

Hatch Dates, Growth, Survival, and Overwinter Mortality of Age-0 Alewives in Lake Michigan: Implications for Habitat-Specific Recruitment Success

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Abstract.—Alewives *Alosa pseudoharengus* are key components of Laurentian Great Lakes ecosystems and spawn in multiple habitat types. Exploration of alewife early life history dynamics within these different habitats should help identify important recruitment processes. During 2001–2003, we quantified physical (temperature, transparency) and biotic (chlorophyll *a*, zooplankton densities) habitat factors and collected age-0 alewives (using ichthyoplankton nets and trawls) in a nearshore region of Lake Michigan and Muskegon Lake, Michigan (a drowned river mouth lake connected to Lake Michigan). We characterized alewife hatch dates, individual condition, growth, mortality, and size-dependent overwinter survival to infer differences in habitat-specific recruitment success. Temperature, turbidity, chlorophyll-*a* concentrations, and densities of zooplankton prey were consistently higher in Muskegon Lake than in nearshore Lake Michigan. On average, young alewives in Muskegon Lake hatched earlier, grew faster, were in better condition (based on a biphasic length–weight relationship), and had greater survival than alewives in Lake Michigan. By the end of the growing season, young alewives in Muskegon Lake obtained a larger size than those residing in nearshore Lake Michigan, suggesting that they were more likely to survive through winter (a period of intense size-selective mortality) and ultimately recruit to the adult population.

Identification of fish nursery habitats that contribute disproportionate (relative to their size) numbers of individuals to the adult population (Beck et al. 2001) can guide habitat management efforts and monitoring activities. Such habitats should not only contain a large number of young fish but also support relatively higher growth and lower mortality rates (Houde 1997). Further, characterization of early life dynamics within such habitats can help elucidate important recruitment processes.

Populations of nonnative alewives *Alosa pseudoharengus* are ecologically important components of

Laurentian Great Lakes ecosystems and constitute the forage base for economically valuable salmonid fisheries (Stewart and Ibarra 1991; Madenjian et al. 2002). Annual recruitment variability of alewives in the Great Lakes is high and appears to be related to spawning stock size, predation by salmonines, summer temperatures, and winter severity (Henderson and Brown 1985; O’Gorman et al. 2004; Madenjian et al. 2005). Unlike in their native range, alewives in the Great Lakes are not anadromous, but they do migrate inshore and into tributary waters to spawn. In turn, young alewives in Lake Michigan hatch in a variety of habitat types (Goodyear et al. 1982), including nearshore Lake Michigan proper (Jude et al. 1981b), bays (Wagner 1972), drowned river mouth lakes (Jude et al. 1981a; Höök 2005), harbors (Norden 1967), and tributaries (Edsall 1964; Brown 1972; Mansfield

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1984). There is evidence that most young alewives in Lake Michigan spend their first few months of life in their natal habitat (Dufour et al. 2005), and it is likely that alewives then migrate into deep offshore waters (where there is some thermal refuge) before winter (Wells 1968; but see Bergstedt and O'Gorman 1989).

Survival of young alewives in Lake Michigan from hatching (May–August) through their first year of life (the subsequent spring) is mediated by seasonal selective processes. During early life, fish probably experience high rates of size-dependent mortality primarily as a result of two processes: starvation and predation (Miller et al. 1988; Houde 1997, 2002). Starvation becomes less likely with increasing size because of greater energy reserves and reduced mass-specific metabolic rates. Similarly, vulnerability of young fish to predators also tends to decrease with size because of (1) greater swimming speeds (thereby enhancing ability to escape from potential predators) and (2) decreased vulnerability to gape-limited predators. In keeping with the expectation that larger individuals have higher survival rates, Mansfield and Jude (1986) found that survival of age-0 alewives increases with size. Further, the condition of alewives in Lake Michigan declines dramatically overwinter (Flath and Diana 1985; Stewart and Binkowski 1986; Madenjian et al. 2006), and several authors have suggested that age-0 alewives must reach some minimum size (sufficient energy reserves and low mass-specific metabolic rate) to survive this period of resource scarcity (Brown 1972; Flath and Diana 1985; O'Gorman and Schneider 1986; Bergstedt and O'Gorman 1989; Höök 2005).

The temporal association between temperature and lakewide alewife recruitment success (e.g., Madenjian et al. 2005) suggests the possibility of a spatial relationship, where warmer habitats confer a recruitment advantage to young-of-the-year (hereafter, age-0) alewives. In keeping with this expectation, Höök (2005) suggested that larval alewife densities are greater in drowned river mouth lakes (warm, sheltered habitats connected to Lake Michigan, analogous to estuaries; Herdendorf 1990) than in nearshore Lake Michigan. In contrast, Klumb et al. (2003b) found that larval alewife densities were similar between embayments and exposed nearshore regions of Lake Ontario. Thus, the overall importance of sheltered habitats for recruitment of alewives in the Great Lakes remains unclear.

