.2% for 2006-2009 (age 10-14 to age 13-17). Annual mortality estimates for the 2002 and 2003 year classes that were estimated in both the 2006 and the 2009 mark recapture study was 4% (the two

Walleye condition and growth rates in Cayuta Lake were high. The average relative weight of walleye was 97-110 in 1995-2008. No weights were taken in 2007 and 2009. Walleye reached 456-496 mm as age-4 fish in the fall, but were smaller in 2008 (413 mm). The most abundant diet item in 145 age-1 and older walleye stomachs with diet items (out of 387 fish analyzed) from fall gillnetted fish in Cayuta Lake was alewife. Of the 108 prey fish that could be identified, 107 were alewife. Length of measureable alewife eaten ranged from 60 to 145 mm, and consisted of slightly more age-0 than older fish (28 age-0 and 15 age-1 and older alewife identified). The 77 fish that were too digested to be identified were likely also alewife as the only other identifiable prey species was one yellow perch. Invertebrates were present in 2 stomachs.

Canadarago Lake. In Canadarago Lake, trap netting during the spawning runs resulted in the capture and marking of 1,742 (2004) and 2,350 (2008) walleye (Table 2). Effort was 53-56 net-nights, and by-catch was similar to Cayuta Lake, consisting mostly of chain pickerel, white suckers, bullhead, yellow perch, bluegill and pumpkinseed (Table 2). The age 3 and older walleye population was estimated to be 24.3 fish/ha in 2004 and 20.5 fish/ha in 2008 (CV in both years 15%), corresponding to a biomass of 19.2 (2004) and 17.6 kg/ha (2008) (Table 2). Walleye growth was lower in Canadarago Lake than in Cayuta Lake for most age classes. Length-at-age 4 increased from 421 mm in 1996 to 457 mm in 2006, but then decreased to 429 mm in 2008 (Figure 2, change over time $r^2=0.36$, $N=12$, $P=0.04$). Mean relative weight of walleye varied between 80 and 94, with the highest value in 2009. Mortality of walleye in Canadarago Lake calculated from the two mark-recapture estimates was 40.5% per year (calculated from the estimated number of age-4 and older fish in 2004 and age-8 and older fish in 2008). Similar mortality rates (34.6% per year) were obtained from the gill net catch curves using the sum of all fish age 3 to 9 caught in 1995 -2008. These mortality rates indicate an exploited population; walleye are often targeted by anglers in Canadarago Lake (Willms and Green 2007).

Alewife

Cayuta Lake: Alewife abundance estimated with hydroacoustics in Cayuta Lake was high through 2004, ranging from 13,140 to 24,470 fish/ha with a corresponding biomass range from 108 to 258 kg/ha (Table 3). Densities decreased to 3,800 fish/ha (44 kg/ha) in 2007 and increased to 5,700 fish/ha (66 kg/ha) in 2009. Abundance in the years after completion of the enhanced walleye stocking program (2006-2009) was lower than in any year prior to this stocking (1995-2003, Table 3). Alewife dominated the catch in the small-mesh gill nets (97-100%, Table 3) supporting our assumption that all acoustic targets were alewife. Catch per unit effort of alewife ranged from 48 to 192 fish/net-hour (Table 3). The proportion of age-0 alewife ranged from 27 to 86% of the catch. Mean length of alewife in the fall ranged from 83 to 102 mm for age-0, from 122 to 143 mm for age-1, and from 131 –162 mm for age-2 (Figure 3). Length-at-age increased significantly over time for age-2 fish - but not for age-0 or age-1 fish (Table 4). Alewife condition measured as percent dry weight in 2002-2009 was similar among age groups (0.22–0.28 for age-0, 0.26–0.29 for age-1, 0.24–0.28 for age 2 and older, Figure 3) and increased significantly for age-1 fish over time (Table 4). Length-at-age for age-1 and age-2 alewife, and condition for age-1 alewife increased significantly with alewife density (Figure 4, Table 4). Recruitment measured as age-0 alewife abundance in the fall was not significantly correlated with the abundance of age-2 and older alewife (r^2=0.19, df=6, P=0.29, Figure 5).

Canadarago Lake. In Canadarago Lake, small-mesh gill nets set to target alewife caught none in 1999 and 2000, a single age-0 alewife in 2001, and none in 2002 (Table 3). During these years, most fish caught were close to the bottom of the nets and consisted primarily of yellow perch and walleye. The catch of alewife began to increase in 2003 and reached 58 fish/net-hour in 2007 (Table 3). Alewife constituted over 95% of the catch from 2006 to 2009 (Table 3). Acoustic surveys started in 2003 and estimates of alewife density at Canadarago Lake were less than 25 fish/ha from 2003-05. Abundance increased to 376 fish/ha in 2006 and to 1,048 fish/ha in 2009 (Table 3, Figure 3). Since we did not catch many other species in the water column in our nets even when alewife catches were low, we considered all acoustic targets to be alewife. Biomass increased two orders of magnitude during the same time period from 0.4 kg/ha in 2003 to over 40 kg/ha in 2008 and 2009 (Table 3). The proportion of the alewife catch consisting of age-0 fish was over 90% until 2006 and then decreased to 54-60% in 2008-2009 (Table 3). Mean length of age-0 alewife averaged 125-140 mm in 2003-2005 (Figure 4) with one age-0 fish reaching 177 mm. Mean lengths of age-1 alewife ranged from 196 to 238 mm (Figure 3) with an individual age-1+ fish as large as 253 mm. There were no time trends in length-at-age or condition (Table 4). Mean length of age-0 alewife, but not mean length-at-age for age 1 and age 2, was marginally negatively correlated with density (Table 4). Alewife condition measured as percent dry weight ranged from 26 to 32 % for age-0 and from 32 to 39 % for age-1 and age-2 and older fish (Figure 3) without a time trend or density effect (Table 4). Recruitment measured as age-0 abundance in the fall was correlated with abundance of age-2 and older alewife (r^2 = 0.89, df = 5, P = 0.001, Figure 5).

