Dynamics of Alewife Recruitment Variability in Lake Michigan

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This project was completed in 2004

Project Rationale

Arguably, the most ecologically important fish species in Lake Michigan is the Alewife *Alosa pseudoharengus* due to its dual role as predator and prey. Alewives are critical for sustaining a diverse planktivore and salmonine community as specified by the Great Lakes Fisheries Commission Fish Community Objectives (FCOs) for Lake Michigan. These FCOs call for annual sustainable salmonine harvests of 2.7 to 6.8 million kg, for self-sustaining lake trout *Salvelinus namaycush* populations, for a diverse planktivore prey base, and for self-sustaining stocks of yellow perch *Perca flavescens* with annual yields of 0.9 to 1.8 million kg. However, objectives for sustainable salmonid and yellow perch fisheries and a diverse planktivore community may be mutually exclusive. An Alewife population of sufficiently high abundance to support adequate growth and survival of salmonids likely will suppress zooplankton biomass, native planktivores, and lake trout populations. This management paradox is recognized in the FCOs for Lake Michigan, but the solution to the problem is not evident. Of premier concern, and at a detriment to our ability to achieve FCOs for Lake Michigan, is the unpredictable and apparent stochastic nature of Alewife recruitment dynamics. Factors controlling abundance of adult alewives include predation by salmon, intra-specific competition, physiological condition and overwinter survival, and upwelling events. However, those factors regulating annual variation in Alewife recruitments are less well understood. Field studies of Alewife early life dynamics in the Great Lakes have been limited, and have revealed little about the mechanisms causing recruitment variability. Furthermore, these earlier studies occurred under conditions of high Alewife abundance; current conditions have changed with alewives less abundant than in the 1980s, thus potentially providing a contrast in density dependent recruitment mechanisms. For example, high overwinter mortality of juvenile alewives was common during the 1960s and 1970s before salmonine predation and a series of cold years decreased Alewife density, increased zooplankton densities, and improved young-of-the-year (YOY) growth rates and overwinter survival. Density dependent effects on recruitment were observed for Alewife in Lake Ontario, where maximum recruitment occurred at intermediate Alewife densities. But, the underlying mechanism for density dependence was not evident.

Objectives

Causes for annual variation in Alewife survival are not well understood, but historically were believed to be related to variation in temperature (duration and severity of winter, upwelling), as well as to salmonine predation and competition from adult alewives. We hypothesize that spatial and temporal variation in thermal habitat and physical advective processes, through their influence on Alewife spawning behavior, larval and juvenile growth rates and spatial distributions, prey and predator availability, and overwinter mortality, determine the temporal and spatial variation in Alewife survival and recruitment. Our overall objective is to identify and quantify those factors that regulate Alewife recruitment in Lake Michigan.

Specific Objectives

- to quantify larval and young-of-the-year (YOY) Alewife abundance, their zooplankton prey, and predators in Lake Michigan proper and in tributary embayments
- to determine origin (lake vs. tributary mouth) and thermal history of surviving late stage larvae and YOY alewives
- to estimate and compare growth, survival, and potential recruitment of larval and YOY Alewife from the lake proper and tributary embayments
- to link origin, abundance, growth, condition and survival of larvae and YOY alewives to overwinter survival and eventual recruitment
- to analyze historical databases on Alewife recruitment variability under low to high Alewife abundances, and compare these patterns with our results at current, low-intermediate Alewife abundances
- to develop regression models to predict Alewife recruitment variability for use in management of Lake Michigan's salmonine fisheries

2004 Progress

Much of our effort has centered on processing the remainder of laboratory samples of alewives, their predators and prey. We have found significant differences in larval fish catch between day and night and are currently adjusting our day catches based on this information. Otolith microchemistry continues to look promising. Oxygen stable isotope (δ18O) in the water differs between drown river months and Lake Michigan proper. Preliminary data suggesting we can discern origin of larvae by looking at δ18O in the otoliths of larval fish. Field observations continue to suggest that there is a size threshold (65mm) that larvae much achieve before winter to survive to spring. Lastly, we have developed as statistical spawner-recruit model that appears to reproduce historical recruitment of Alewife in Lake Michigan.