Habitats that support early hatching and fast growth of young alewives should favor higher survival from summer to fall and overwinter. Age-0 alewives that occupy such habitats may thus obtain a recruitment advantage over individuals that occupy habitats

supporting late hatching and slow growth. During 2001–2003, we studied young alewives in two habitats: Muskegon Lake, Michigan, a drowned river mouth lake connected to Lake Michigan, and the nearshore area of Lake Michigan proper, adjacent to Muskegon Lake. Past studies suggest that (1) there is limited movement between these two habitats by alewives during early life (i.e., within ~20 d posthatch; Dufour et al. 2005) and (2) water currents rapidly advect larval alewives throughout Lake Michigan proper (Höök et al. 2006). Thus, while larval alewives captured in Muskegon Lake have probably spent their entire life within this habitat, larval alewives captured within a nearshore area of Lake Michigan may have hatched throughout the lake proper (i.e., characteristics of these alewives reflect conditions in various areas of Lake Michigan). We measured physical and biological attributes of these two environments and collected young alewives throughout the entire growing season and subsequent spring. Our objectives were to characterize growth environments, hatch dates, condition, early growth and mortality rates, and size-dependent overwinter survival of age-0 alewives to infer differences in habitat-specific recruitment success.

Methods

During 2001–2003, we sampled young alewives and their ambient environments in (1) Muskegon Lake (1,712-ha drowned river mouth lake connected to Lake Michigan at the mouth of the Muskegon River) and (2) the nearshore Lake Michigan area (28,500 ha; depth < 50 m) adjacent to Muskegon Lake (Figure 1). Details of sampling are presented by Höök (2005). In summary, during 2001 and 2002, we used a random survey design to characterize the two habitats. Each sampling week, we randomly selected four stations per habitat. Habitats were sampled weekly during mid-May through July and biweekly during August–October. At each station, we collected larval fish and zooplankton with plankton nets and measured temperature (surface and entire water column), light attenuation, and chlorophyll *a* throughout the water column. In addition, during late summer and fall 2002 and spring 2003, we used midwater and bottom trawls in these two habitats to collect larger age-0 and age-1 alewives. Finally, to increase the spatial breadth of habitat comparisons, we also conducted less-frequent sampling (approximately biweekly from mid-May to mid-August) of two other drowned river mouth lakes (Pigeon and Manistee lakes, Michigan) and Muskegon Channel (connecting channel draining Muskegon Lake into Lake Michigan; Figure 1).

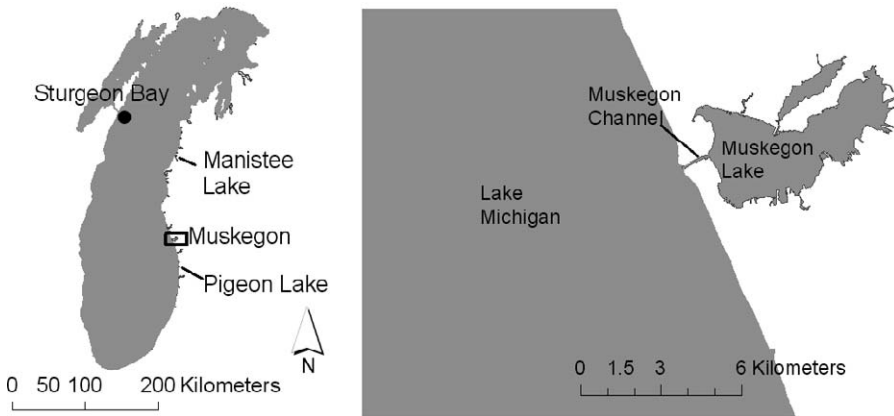


FIGURE 1.—Maps depicting Lake Michigan alewife sampling locations (left) and the Muskegon Lake, Michigan, and nearshore Lake Michigan study area (right).

Physical and biological environments.—We characterized thermal and light environments by measuring (1) surface water temperatures (0.5 m below the surface); (2) thermal profile (measurements at 1-m depth intervals) with a Sea-Bird conductivity, temperature, and depth (CTD) profiler; and (3) Secchi disk depth. We quantified biological environments with measures of fluorescence (a proxy of chlorophyll *a*) and zooplankton biomass. Fluorescence was measured with a Sea-Tech fluorometer mounted on the CTD profiler (at 1-m depth intervals).