Density effects. Comparisons across the alewife populations in the two lakes show highly significant effects of alewife density on growth and condition, but no significant effects of time (Figure 4, Table 4). Density explained between 48 and 84% of the variation in condition and between 77 and 84% of the variation in length (for age-0, age-1 and age-2 alewife) when combining data from both lakes. A linear function of spawner density explained 45% of the variation in recruitment in the combined data set (r^2 = 0.45, df = 13, P = 0.006), but the relationship is non-linear (Figure 5) and recruitment per spawner declined as a power function of spawner density ($R/S = 20.3\ S^{-0.32}$, $r^2 = 0.69$). The Beverton-Holt stock-recruitment curve fit to the combined data set is (Jmpv8.0, non-linear least-squares fit, df=13):

$$R = 13.8\ S\ /\ (1+0.00255\ S)$$

where R is the number of age-0 alewife in the fall (fish/ha), S is the number of age 2 and older alewife in the fall (fish/ha). This curve reaches 50% of maximum recruitment rates at a spawner density of 391 fish/ha.

Estimated alewife mortality in Cayuta Lake (2002-2009) was between 38 and 87% for age 0 to age 1, and between 20 and 89% for age 1 and older fish. The highest mortality rates were observed between 2005 and 2007 for both age groups. Catches were too variable

Angler Diary Program

Three to ten anglers per year returned diaries with a total annual effort of 155-558 angler hours (Table 5). Effort specifically targeting walleye was 121-215 angler-hour per year. Catch rates of walleye by anglers targeting walleye were only 0.01 walleye/hour in 2004, but increased significantly to 0.13 walleye/hour in 2008-09 (r^2=0.84, df=4, P=0.036). Catch rates of largemouth bass were 0.3-0.6 fish/hour, and chain pickerel catch rates were 0.1-0.3 fish/hour. The bass catch rate increased significantly from 2004-2009 (P=0.04).

Discussion

The alewife populations in the two lakes were at different stages of population development. Alewives have been in Cayuta Lake for at least three decades and exhibit characteristics of other landlocked alewife populations – high abundance, slow growth and relatively poor condition (Graham 1954; Anderson and Neumann 2002; Post et al. 2008). Zooplankton in Cayuta Lake were small, phytoplankton abundant, and water clarity poor; classic responses to size-selective alewife predation and the resulting cascading trophic interactions (Hrbaček et al. 1961; Brooks and Dodson 1965; Carpenter et al. 1985). Walleye feeding on these abundant alewives exhibited fast growth and excellent condition, but produced no recruits, also a common observation in lakes with abundant alewives (Mason and Brandt 1986, Fielder et al. 2007). In contrast, the alewife population in Canadarago Lake was established in the late 1990s and was still increasing in 2009. Alewife growth rates and condition in Canadarago Lake were high, zooplankton were dominated by large *Daphnia* and large calanoid copepods (until fall of 2009) and water clarity was high. Walleye grew more slowly than in Cayuta Lake and we caught age-0 walleye in our annual electrofishing surveys in all years from 1990 to 2008 except one (2006) (Brooking et al. 2008). Biomass of adult walleye was similar in Canadarago and Cayuta Lake (18-24 kg/ha) indicating that the alewife populations in the two lakes experienced similar predation pressure.

We believe the limnological characteristics of the two lakes primarily reflect the differences in alewife populations. Although Cayuta Lake is more productive with higher spring TP than Canadarago Lake, the zooplankton biomass was higher in Canadarago and was dominated by large zooplankton, in particular *Daphnia pulicaria*. No *Daphnia* were present in Cayuta Lake. This is a well documented zooplankton community response to high alewife abundance (Brook and Dodson 1965, Kohler and Ney 1981, Post et al. 2008). Recent changes in Canadarago Lake zooplankton further support the alewife effect. In 2008, the dominant *Daphnia* species in Canadarago Lake shifted from the larger *Daphnia pulicaria* to the smaller *Daphnia mendotae*, also a common response to high planktivory (Mills and Forney 1983, Rudstam et al. 1993). By the fall of 2009 *Daphnia* were no longer detectable in Canadarago Lake and the zooplankton species composition and size structure resembled that in Cayuta Lake. Similar abrupt changes in zooplankton community structure in late summer were observed the year a strong year class of alewife was produced in Onondaga Lake, New York (Wang et al. 2010).

Water clarity was substantially higher in Canadarago Lake than in Cayuta Lake, as expected when large *Daphnia* are present (Carpenter et al. 1985, McQueen et al. 1986) increase in water clarity observed since 2002 is likely the result of increased zebra mussel grazing (Karatayev et al. 2002; Mayer et al. 2001). It remains to be seen if phytoplankton abundance will increase and water clarity decline in Canadarago Lake as a response to alewife-initiated trophic cascades, or if zebra mussel grazing will be sufficient to maintain the current high water clarity in the lake.

In Cayuta Lake, there was no change in the zooplankton assemblage or water clarity after a 6-fold decline in alewife abundance, suggesting that there is a threshold alewife density at which large zooplankton are eliminated from a lake. It is also possible that *Daphnia* were no longer present in the lake, as alewife have been abundant for at least 2 decades; however, *Daphnia* resting eggs can survive for several decades in sediments (Hairston and Fox 2009). Our data suggest that a threshold at which alewives eliminate large zooplankton from lakes is at a biomass of around 30 to 40 kg/ha, as this alewife biomass was correlated with the decline of first *Daphnia pulicaria* and then *Daphnia mendotae* in Canadarago Lake. This is similar to the threshold of age-0 yellow perch that caused declines of *Daphnia pulicaria* in Oneida Lake (Mills and Forney 1988). We note that this threshold likely depends on lake productivity and on the availability of refuges for *Daphnia* (nearshore or in low oxygen water, Jeppesen et al. 1997; Klumb et al. 2004).

Walleye grew faster and were in better condition in Cayuta than in Canadarago Lake, although the difference between the lakes declined by the end of the study period. Growth rates in both lakes were higher than in nearby Oneida Lake (He et al. 2005) and length-at-age 4 (456-491 mm) in Cayuta Lake prior to 2009 was among the highest observed in inland New York lakes (Rudstam et al. 1996b). These growth rates are similar to growth rates in Lake Ontario (Hoyle et al. 2010) but lower than growth rates in western Lake Erie and Green Bay, Lake Michigan (Kapucinski et al. 2010, Vandergroot et al. 2010). Walleye relative weight was higher in Cayuta (97-110) than in Canadarago Lake (80-94) which is consistent with observed relative weight of walleye of 101-112 in Lake Conaughy, Nebraska after alewife introduction (Porath et al. 2003, Cade et al. 2008). Walleye growth and condition is related to prey abundance (VanDeValk et al. 2008; Kaufman et al. 2009) and the high growth rates in Cayuta Lake indicate that this walleye population was not prey limited. As a result, angler catch rates were relatively low. Catch rates of walleye are negatively correlated with prey fish abundance in Oneida Lake (VanDeValk et al. 2005), a relationship that is also observed in other walleye fisheries (Beard et al. 1997; Newby et al. 2000). Mortality rates of adult walleye in Cayuta Lake (6-13%) were low and similar to natural mortality rates measured in Oneida Lake (10%, Irwin et al. 2008), another indication of low catchability to the sport fishery. Walleye mortality in Canadarago Lake (40% per year 2004-2008) is more typical of exploited populations (Carlander 1997). We did observe an increase in catch rates over time in Cayuta Lake which could be the result of decreasing alewife density, but it is also possible that angler catch rates increased as anglers became more adept at catching walleye in that lake.