Objective: Quantify, Fish Larvae, Predators and Zooplankton Prey

Much of our effort has centered on processing the remainder of laboratory samples of alewives, their predators and prey. We are now revising estimates of YOY Alewife abundance based upon suspected extrusion of larvae through the larger mesh sizes, and avoidance of sampling gear by late larvae and early juveniles. Data illustrating potential extrusion and avoidance by larvae of gear are shown in Figures 1-3. Figure 1 indicates catches of small larvae were highest in 335 µm mesh nets, catches of intermediate sized larvae were highest in 500 µm mesh nets, and catches of larger larvae and small juveniles were highest in the 700 µm Tucker trawl sampler. Catches of large larvae and small juveniles were much higher during night than during day, indicating net avoidance (Figures 2 and 3). We are currently developing regression equations relating relative size-specific catches of larval alewives to mesh size and time of day. We will use these equations to adjust densities, thereby providing more accurate estimates of size-specific abundances. The adjusted densities will also improve our estimates of larval mortality rates.

We are beginning to analyze hydroacoustic estimates of potential predator abundances of YOY alewives in nearshore Lake Michigan and Muskegon Lake. We completed analysis of zooplankton prey samples from 2001, and are finishing analysis of the 2002 samples. We will use these to relate larval growth rates of Alewife cohorts to zooplankton prey densities and temperatures, as part of an effort to quantify the relative importance of habitat factors affecting Alewife larvae survival.

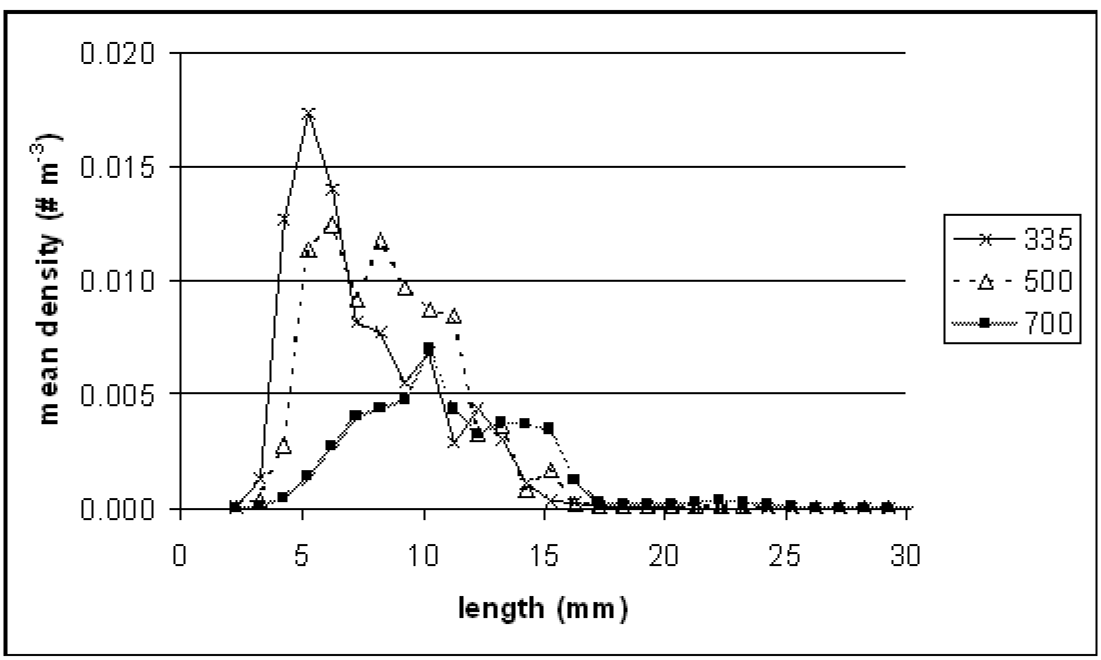

***Figure1**: Density (No. m-3) of Alewife larvae and juveniles collected in 335-µm, 500-µm and 700-µm mesh sizes at the same dates and locations during summer, 2002 in Muskegon Lake and Lake Michigan.*