Zooplankton biomass was determined from vertical tows (from 1 m above bottom to surface) with the use of two zooplankton nets (0.31-m diameter and 64- μm mesh; 0.5-m diameter and 153- μm mesh), both fitted with flowmeters. We deployed each net one time at each station (within a habitat, we collected four zooplankton samples per net per week). Upon retrieval of the nets, samples were concentrated, zooplankton were anesthetized with carbonated water, and contents were preserved in 10% sugar-buffered formalin. In the laboratory, we removed 1-mL aliquots from preserved zooplankton samples of known volume (before removing aliquots, samples were neither diluted nor concentrated). We counted all animals within aliquots. If a single aliquot did not contain at least 600 animals, we removed and counted animals from additional aliquots until this minimum count was surpassed (for the vast majority of samples, we examined more than one aliquot to count 600 animals). For samples from the 153- μm -mesh net, we used a dissecting microscope to identify all zooplankters from each aliquot to the lowest possible taxonomic level, primarily by use of keys in Edmondson (1959), Balcer et al. (1984), and Hudson et al. (1998). For samples from the 64- μm -

mesh net, we focused on very small zooplankton that would easily pass through the 153- μm -mesh net. Based on our assessments, the very small-bodied zooplankton overwhelmingly consisted of three categories (rotifers, copepod nauplii, and veligers of zebra mussels *Dreissena* spp.); thus, we only identified and counted these three types of small-bodied zooplankton. We converted densities (number/ m^3) to biomass (g/m^3) using published taxa-specific individual masses (Hall et al. 1970; Nalepa 1972; Hawkins and Evans 1979; Sprung 1993; Burkhardt and Lehman 1994; Makarewicz et al. 2001; H. Vanderploeg, National Oceanic and Atmospheric Administration [NOAA] Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan, unpublished data).

Larval alewife collections.—We sampled alewives by use of (1) a 60-cm-diameter bongo sampler with paired 335- and 500- μm -mesh nets and (2) a 2.0- m^2 Tucker trawl sampler with 700- μm mesh (to collect larger fish that were able to avoid the bongo sampler). During 2001, we used the bongo sampler to collect alewife larvae in Muskegon Lake and Lake Michigan from 14 May to 14 September and used the Tucker trawl from 9 July to 30 October. During 2002, we deployed the bongo sampler from 13 May to 27 August and the Tucker trawl from 24 June to 28 August. We towed all ichthyoplankton samplers obliquely at 0.5–1.0 m/s (1–2 knots) for 5 min from near bottom to surface. All specimens were preserved in 90% ethanol. In the laboratory, we identified alewife larvae and juveniles by use of taxonomic keys (Auer 1982; Wallus and Kay 1990). We measured total lengths (nearest 0.1 mm) and wet weights (nearest 0.05 mg) of 30 randomly selected individual alewives from each net sample. Lengths were measured with a dissecting microscope

and camera with Optimus image analysis software, and weights were measured after blotting individuals to remove excessive liquid. If fewer than 30 alewives were caught in a sample, we measured lengths and weights of all individuals. To account for specimen shrinkage due to preservation in ethanol, we adjusted lengths by multiplying postpreservation measures by 1.1 (S. Ludsin, NOAA Great Lakes Environmental Research Laboratory, unpublished data).

Hatch dates.—To compare temporal hatching distributions among habitats, we noted sampling weeks when at least one alewife larva smaller than 6.0 mm was captured in a given habitat. We chose this length threshold to index recent hatching, in part because the majority of otoliths examined from alewives smaller than 6.0 mm had no growth increment or only one increment (i.e., maximum age of 3 d; see below). On the other hand, the duration of yolk sac absorption can be more variable (sometimes >3 d). We estimated the average hatch date (hatch) in Muskegon Lake and Lake Michigan as

$$\text{hatch} = \frac{\sum \text{day}_i \times \text{dens}_i}{\sum \text{dens}_i}, \quad (1)$$

where day_i is the day of year (days 1–365) of a sampling trip and dens_i is the mean density of larval alewives smaller than 6.0 mm collected in the 335- μm net (i.e., the finest-mesh net) during day_i .

Fish condition.—We evaluated differences in the condition of young alewives by comparing length–weight relationships between individuals captured in Lake Michigan and Muskegon Lake. We initially assumed a single-phase exponential relationship between length (L) and weight (W). To estimate such a relationship, we plotted $\log_e(L)$ versus $\log_e(W)$ for individual alewives between 3.5 and 30.0 mm. This plot revealed a clear biphasic length–weight relationship. We used a nonlinear fitting routine to estimate the biphasic break point for the $\log_e(L)$ – $\log_e(W)$ relationship. We then compared differences in $\log_e(W)$ among habitats with analyses of covariance (ANCOVAs) using $\log_e(L)$ as a covariate and habitat as a factor. In total, we conducted four ANCOVAs (i.e., separate analyses for 2 years [2001 and 2002] and two size ranges [i.e., individuals above and below the biphasic break point]).