We used the contrast between these two alewife populations to explore the range of density-dependent compensatory responses possible in alewife populations. We expected compensatory responses to include increased growth and condition and decreased cannibalism at low density. Growth rate and condition of the three age groups of alewife investigated was strongly density dependent. For age 0, age 1, and age 2 and older, 77-84% of the variation in length-at-age and 48-84% of variation in condition was predicted by locked populations (Odell 1934; Anderson and Neumann 2002), Canadarago Lake alewives grew very fast, reaching lengths typically observed in anadromous alewife (Scott and Crossman 1992). The Canadarago Lake population may be among the fastest growing land-locked alewife populations reported in the primary literature, but anecdotal evidence indicates that this growth rate is not unusual shortly after invasions. Large alewives were observed in several New York lakes (Otsego, Champlain, and Onondaga) shortly after alewives were first reported in these lakes (Harman et al. 2002; Simonin 2010; Wang et al. 2010). Condition measured as percent dry weight was also high in Canadarago Lake compared to other alewife lakes, including Lake Michigan (Flath and Diana 1985; Rand et al. 1994). Increased growth and condition lead to higher fecundity – the number of eggs produced in a 300 mm alewife could be an order of magnitude higher than in a 130 mm fish (Norden 1967; Loesch 1987; Jessop 1993). Clearly, alewife populations show substantial ability to compensate for high mortality and low density by increased growth rates. In addition, cannibalism must be important in alewife as they are known larval fish predators (Crowder 1980; Mason and Brandt 1986; Kohler and Ney 1981; Brooking et al. 1998) and cannibalism must be lower at low adult densities, further increasing the compensatory response of this species at low densities.

Given these possible compensatory responses, we expect the stock-recruitment curve for alewife to rise steeply at low spawner densities. Such a curve has been derived for alewife in Lake Ontario (O'Gorman et al. 2004) and is evident in our relationship between the number of likely spawners (age-2 and older) and the number of age-0 fish present in the fall. Our stock recruitment curve increases rapidly to a plateau – a shape typical of the Beverton-Holt formulation of the stock-recruitment curve. The Beverton-Holt stock-recruitment curve fitted to these data indicate that alewife average recruitment is 50% of their maximum at spawner densities as low as 390 fish/ha. Similarly, anadromous alewife had a positive relationship between spawner abundance and recruitment only when spawner abundance varied between 0.2 and 8.7 fish/ha (Love Lake, Maine, Havey 1973) and not when spawner abundance varied between 11 and 38 fish/ha (Damariscotta Lake, Maine, Walton 1987). Further, our stock recruitment data showed no decrease in number of recruits per spawner at low abundances (the Allee effect, Stephens et al. 1999). The shape of the stock-recruitment curve at low densities determines the dynamics of newly established populations and of populations after a strong decline (discussed in relation to over-fishing by Myers 2001). If there is a decrease in recruits per spawner at low densities, an alewife population will take longer to return to high abundance if pushed to low density by predation, making alewife more likely to be controlled by predation. However, our data as well as the fast return of alewife abundance following large scale winter mortality events (O'Gorman and Schneider 1986; Ridgeway et al. 1990) suggest a steeply sloped stock –recruitment curve without an Allee effect. On the other hand, the lack of a return of alewife after the population crash in Lake Huron in 2004 (Schaeffer and Warner 2007, Riley et al. 2008) does indicate that an alewife population can be slow to recover under some conditions possibly associated with high predation rates. Also, we note that it took 7 years for the alewife population to increase in Canadarago Lake, compared to a few years between first observation and abundant populations in some other lakes (Lake Champlain, Simonin 2010; Lake St Catherine, Good and Cargnelli 2004) suggesting that the Canadarago Lake walleye in an alewife population at low density likely depends on the productivity of the lake and the overall abundance of predators. Although walleye density was relatively high in both our study lakes compared with many other walleye lakes (Nate et al. 2001), it is not as high as observed in some systems (Carlander 1997). Finally we note that our stock-recruitment relationship indicates that the Canadarago Lake alewife population is no longer limited by spawner biomass and we can expect the alewife population to now increase quickly and develop an abundant and slow growing population that is typical of land-locked populations.

We were unable to increase the walleye population in Cayuta Lake despite stocking rates 7 times higher than the standard rates used in 1992-1996. Survival from stocked fingerling to age-4 was only 0.0034% (range 0.002 to 0.008%); an order of magnitude lower than the survival of the 1992-1996 year classes to ages 6 to 10 (0.031%, range 0.002 to 0.07%). We believe this is due to high mortality during the first year in the lake. Although stocked fall fingerlings did relatively well in Cayuta Lake in the past (Olson et al. 2000), it is likely that the large population of adult walleye present in the lake consumed the newly stocked fingerling; cannibalism is common in walleye (Chevalier 1973) and this source of mortality would continue through their second year of life given that walleye feeding rates decline only after the prey/predator length ratio increases over 0.30-0.40 (Nielsen 1980; Knight et al. 1984; Campbell 1998). Age-1 walleye in the fall averaged 216 mm in 1993-2007 in Cayuta Lake, which is about 40% of the length of the average adult walleye in the lake. Although alewife should buffer cannibalism (Nielsen 1980; Hall and Rudstam 1999), newly stocked fingerling walleyes may be particularly vulnerable to predation (Olson et al. 2000). As observed elsewhere, it is difficult to build a dense walleye population through stocking in small lakes (Laarman 1987; Li et al. 1996), possibly due to cannibalism.