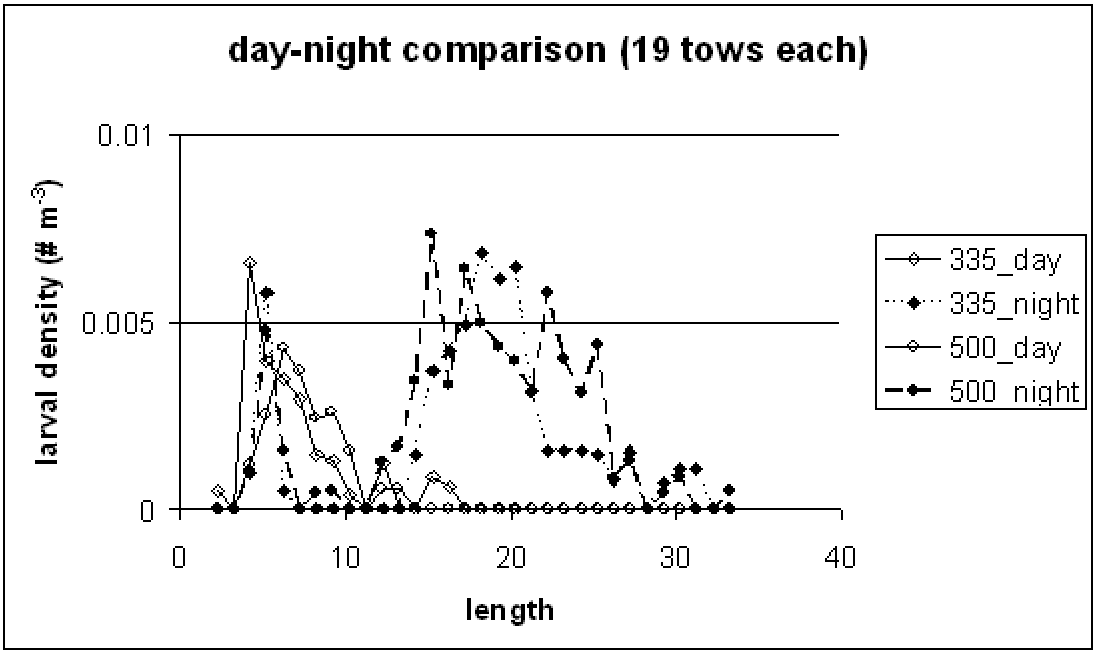

Figure 2: *Density (No. m-3) of Alewife larvae collected during day and night tows in 335- and 500-µm mesh nets of the 0.6-m diam. bongo sampler during summer 2002.*