Growth rates.—We used individual alewife lengths and counts of daily growth increments on otoliths to generate estimates of growth rates for alewife cohorts. We removed both sagittal otoliths from individual alewives (3.5–30.0 mm in length; $n = 485$) under a dissecting microscope. We placed individual otoliths in immersion oil on a microscope slide, covered otoliths

with epoxy and a coverslip, and allowed the epoxy to harden in a drying oven. Otoliths were examined with a compound light microscope to count daily growth increments. For each otolith, growth increments were counted on two occasions (on separate dates) by different individuals. If counts did not agree, then growth increments were counted a third time and the median count was assigned to the individual. Daily growth increments have previously been used as proxies for larval alewife ages; larvae probably begin to deposit daily growth increments on approximately their second day of life (Essig and Cole 1986; D. Jude, University of Michigan, Ann Arbor, personal communication). Thus, to assign ages (d) to individual larvae, we added 2 to the number of growth increments counted.

The effect of growth rate on individual alewife recruitment success is partially dependent on hatch date, which determines time duration of growing season for reaching a sufficient size by winter. Thus, habitat-specific growth rates and hatch dates should be considered concomitantly (i.e., it is less meaningful to compare growth rates of larvae hatching in May in one habitat with those of larvae hatching in August in another habitat; see Ludsin and DeVries 1997). Therefore, we compared growth rates of alewives from Muskegon Lake and Lake Michigan at three temporal scales: (1) all larvae captured in a specific habitat during a single year; (2) larvae with an estimated hatch date between 15 June and 15 July (i.e., the peak hatching period in both habitats); and (3) weekly cohorts (i.e., larvae grouped by estimated hatching week). Larval alewives with no apparent growth increments on their otoliths could be 0, 1, or 2 d old; thus, we excluded such individuals when estimating cohort-specific growth rates. By plotting individual lengths versus estimated age, we found that larval alewife growth in length appears to be fairly well described by a linear model (at least up to 30 mm total length). However, for many weekly cohorts, variation among individuals' ages and lengths was not sufficiently broad to allow realistic estimation of mean growth rates using a regression approach. Instead, we calculated individual growth rates (IG; mm/d) of alewives as

$$\text{IG} = (L - 3.5)/A, \quad (2)$$

where A is age (d) and 3.5 mm is the approximate size of alewives at hatch (Auer 1982). We used two-sample t -tests ($\alpha = 0.05$) to compare mean cohort growth rates.

Mortality.—We used catch curve analyses (i.e., change in density with size and age; Quinn and Deriso 1999) to estimate habitat-specific mortality rates. We grouped alewife larvae into 1-mm length bins (LBs);

for each net tow, we calculated density for the individual LBs. We relied on catches of 6–14-mm larvae in the 335- and 500- μm nets to estimate mortality rates. These two nets were mounted on the same bongo frame and were always deployed simultaneously. We did not use catches in the 700- μm net because this net was not used throughout our sampling season. In addition, Höök (2005) demonstrated that the 335-, 500-, and 700- μm -mesh nets were highly size selective and most adept at capturing small, intermediate, and large alewife larvae, respectively. Larvae were fully recruited to the gear at 5 mm, and we followed Everhart and Youngs' (1981) suggestion to use the bin after the point of full recruitment (i.e., 6 mm) as the initial bin for catch curve analysis. We did not use density estimates for LBs over 14 mm because catches of these larger sizes were significantly higher in the 700- μm net, suggesting that larger larvae could avoid capture in the finer-mesh nets (and bias mortality estimates). Höök (2005) also demonstrated that large (>14 mm) alewife larvae were more likely to be caught at night than during the day (this pattern did not hold for small larvae), suggesting that daytime density estimates for large larvae were negatively biased.

We calculated average density (335- and 500- μm -net catches combined) by LB for 15 June–25 July (i.e., when we would expect to collect larvae from the peak hatching period). We then used estimates of growth rates (GR; mm/d) during the peak hatching period to estimate the mean A (d) associated with each LB (mm) using equation (3). Again, we assumed that alewife larvae hatch at a length of 3.5 mm (Auer 1982).

$$A = (\text{LB} - 3.5)/\text{GR}. \quad (3)$$

We calculated the natural logarithm of LB density ($\log_e(D)$), and we estimated instantaneous daily mortality (Z) as the slope of a regression line relating A (independent variable) and $\log_e(D)$ (dependent variable). We used regression models with indicator variables to compare Z estimates between habitats (Neter et al. 1996).