The alewife population did decline in Cayuta Lake from 2002 to 2007. Could this decline be attributed to walleye predation? Although the adult walleye biomass only increased from 11.6 in 2002 to 13.8 kg/ha in 2009, the actual walleye population preying on alewives could have been higher because these estimates do not include sub-adult walleye. We can estimate biomass of walleye age-1 and older in the spring using the mark-recapture estimates, the age structure in the aged population, and the calculated mortality estimates. Average weight of an age class was estimated from the size of the year class in the previous fall. With these assumptions, the walleye biomass was predicted to increase to 17 kg/ha by year 2000 due to the 1992-1996 stocking, stay relatively stable from 2000 to 2004 at 16-17 kg/ha, and then increase to a peak of 22.8 kg/ha in 2009 as the 2002-2006 stocked fish grew in size. After 2009, the biomass is expected to slowly decline. The increase from 17 to 22 kg/ha from 2004 to 2007 does coincide with a decline in alewife abundance from 15,000 fish to less than 4,000 fish/ha (Figure 6) and with alewife mortality estimates over 80% per year for both age-0 to age-1 alewife and for age-1 and older alewife. However, alewife abundance increased from 2008 to 2009 even though walleye biomass remained above 22 kg/ha, suggesting that a walleye biomass of 22-23 kg/ha is not sufficient to decrease an alewife population sufficiently to limit alewife recruitment. Similarly, a walleye biomass of 18-19 kg/ha in Canadarago Lake was not sufficient to prevent an increase in density of alewives in that lake, although it may have slowed the rate of the increase by several years.

Winter mortality is likely high for alewife in New York and the Great Lakes (Flath and Diana 1985; O'Gorman and Schneider 1986; Höök et al. 2007), and winter die-offs have been observed in both the winter of 2007-08 and 2008-09 in Canadarago Lake. Clearly the

Lake. Winter mortality of alewife increases at temperature below 2°C (Colby 1971; Snyder and Henderson 2006; but see Lepak et al. 2008) and most winter days had water temperature above 2°C in our two study lakes (Table 1). Severe winters may limit alewife abundance in some lakes. In Oneida Lake, NY alewives have been caught occasionally in bottom trawls since 1974 (Rudstam and Jackson 2008), but a population has not become established. This could be due to winter temperatures, as water temperatures are below 1 °C for substantial time periods in Oneida Lake and over-winter mortality of another clupeid, gizzard shad *Dorosoma cepedianum* is very high in that lake (Fitzgerald et al. 2006; Fetzer 2009).

This study revealed strong compensatory responses of land-locked alewife and provided a stock –recruitment curve for alewife that included quantitative estimates of the number of recruits and spawners at both low and high spawner densities. By following two populations at different stages of the invasion process over a decade, we were able to get information on both the ascending limb of the stock –recruitment curve and the alewife density that limits recruitment per spawner. We did not observe a decline in alewife total recruitment at high alewife densities that has been suggested elsewhere (O'Gorman et al. 2004), either because the alewife population was still not sufficiently high, or that factors other than cannibalism are more important regulators of recruitment at high densities.

Experiences from the Great Lakes suggest that alewife populations can be depressed through predator stocking (Kitchell et al. 1994). Whether this is desirable or not depends on management goals. In any case, we have shown some of the range of compensatory responses possible by alewife populations at low densities (increased growth, condition and number of recruits per spawner). These compensatory responses should be taken into account when considering the risks involved with various stocking levels of predators, in the Great lakes and elsewhere, or conversely, when designing management goals to control alewife. Our results indicate that 50% of the full recruitment potential of alewife is reached at relatively low densities (around 400 spawners/ha) in productive small lakes. Whether these results can be extrapolated to larger water bodies remains to be investigated.

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s and Figures

1. Limnological characteristics of Cayuta and Canadarago Lakes. Average and range of annual values are included for most ieters. The number of years and the range of years are in the footnotes. The range is in parenthesis.

	Cayuta Lake	Canadarago Lake
ition	42°21.99 N, 76°44.10 W	42°49.05 N, 75°00.24 W
(ha)	152	770
depth (m)	8	13.4
n depth (m)	4.8	7.5
ıg TP (May-June, µg/L)	64 (5-320) [a]	9.9 (6.1-18.3) [e]
n annual Secchi depth (m)	1.2 (0.8-1.4) [b]	4.0 (2.9-5.6) [f]
zooplankton biomass (µg/L)	144 (27-226) [c]	231 (119-452) [g]
zooplankton density (#/L)	115 (26-192) [c]	30 (15-80) [g]
zooplankton mean size (mm)	0.35 (0.32-0.38) [c]	0.87 (0.37-1.35) [g]
ys below 1°C	0 (0-0) [d]	3 (0-21) [h]
ys below 2°C	5 (0-11) [d]	90 (39-109) [h]
ys below 3°C	52 (31-84) [d]	124 (114-127) [h]
ys below 4°C	118 (97-134) [d]	133 (125-143) [h]

ears between 1994 and 2008
ears between 1988 and 2008
ears between 1992 and 2009
inters from the winter of 2002-2003 to the winter of 2006-2007
ears between 1990 and 2008
ears between 1988 and 2009
ears between 1990 and 2009
inters from the winter of 2002-2003 to the winter of 2002-2009

2. Spring trap net catches in Cayuta and Canadarago Lakes during mark-recapture years. Also included are the number of fish capture and recaptures samples obtained with electrofishing and gill nets and the abundance estimates. Other fish species les carp, chub sucker, golden shiner, rudd, and alewife. By-catch was not recorded in 2004 in Canadarago Lake.

Species	Cayuta 2002	Cayuta 2006	Cayuta 2009	Canadarago 2004	Canadarago 2008
Total walleye marked	461	694	760	1742	2350
Proportion males marked (%)	58	62	65	74	76
Number in capture sample	183	138	153	449	241
Number recaptured	47	47	55	41	35
Estimated population age-3 and older	1770	2012	2092	18674	15803
95% confidence interval	1356-2184	1560-2463	1665-2518	13260-24088	10974-20632
Density (#/ha)	11.6	13.2	13.8	24.3	20.5
Biomass (kg/ha)	20.1	23.4	24.2	19.2	17.6
Trapnet catch per net night:					
Walleye	3.9	11.6	27.1	31.1	44.3
Yellow perch	4.8	18.5	10.1	-	95.9
Chain pickerel	1.9	8.1	9.2	-	0.1
White sucker	5.8	8.2	12.8	-	17.0
Brown/yellow bullhead	9.2	15.2	26.2	-	17.7
Black crappie	11.0	40.8	17.9	-	0.1
Largemouth bass	0.6	2.0	1.7	-	0.6
Smallmouth bass	0.0	0.0	0.0	-	1.3
Bluegill	2.8	25.8	18.0	-	2.9
Pumpkinseed	0.2	6.8	6.6	-	1.2
Rock bass	0.0	0.3	0.3	-	7.0
Other species	0.5	1.0	0.8	-	0.1
Total number of net-nights	117	60	28	56	53

e 3. Catches in vertical gill nets and acoustic estimates of alewife abundance in Cayuta and Canadarago Lake. Abundance ates are based on combined acoustics – gill net surveys.