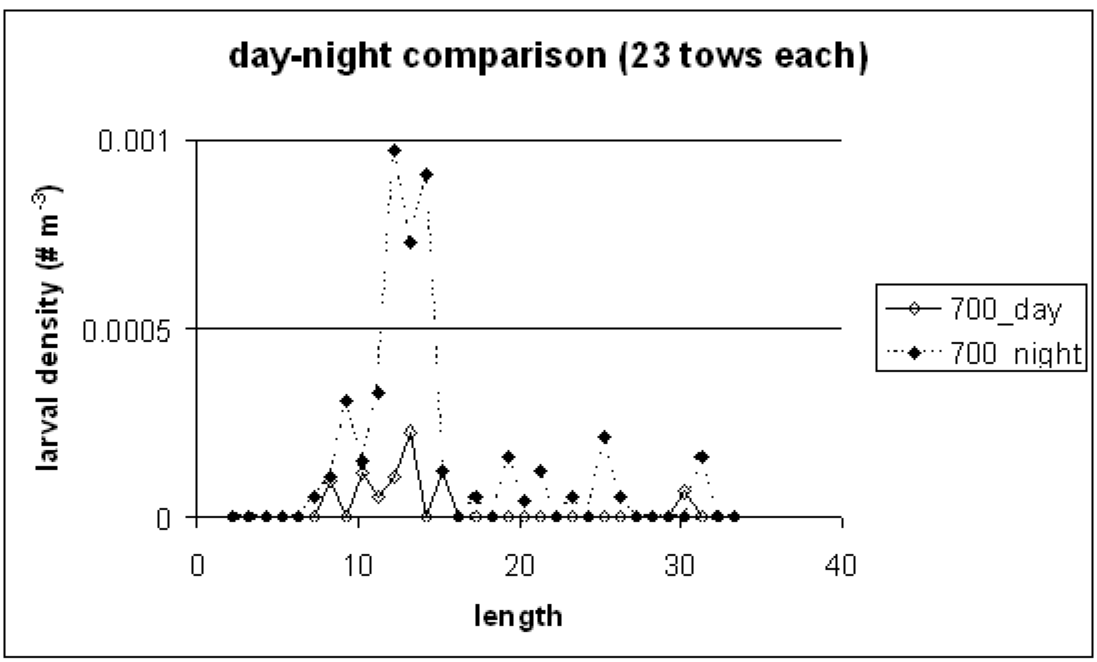

Figure 3: *Density (No. m-3) of Alewife larvae collected during day and night samples by the 700-mm mesh, 2m2 Tucker trawl during summer, 2002.*

Objective: Determine origin (lake vs. drowned river mouth) and thermal history of surviving late stage larvae and YOY alewives:

In order to determine the natal origin and preferred larval temperature of surviving YOY alewives captured in Lake Michigan and Muskegon Lake, YOY otoliths were micro-sampled and isotopically measured. One hundred thirty six out of 163 specimens provided valid core values. Sixty-two water samples collected during 2002 and 2003 were analyzed to assess oxygen isotope variability in source waters. Water samples collected in 2003 confirm that discernable variation in ?18Owater exists among the different collection sites. Moreover, ?18O values for Lake Michigan proper did not vary greatly between years (2002 and 2003) or among depths.

Objectives: Estimate vital rates of larvae, and link origin, abundance, growth, condition and survival of larvae and YOY alewives to overwinter survival and eventual recruitment, and identify factors influencing recruitment variability in the first year of life:

We compared length distributions of YOY alewives collected in nearshore Lake Michigan and Muskegon Lake in 2002 with length distributions of alewives that survived to spring 2003. The comparison suggested that YOY alewives that survived overwinter exceeded 65 mm, and were similar in length to alewives sampled from Muskegon Lake. Environmental temperature reconstructions of survivors from Lake Michigan also indicate that most individuals inhabited warm areas of Lake Michigan during summer. These results suggest that warm environments that promote growth of larvae are important to survival and potential recruitment of Lake Michigan alewives. We are presently analyzing survival and growth of Alewife cohorts born over late spring and summer in 2001 and 2002 to infer which cohorts contribute the majority of survivors.

Objective: Analyze historical databases on Alewife recruitment variability under low to high Alewife abundances, and compare these patterns with our results at current, low-intermediate Alewife abundance:

We conducted an analysis of Alewife recruitment variability using annual indices of Alewife abundance as indexed in USGS monitoring surveys. The analysis has been completed. The manuscript is “In Press” in Transactions of the American Fisheries Society.

We used a long-term series of observations on Alewife *Alosa pseudoharengus* abundance, based on fall bottom trawl catches, to assess the importance of various abiotic and biotic factors on Alewife recruitment in Lake Michigan during 1962-2002. We fit a basic Ricker spawner-recruit model to the lakewide biomass estimates of age-3 recruits and the corresponding spawner stock size, and then fit models for all possible combinations of the following four external variables added to the basic Ricker spawner-recruit model: an index of salmonine predation on an Alewife year-class (PRED), an index for the spring-summer water temperatures experienced by alewives during their first year in the lake (SUMMER), an index of severity of the first winter experienced by alewives in the lake (WINTER), and an index of lake productivity during an Alewife year-class’s second year in the lake (TP). Based on an information criterion, the best model for Alewife recruitment included PRED and SUMMER as external variables. Our analysis corroborated the contention that the decline in Alewife abundance during the 1970s and early 1980s in Lake Michigan was driven by salmonine predation. Furthermore, our findings indicated that the extraordinarily warm water temperatures during spring and summer of 1998 likely led to a moderately high recruitment of age-3 alewives in 2001, despite the high level of salmonine abundance.