Age-0 and yearling characteristics.—To compare relative habitat-specific densities and to characterize size distributions of surviving alewives, we towed a midwater trawl (6.40- \times 6.40-m net opening; 6.35-mm cod liner; tow speed \sim 2.5 knots) at night to collect age-0 and yearling alewives in Muskegon Lake, Muskegon Channel, and Lake Michigan during late summer and fall 2002 and spring 2003 (number of tows varied by sample date). Midwater trawling at night in Lake Michigan yielded relatively few alewives. Therefore, to obtain sufficient numbers of individuals for comparison of size distributions among habitats, we supplemented our midwater sampling with daytime

bottom trawling (7.62-m net opening; 12.70-mm cod liner; tow speed \sim 2.5 knots) in this habitat. For each sampling day, we calculated mean age-0 and age-1 alewife catches per 10 min of nighttime midwater trawling, and (due to seasonality of these data) we used paired t -tests to compare mean catches among habitats (catches paired by sampling day).

Upon collection, we froze alewives in the field and subsequently measured their total lengths and wet weights. We used these individual measures to compare size distributions of age-0 and yearling alewives. In addition, to expand the spatial and temporal breadth of these comparisons, we augmented these data with 66 age-0 alewives collected in Lake Michigan (near Sturgeon Bay, Wisconsin) on 15 October 2002 by C. Madenjian (U.S. Geological Survey [USGS] Great Lakes Science Center, Ann Arbor) and 20 yearling alewives collected within our nearshore Lake Michigan study area on 13 April 2003 by S. Pothoven (NOAA Great Lakes Environmental Research Laboratory Field Station, Muskegon).

Results

Physical and Biological Environments

During 2001 and 2002, Muskegon Lake warmed sooner and reached a greater maximum temperature than nearshore Lake Michigan (Figure 2; Table 1). Fluorescence and Secchi depth measures indicated consistently higher chlorophyll- a concentrations and lower transparencies in Muskegon Lake than in nearshore Lake Michigan (Table 1).

In general, densities of small-bodied zooplankton (collected in 64- and 153- μm nets) were higher in Muskegon Lake than in Lake Michigan, and densities of large-bodied zooplankton (collected in 153- μm net) were similar between the two habitats (Figure 3). In both habitats, rotifers were the dominant small zooplankton sampled on virtually all dates in the 64- μm net. Zebra mussel veligers and copepod nauplii alternated as the second-most abundant zooplankton type in the 64- μm net. To consider the relative availability of alewife prey, we grouped zooplankton catches in the 153- μm net into two size-based categories (with a taxa dry weight of 2.0 μg as an arbitrary cutoff between categories). This grouping suggested that during both 2001 and 2002, densities of small-bodied zooplankton (i.e., those likely to be consumed by small larval alewives) were higher in Muskegon Lake than in Lake Michigan. Densities of large-bodied zooplankton were not consistently different between habitats (i.e., mean density was higher in Muskegon Lake during 2001 and higher in Lake Michigan during 2002).

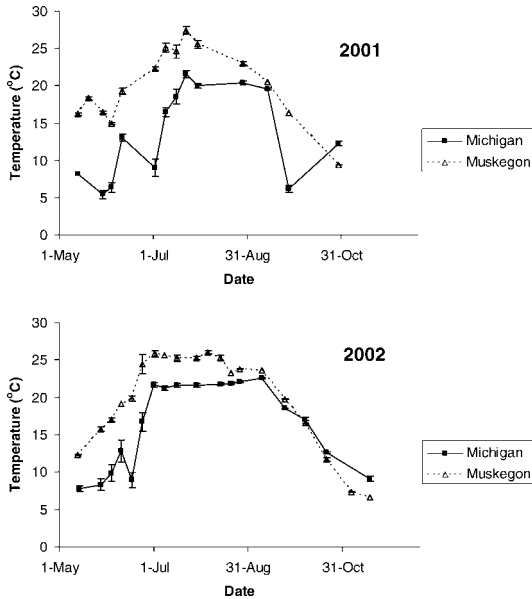


FIGURE 2.—Mean epilimnetic temperature (°C; ± SE) based on temperature and depth profiler casts in nearshore Lake Michigan and in Muskegon Lake, Michigan, during 2001 (upper panel) and 2002 (lower panel). Note the likely occurrence of upwelling events (three during 2001 and one during 2002) in Lake Michigan.