	# net sites	Soak time (hour)	Average proportion alewife % (range)	Alewife catch per net-hour Total (range)	Age-0 % (range)	0-2 m % (range)	TS minimum (dB)	Abundance 2m-bottom fish/ha mean (SE)	Abundance surface-bottom fish/ha mean (SE)
ke									
	1	2	99 (99-100)	111 (-)	74 (-)	36 (-)	-61	8369 (1943)	13139 (6560)
	2	2	99 (98-100)	192 (151-234)	82 (81-82)	67 (55-78)	-61	8090 (1421)	24472 (10692)
	2	2	99 (99-100)	76 (41-111)	42 (40-44)	62 (55-69)	-61	7180 (1892)	18867 (6272)
	3	2.5	99 (99-99)	59 (12-100)	60 (57-64)	88 (84-93)	-61	1802 (834)	14469 (9835)
	3	3.1	100 (100-100)	74 (69-81)	27 (16-34)	76 (65-84)	-61	3497 (1001)	14386 (6542)
5	3	1.9	99 (98-100)	109 (69-118)	46 (15-67)	71 (50-82)	-61	2432 (378)	8298 (1474)
	3	1.5	99 (98-100)	179 (105-253)	40 (34-45)	59 (52-63)	-61	1931 (453)	4688 (1171)
7	3	3.2	99 (99-100)	70 (62-82)	86 (83-89)	79 (77-83)	-61	780 (318)	3798 (1650)
	3	5.1	97 (95-100)	102 (74-132)	50 (33-67)	57 (44-74)	-61	1655 (474)	3845 (1794)
	4	2.3	99 (98-100)	48 (13-121)	49 (41-62)	43 (14-67)	-54	3263 (709)	5711 (2495)
Lake									
	4	12	0 (0-0)	0	-	-	-	-	-
	4	12	0 (0-0)	0	-	-	-	-	-
	4	12	2 (0-14)	<0.1 (-)	100 (-)	100 (-)	-	-	-
	4	12	0 (0-0)	0	-	-	-	-	-
	5	14	47 (0-100)	0.4 (0-2)	100 (-)	15 (5-25)	-50	22 (8)	26 (10)
	4	15.8	79 (50-86)	2.4 (0-6)	88 (67-99)	39 (19-67)	-50	9.2 (7)	15 (13)
	4	16.4	76 (2-99)	4.8 (0-13)	99 (99-100)	33 (27-38)	-50	5.9 (3)	9 (5)
	4	4.3	95 (66-100)	11 (0-24)	78 (50-91)	51 (31-75)	-60	183 (99)	376(261)
	4	4.6	99 (92-100)	58 (5-134)	81 (70-97)	47 (42-58)	-50	156 (52)	293 (101)
	4	4.6	97 (0-100)	4.9 (0-13)	60 (18-89)	33 (27-50)	-52	426 (181)	691 (306)
	4	5	99 (63-100)	42 (0-107)	54 (20-79)	31 (0-50)	-61	723 (209)	1048 (378)

4. Regressions of total length (mm) and condition (% dry weight) for age-0, age-1 and age-2 alewife as a function of time (year) s a function of $\log_{10}$ transformed total alewife density (fish/ha). Fish length, condition and density were measured in September-ber (see Table 3). Statistics given are variance explained (r^2), direction of density dependence when r^2 >0.25, number of years ded (N), and significance level (P, two-tailed). Significant relationships at the 0.10 (two tailed test) and below are in bold.

bute	Cayuta Lake	Canadarago Lake	Both lakes combined
ionship with time			
th age-0	r^2=0.21, (+), df=8, P=0.179	r^2=0.46, (-), df=4, P=0.146	r^2=0.07, (0), df=14, P=0.30
th age-1	r^2=0.26, (+), df=6, P=0.198	r^2=0.49, (0), df=3, P=0.186	r^2=0.05, (0), df=11, P=0.48
th age-2	**r^2=0.85, (+), df=6, P=0.001**	r^2=0.33, (0), df=2, P=0.422	r^2=0.20, (0), df=10, P=0.14
lition age-0	r^2=0.08, (0), df=6, P=0.489	r^2=0.01, (0), df=4, P=0.838	r^2=0.02, (0), df=12, P=0.60
lition age-1	**r^2=0.56, (+), df=6, P=0.032**	r^2=0.52, (0), df=3, P=0.171	r^2=0.05, (0), df=11, P=0.46
lition age-2 and older	**r^2=0.40, (-), df=6, P=0.093**	r^2=0.12, (0), df=2, P=0.649	r^2=0.06, (0), df=10, P=0.46
ionship with density			
th age-0	r^2=0.29, (-), df=8, P=0.107	**r^2=0.59, (-), df=4, P=0.074**	**r^2=0.84, (-), df=14, P<0.001**
th age-1	**r^2=0.64, (-), df=6, P=0.017**	r^2=0.42, (0), df=3, P=0.237	**r^2=0.81, (-), df=11, P<0.001**
th age-2	**r^2=0.81, (-), df=6, P=0.002**	r^2=0.23, (0), df=2, P=0.519	**r^2=0.77, (-), df=10, P<0.001**
lition age-0	r^2=0.16, (0), df=6, P=0.321	r^2=0.05, (0), df=4, P=0.678	**r^2=0.48, (-), df=12, P=0.006**
lition age-1	**r^2=0.63, (-), df=6, P=0.019**	r^2=0.50, (-), df=3, P=0.203	**r^2=0.84, (-), df=11, P<0.001**
lition age-2 and older	r^2=0.29, (+), df=6, P=0.166	r^2=0.01, (0), df=2, P=0.881	**r^2=0.61, (-), df=10, P=0.003**