Prior Accomplishments

During the spring, summer, and fall of 2001 and 2002, we sampled age 0 alewives (using plankton nets, hydroacoustics and trawls) in near shore Lake Michigan and three drowned river mouths (Muskegon Lake, Manistee Lake, and Pigeon Lake). We characterized and related physical (temperature, transparency, etc.) and biotic (zooplankton, fish predators, etc.) habitat factors to habitat-specific hatch dates, growth rates and mortality rates, estimated from otolith increment patterns and temporal changes in densities at age. We completed the thrust of our field work during fall 2002. However, for the purpose of characterizing surviving alewives from the 2002 year-class, we augmented our field sampling by trawling for yearling alewives in Lake Michigan during spring 2003. Our laboratory analyses of samples collected during 2001-2003 are ongoing.

Quantify Fish Larvae, Predators and Zooplankton Prey: Surveys to sample ichthyoplankton and zooplankton were conducted on a weekly basis from May through July, biweekly in August and September, and once in October. Surveys were conducted using a combination of NOAA vessels RV Cyclops (7-m), RV Remorse, and RV Shenehon (16-m). We used a stratified random design to sample zooplankton and larval Alewife in Muskegon Lake and Lake Michigan. At each station, we estimated densities of Alewife larvae and their zooplankton prey, and made a CTD cast from surface to bottom to profile temperature and chlorophyll a. We estimated zooplankton prey densities by taking bottom-to-surface, vertical tows with 64 and 153-mm zooplankton nets. We estimated ichthyoplankton densities at each site with a 60-cm diameter bongo sampler with 335 and 500-mm mesh nets. To catch larger alewives that would avoid the bongo sampler, we also used a 2-m2 Tucker trawl sampler of 700-mm mesh. We towed all ichthyoplankton samplers obliquely for 5-minutes from bottom to surface. We measured the volume of water filtered by plankton samples with flow meters placed inside the nets. The volume of water filtered by zooplankton nets varied with station depth. The bongo and Tucker trawl samplers filtered approximately 100 m3 and 1000 m3 of water, respectively. In addition to the randomly selected stations, we collected bi-monthly samples of zooplankton and fish larvae at 3 fixed stations (15, 45, 110 m) in Lake Michigan and at 1 station in Muskegon Lake.

Physical and Biological Environment: During both 2001 and 2002, Muskegon Lake warmed sooner, reached a greater maximum temperature, and subsequently cooled at an earlier date than nearshore Lake Michigan. Chlorophyll a measurements indicated consistently higher productivity in Muskegon Lake and measures of secchi depth in Muskegon Lake and Lake Michigan also suggested that Muskegon Lake was far more productive. Annual differences in primary and secondary productivity were not as evident as habitat differences, but on average chlorophyll a concentrations were higher in 2002 than in 2001.

Zooplankton prey in Muskegon Lake and Lake Michigan were analyzed from net tows taken at our icthyoplankton sampling stations (augmented by tows taken at NOAA monitoring stations). Zooplankton prey densities were remarkably similar between years, and between inshore and offshore areas of Lake Michigan. During 2001 and 2002, rotifers, zebra mussel (Dreissena polymorpha) veligers (referred to hereafter as veligers), and to a lesser degree copepod Nauplii were the dominant zooplankton captured in nearshore Lake Michigan. During both years, rotifers were the dominant zooplankter sampled on virtually all dates. In 2001, densities of veligers and cladocerans (mostly Bosmina) were also relatively high. To consider the relative availability of Alewife prey, we grouped zooplankton into two size-based categories. This grouping suggested that during both 2001 and 2002 densities of small-bodied zooplankton (i.e. those likely to be consumed by larval alewives) tended to be higher in Muskegon Lake (relative to Lake Michigan). Densities of large-bodied zooplankton however were not dramatically different between the two habitats.

We indexed potential predator abundances of YOY alewives using hydroacoustics. We have not yet processed these data, but initial inspection suggests that during both years potential predator densities were dramatically greater in Muskegon Lake than nearshore Lake Michigan.