Hatch Dates

During 2001 and 2002, larval alewives in Muskegon Lake (and other drowned river mouth lakes) hatched earlier and reached greater peak densities than larvae in nearshore Lake Michigan (Table 1; Figure 4). During both years, we initially collected larval alewives

approximately 6 weeks earlier in Muskegon Lake than in nearshore Lake Michigan, and average hatching dates (see above for description) were earlier in Muskegon Lake (27 June 2001 and 22 June 2002) than in Lake Michigan (1 July 2001 and 1 July 2002). We also observed early hatching in other tributary systems (i.e., Pigeon Lake, Manistee Lake, and Muskegon Channel) relative to Lake Michigan (Figure 4).

Condition

We used a nonlinear fitting routine to analyze biphasic length–weight relationships (Figure 5, upper panel). This biphasic model removed systematic biases in the distributions of residuals that were evident when a single regression line was fit to the entire range of data. In addition, the biphasic model dramatically reduced the sum of residual squares and led to a lower Akaike’s information criterion score than did a single-phase growth model. This analysis suggested that with outliers included, the break point was 9.35 mm (below break point: $W = 0.0000355 \times L^{1.249}$; above break point: $W = 0.0000002 \times L^{3.553}$).

Length-specific mass of young alewives tended to be higher in Muskegon Lake than in Lake Michigan (Table 2; Figure 5, lower two panels). Length was a significant covariate in all four ANCOVAs (separate analyses by year and alewife size range: 2001 small alewives: $F_{1,409} = 206.0, P < 0.01$; 2001 large alewives: $F_{1,515} = 1,324.3, P < 0.01$; 2002 small alewives: $F_{1,756} = 274.3, P < 0.01$; 2002 large alewives: $F_{1,718} = 2,848.9, P < 0.01$). Further, length-specific mass of individual alewives smaller than 9.35 mm was significantly greater in Muskegon Lake than

TABLE 1.—Mean (±SE) habitat characteristics (surface temperature, Secchi depth, and epilimnetic chlorophyll-*a* concentration) and alewife density (based on catches in three ichthyoplankton nets) during May–August 2001–2002 in nearshore Lake Michigan, Muskegon Channel, Muskegon Lake, Manistee Lake, and Pigeon Lake, Michigan. Asterisks indicate no data available.

Year and variable	Lake Michigan	Muskegon Channel	Muskegon Lake	Manistee Lake	Pigeon Lake
2001					
Temperature (°C)	15.8 ± 1.7	21.9 ± 1.1	23.3 ± 1.1	21.0 ± 1.5	17.8 ± 2.1
Secchi depth (m)	6.6 ± 0.3	*	1.8 ± 0.1	1.9 ± 0.1	2.3 ± 0.5
Chlorophyll <i>a</i> (µg/L)	1.8 ± 0.2	*	9.8 ± 1.5	*	*
Mean alewife density (fish/m ³)					
335-µm net	0.5 ± 0.2	1.8 ± 1.0	18.0 ± 11.9	2.6 ± 2.0	4.8 ± 3.4
500-µm net	0.8 ± 0.3	1.2 ± 0.6	28.2 ± 18.6	1.3 ± 0.7	0.5 ± 0.4
700-µm net	0.4 ± 0.1	11.7	1.8 ± 1.0	*	*
2002					
Temperature (°C)	16.9 ± 1.5	21.8 ± 1.2	22.2 ± 1.3	22.5 ± 1.6	21.5 ± 1.5
Secchi depth (m)	6.5 ± 0.4	*	2.1 ± 0.1	2.4 ± 0.1	2.2 ± 0.1
Chlorophyll <i>a</i> (µg/L)	2.7 ± 0.3	*	9.4 ± 1.8	*	*
Mean alewife density (fish/m ³)					
335-µm net	2.5 ± 1.1	2.8 ± 1.6	9.2 ± 4.7	46.2 ± 39.6	28.7 ± 15.1
500-µm net	2.0 ± 0.9	2.4 ± 1.6	8.3 ± 5.0	6.0 ± 2.3	30.4 ± 20.6
700-µm net	0.5 ± 0.2	3.1 ± 2.5	13.9 ± 10.9	*	*