ᵉ 5. Catch per angler hour in Cayuta Lake obtained from the angler diary program. Both catch rates for anglers targeting walleye ᶠor all angler hours are reported. Catch rates of other fish species are based on all angler hours. In 2004, anglers only kept diaries ı fishing for walleye.

ear	Number of cooperators	Number of trips	Total angler-hour	Angler -hour targeting walleye	All walleye (#/hour)	Target walleye (#/hour)	Largemouth bass (#/hour)	Chain pickerel (#/h)	Yellow perch (#/hour)	Sunfish (#/hour)	I c (#
04	3	62	155.0	155.0	0.013	0.013	-	-	-	-	
05	10	152	424.0	122.5	0.024	0.057	0.314	0.191	0.073	0.156	0.
06	5	143	359.0	121.3	0.022	0.033	0.337	0.145	0.042	0.022	(
07	6	184	468.3	184.2	0.019	0.043	0.500	0.175	0.070	0.132	(
08	7	261	558.3	215.4	0.061	0.144	0.638	0.161	0.113	0.052	(
09	3	211	445.8	158.5	0.045	0.126	0.556	0.348	0.070	0.002	(
rage	5.7	168.8	401.7	159.5	0.031	0.069	0.469	0.204	0.074	0.073	(

Figure 1. Average April – October Secchi disk transparency and October zooplankton biomass, density and mean size from 1988 to 2008 in Cayuta and Canadarago Lakes.

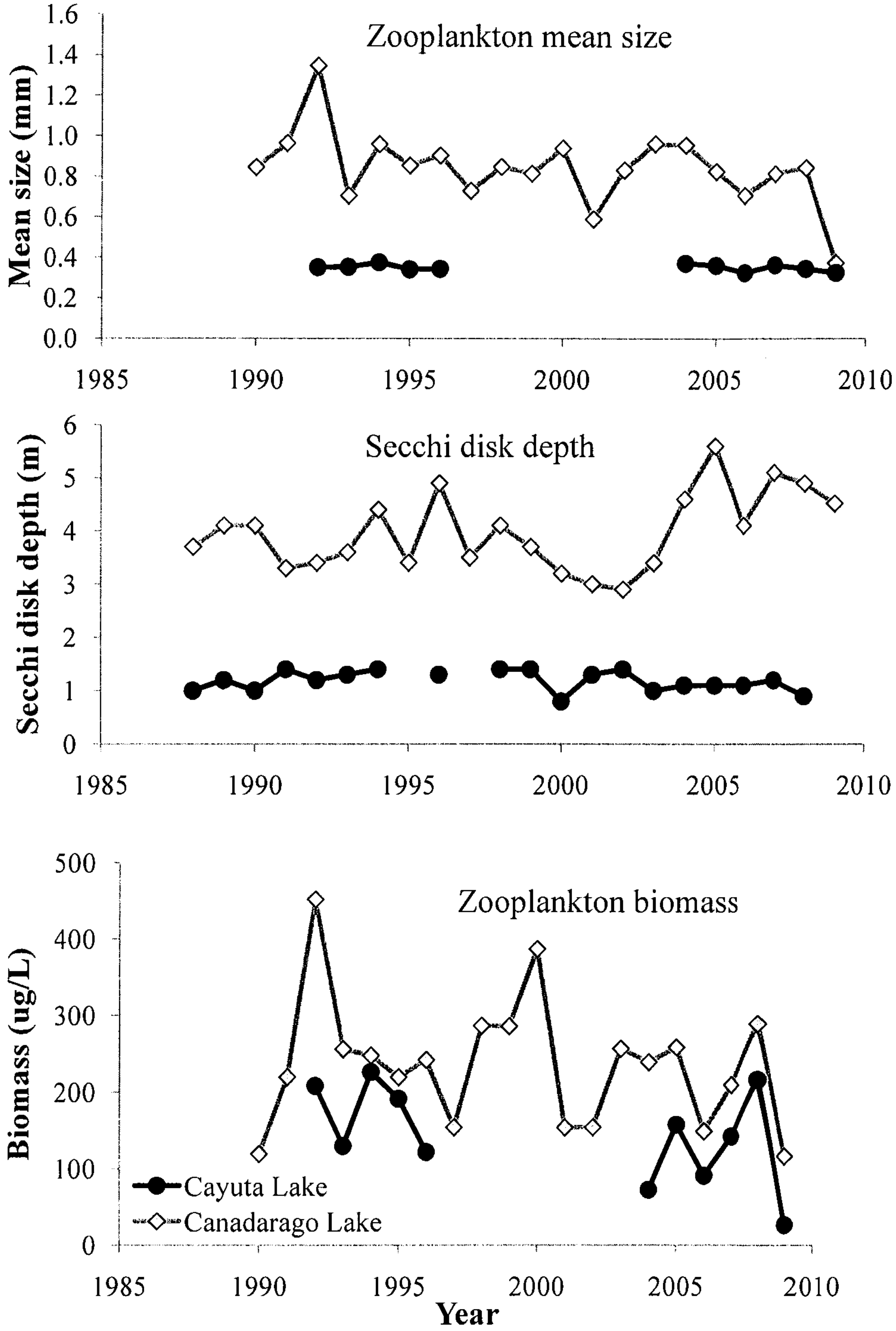

Figure 2. Walleye growth (length at age 4) and condition (relative weight) in Cayuta and Canadarago Lakes from 1995 to 2009. Calculations are based on fall samples (9/30 to 10/27 in Cayuta Lake and 9/27 to 11/4 in Canadarago Lake).