Alewife Larvae and Juveniles: During both 2001 and 2002, larval Alewife peak densities were greater in Muskegon Lake than nearshore Lake Michigan. In addition, larval alewives in drowned-river mouths (Muskegon, Manistee, and Pigeon lakes) began to emerge earlier relative to Lake Michigan.

Fall trawling suggested that YOY Alewife densities were not dramatically different among habitats. However, size-distributions indicated that YOY alewives in Muskegon Lake were larger compared to individuals in Lake Michigan.

Estimate and compare growth, survival, and potential recruitment of larval and YOY Alewife from the lake proper and tributaries: To facilitate estimation of habitat-specific growth, mortality, and recruitment rates, we have measured the total lengths and wet weights of thousands of larval alewives captured during our field sampling. We use these measurements together with counts of daily growth rings on sagital otoliths to generate growth rate estimates. Based on individuals analyzed to date, we estimate that larval alewives in Muskegon Lake grew faster (2001: 0.66 mm day-1, n=117, R2=0.77; 2002: 0.84 mm day-1, n=42, R2=0.95) compared to individuals captured in Lake Michigan (2001: 0.59 mm day-1, n=43, R2=0.72). This pattern is consistent with warmer summer temperatures (Figure 1) and greater densities of small-bodied zooplankton in Muskegon Lake. We rely on temporal changes in densities to estimate mortality rates. Based on this approach, we estimate higher instantaneous mortality rates (Z) for Lake Michigan (2002: Z=0.31) compared to Muskegon Lake (2001: Z=0.15; 2002: Z=0.20). This result is somewhat surprising given that acoustic surveys suggest that densities of potential larval Alewife predators are greater in Muskegon Lake. Perhaps other non-predatory sources of mortality (e.g. starvation and upwelling events) are more important in Lake Michigan. We enumerated prey items in the stomachs of larval alewives captured during July 2001, and found a greater percentage of empty stomachs among Lake Michigan fish (47%, n=15), relative to Muskegon Lake fish (13%, n=39). In addition, upwelling events (a hypothesized source of mortality for age-0 alewives) occur with some frequency in Lake Michigan, but not Muskegon Lake.

In order to estimate the ultimate habitat-specific contribution of recruits to the adult Alewife population, we have built a cohort-based model that simulates daily cohorts of age-0 alewives in two habitat-types (nearshore Lake Michigan and drowned-river mouth lakes) from emergence to the beginning of winter. This model uses our field and laboratory derived estimates of habitat-specific larval densities, emergence dates, and growth and mortality rates as inputs. The model is still being refined, but initial simulations suggest that drowned-river mouth lakes yield a disproportionate (relative to volume) number of recruits to the adult population, and that the recruits from this habitat-type tend to be larger. Nonetheless, given that nearshore Lake Michigan contains a much greater volume of water this habitat-type may ultimately produce a much greater number of overall recruits at the beginning of winter.

Identify factors influencing Alewife recruitment variability. We have compiled data from several sources in order to identify factors which affect annual variation in Alewife recruitment success. We rely upon historical USGS fall bottom-trawling survey data to index annual variation in Alewife year-class strength. We are exploring potential links between year-class strength and the following variables; annual consumption of alewives by salmonines (based on published mixed-models), annual indices of summer temperature (based on water intake data), annual indices of winter severity (based on water intake data), annual variation in water levels, and annual indices of river discharge (based on USGS gauging stations).

Products

Publications

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

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Reports

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Presentations

Höök, Tomas, Edward Rutherford, Doran M. Mason, Charles P. Madenjian, and Jeffrey A. Tyler. *Annual variation in habitat-specific contributions of Alewife recruits in Lake Michigan*. 134th Annual Meeting of the American Fisheries Society. Madison WI. August 21-26, 2004.

Höök, Tomas, Edward Rutherford, Michael McCormick, Dmitry Beletsky, David Schwab, Glenn Carter, and Doran Mason. 2004. *Using hydrodynamic models and satellite-tracked drifter buoys to estimate larval Alewife transport and mortality rates in Lake Michigan*. 47th Annual Conference of the International Association of Great Lakes Research. Waterloo, Ontario, Canada. May 24-28, 2004.