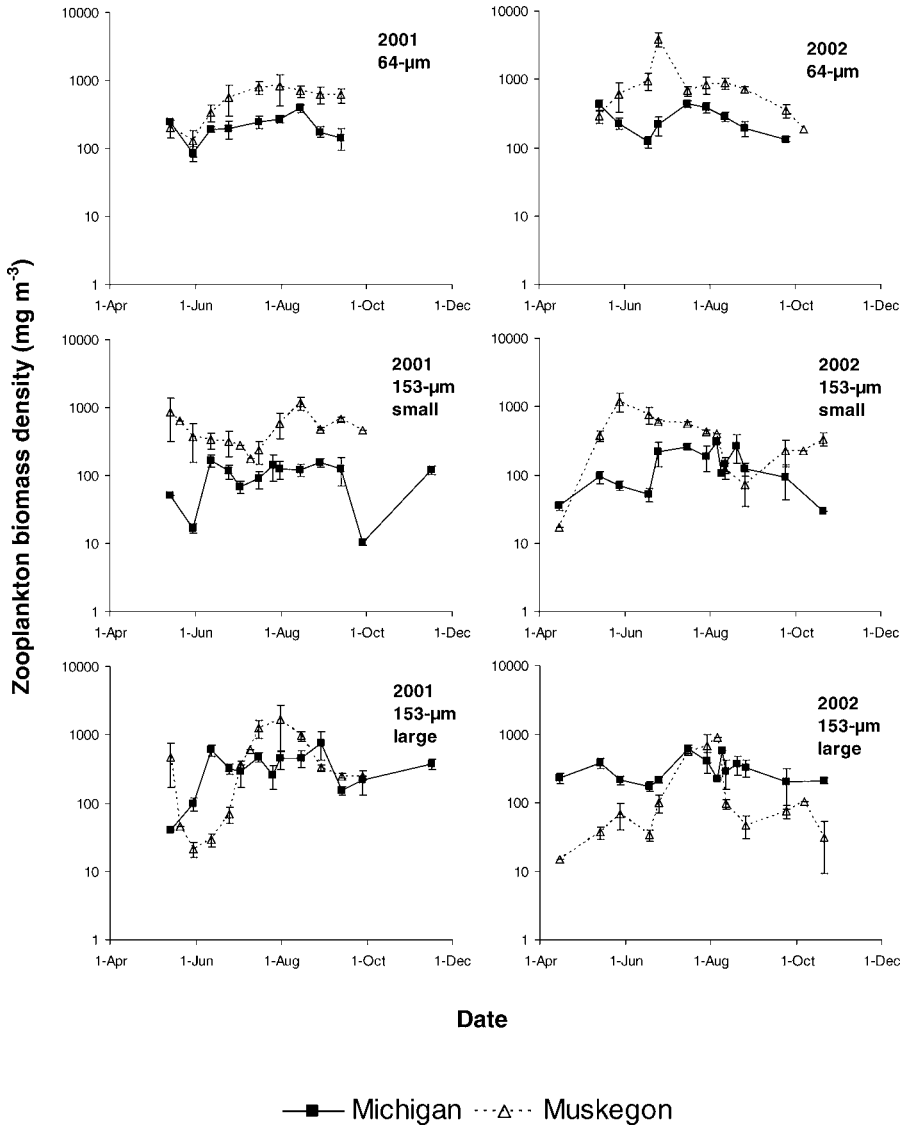


FIGURE 3.—Mean zooplankton wet biomass density (mg/m^3 ; $\pm\text{SE}$) in Muskegon Lake, Michigan, and nearshore Lake Michigan, 2001–2002. The uppermost plots depict combined densities of rotifers, copepod nauplii, and zebra mussel veligers based on catches in a 64- μm plankton net. The middle and lower plots depict catches of small- and large-bodied zooplankton, respectively (based on an arbitrary size cutoff; mean taxa dry weight of 2.0 μg), in the 153- μm net. Note the logarithmic scales.

in nearshore Lake Michigan during 2001 (but not during 2002). During both years, length-specific mass of individual alewives between 9.35 and 30.0 mm was significantly greater in Muskegon Lake than in nearshore Lake Michigan (Table 2).

Growth Rates

During 2001 and 2002, mean ($\pm 95\%$ confidence interval) growth rates (estimated based on larvae captured throughout our sampling period) were not

significantly different (2001: $P = 0.99$; 2002: $P = 0.05$) between Muskegon Lake (2001: 0.89 ± 0.04 mm/d, $n = 151$; 2002: 0.89 ± 0.04 mm/d, $n = 102$) and Lake Michigan (2001: 0.89 ± 0.06 mm/d, $n = 58$; 2002: 0.84 ± 0.06 mm/d, $n = 87$). However, growth rates varied seasonally. For example, within Muskegon Lake, alewives emerging in May and early June generally grew slower than those emerging in late June and July (Figure 6). Comparisons of growth rates of alewives that hatched concomitantly (but in different

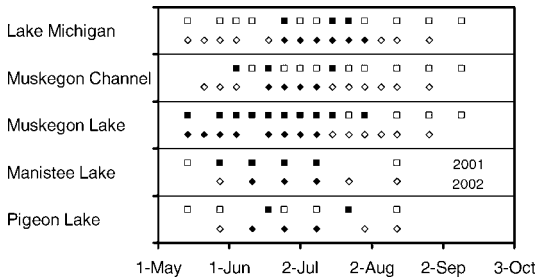


FIGURE 4.—Larval alewife hatching distributions in near-shore Lake Michigan, Muskegon Channel, Muskegon Lake, Manistee Lake, and Pigeon Lake, Michigan, during 2001 (squares) and 2002 (diamonds). Solid points represent weeks when at least one larval alewife smaller than 6.0 mm was captured in the corresponding body of water. Open points represent weeks when sampling took place but failed to capture an alewife larva smaller than 6.0 mm.