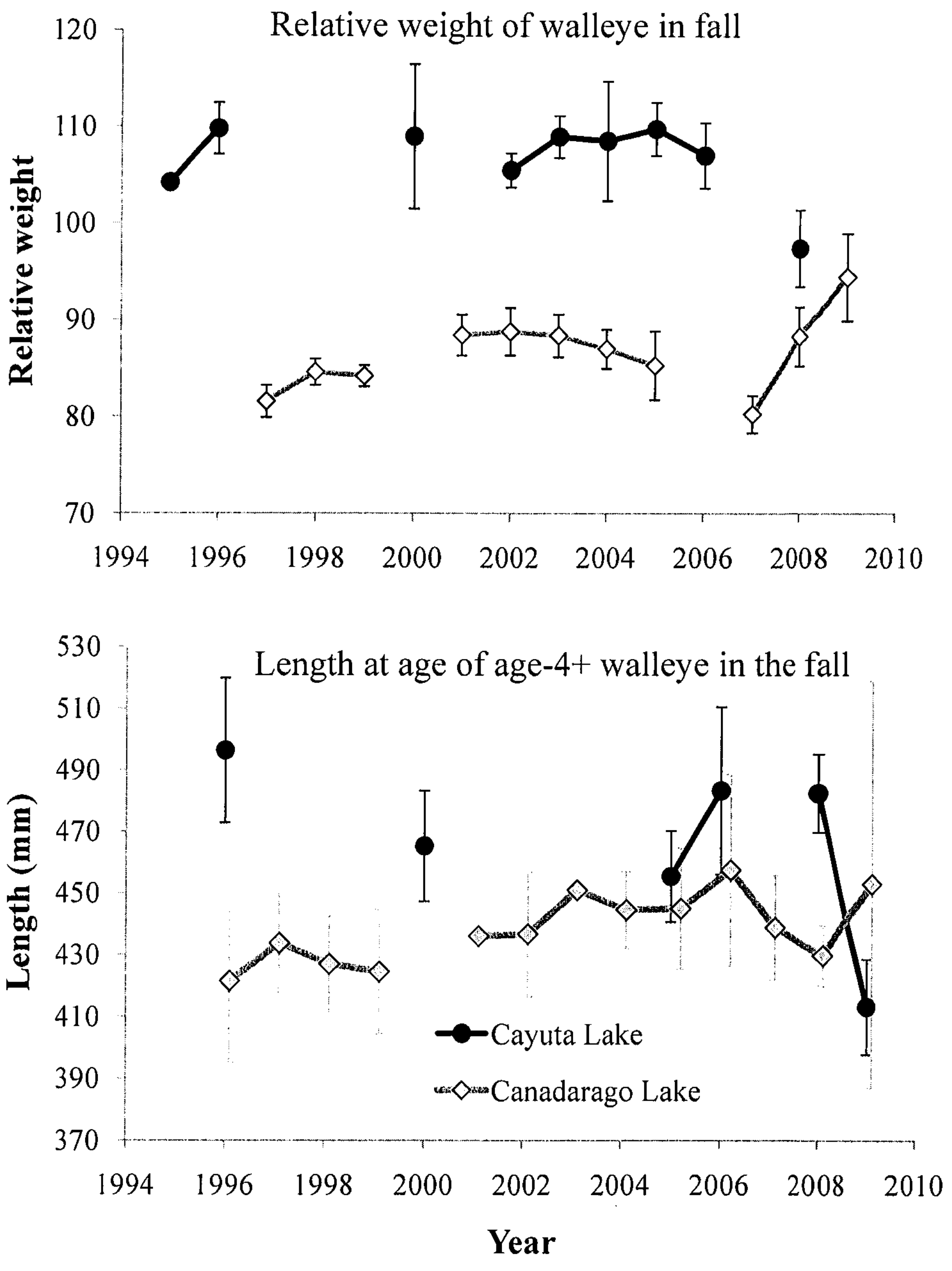

Figure 3. Alewife in Cayuta and Canadarago Lakes A) Alewife abundance, note different scales for the two lakes. B) Alewife length at age 0, age 1 and age 2. C) Alewife condition measured as percent dry weight for age 0, age 1, and age 2+. Symbols are explained in Panel C. There is no growth and condition data from Canadarago Lake for the year 2006.

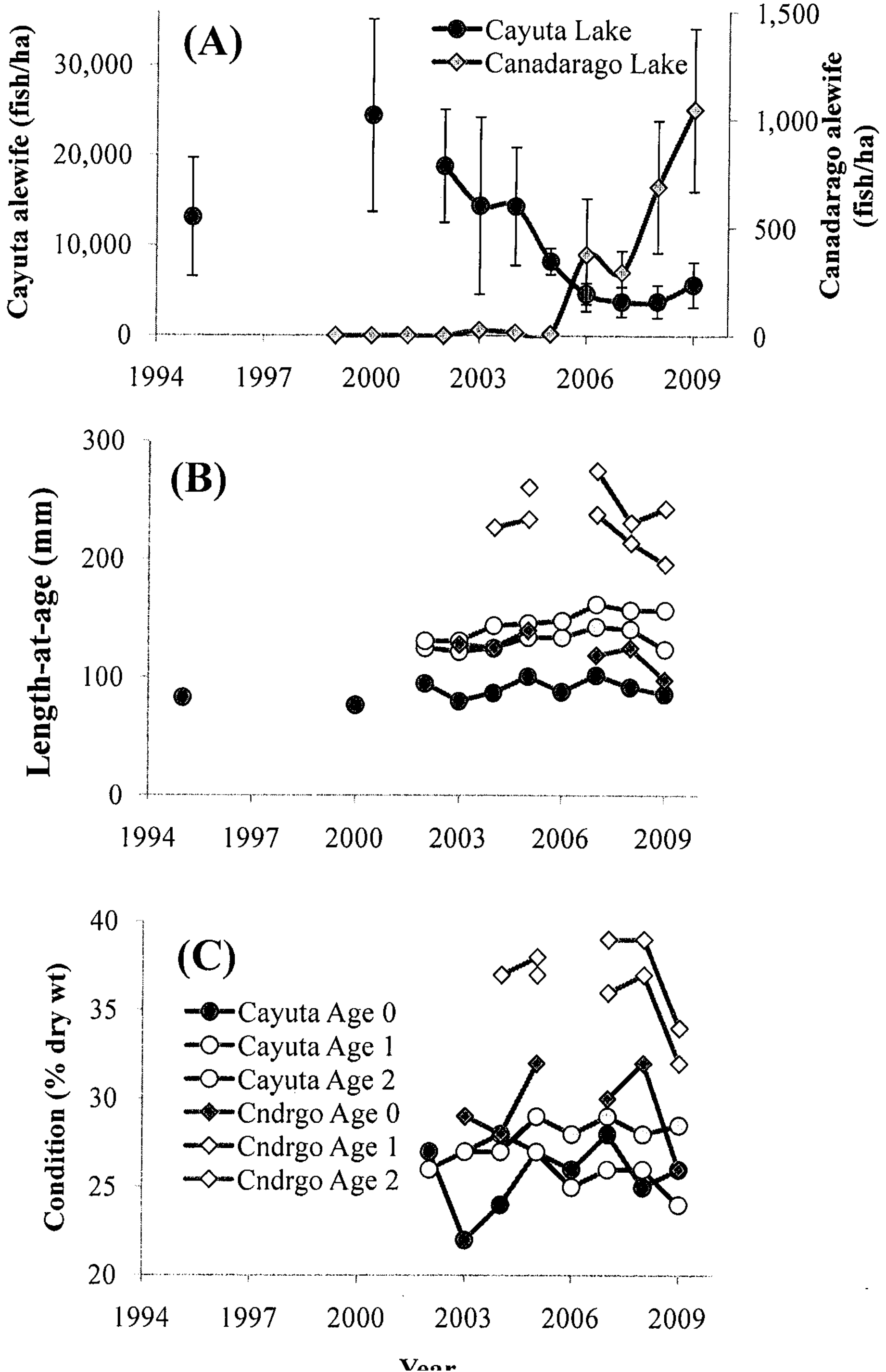

Figure 4. Alewife growth and condition as a function of alewife fall density (all age classes). A) Length at age for age-0, age-1 and age-2 alewife as a function of alewife density. B) Condition measured as percent dry weight as a function of alewife density.

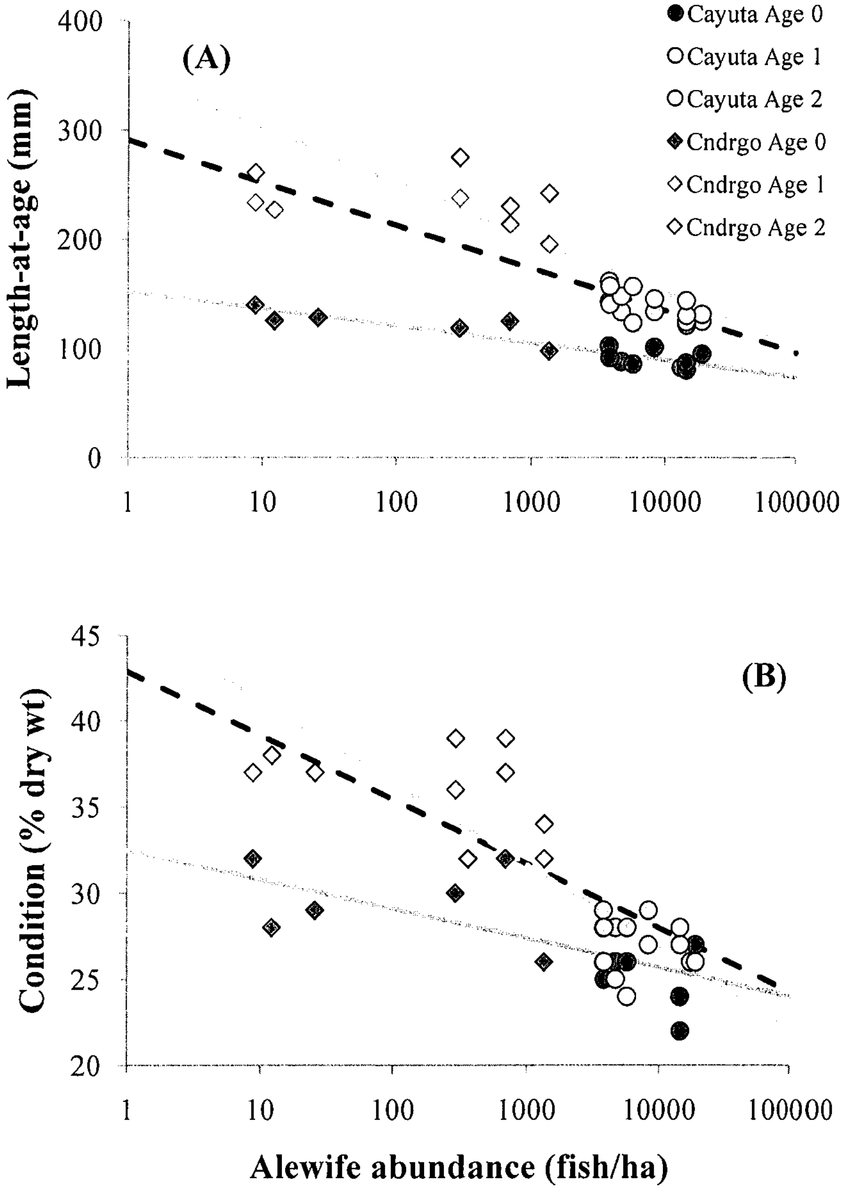

Figure 5. Alewife recruitment as a function of abundance of age-2 and older fish. The line is the Beverton-Holt spawner-recruit curve fitted to the data (see text). Note the logarithmic scale on both axes.

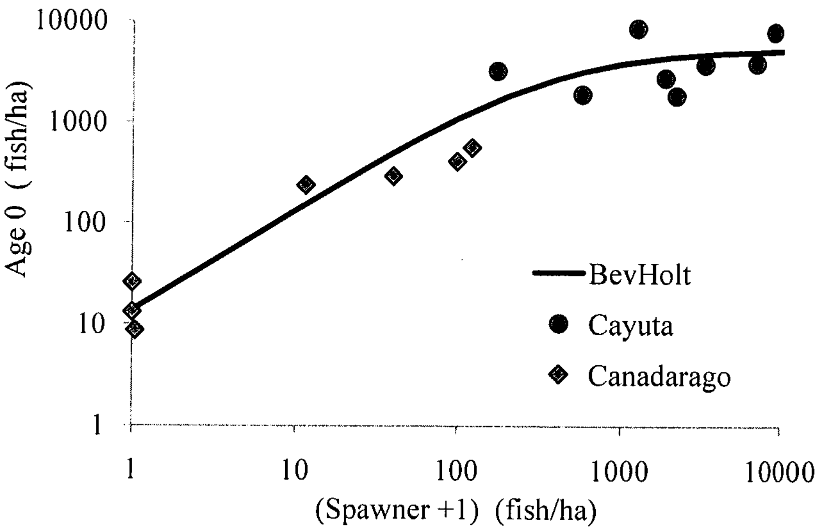

Figure 6. Development of the walleye population in Cayuta Lake New York from 1992 to 2009 based on extrapolation of mortality and abundance data. Alewife abundance (grey squares) is from Table 3. Density (dashed line) and biomass (solid line) of walleye refer to the spring whereas the alewife abundance is for the fall or the same year.