habitats) revealed significant differences. During 2002 (but not 2001), individuals hatching during the peak period (15 June–15 July) grew significantly faster in Muskegon Lake than in Lake Michigan (Table 2). In addition, there were significant differences between growth rates of temporally paired weekly cohorts (Figure 6). Although one 2001 Lake Michigan cohort grew significantly faster than its Muskegon Lake counterpart, four Muskegon Lake weekly cohorts (two during 2001 and two during 2002) grew significantly faster than the corresponding Lake Michigan cohorts.

Mortality

During 2001, alewife *Z* (mean ± SE) was not significantly different between Muskegon Lake (0.14 ± 0.06 per day) and Lake Michigan (0.22 ± 0.06 per day). During 2002, however, estimated *Z* was significantly higher for Lake Michigan fish (0.30 ± 0.04 per day) than for Muskegon Lake fish (0.16 ± 0.03 per day; Table 2).

Age-0 and Yearling Characteristics

Nighttime midwater trawling during late summer and fall 2002 suggested that age-0 alewife densities differed among habitats (Table 3). Paired *t*-tests comparing mean age-0 alewife catches per 10 min of trawling suggested that catches in Muskegon Lake tended to be higher than in nearshore Lake Michigan (*n* = 8; *t* = 4.1; *P* < 0.01). However, catches in Muskegon Channel were not significantly different from catches in either Muskegon Lake (*n* = 7; *t* = 1.1; *P* > 0.05) or Lake Michigan (*n* = 7; *t* = 1.97; *P* > 0.05). During spring 2003, we used a bottom trawl in Lake Michigan and a midwater trawl in Muskegon

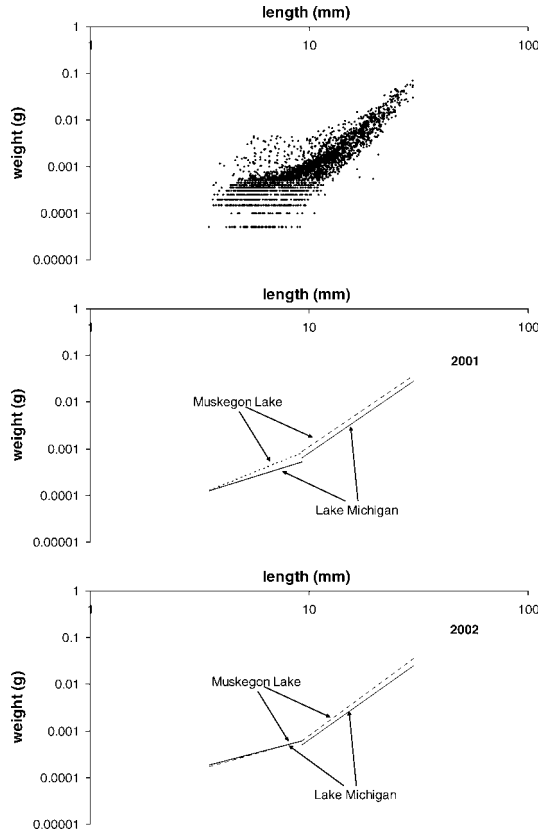


FIGURE 5.—Larval alewife length–weight relationships (log–log scale): uppermost panel shows individual lengths and wet weights (*n* = 3,046) and lower two panels show regression lines fitted separately for small (<9.35 mm total length) and large (≥9.35 mm total length) individuals captured in Muskegon Lake, Michigan (dashed lines), and nearshore Lake Michigan (solid lines) during 2001 and 2002.

Lake and thus we could not directly compare densities among habitats. Nonetheless, it is noteworthy that we caught no yearling alewives in Muskegon Lake during spring 2003 (Table 3).

Comparisons of size distributions indicated that during late summer and fall, age-0 alewives in Muskegon Lake tended to be larger than individuals in Lake Michigan. Further, all spring-caught age-1 individuals were 65 mm and larger (Figure 7).

Discussion

Muskegon Lake (and perhaps other drowned river mouth lakes) appeared to be a more favorable rearing environment for young alewives than nearshore Lake Michigan. Alewife larvae in Muskegon Lake experienced relatively high water temperatures, primary productivity, and densities of small-bodied zooplank-

TABLE 2.—Comparisons of mean (\pm SE) larval alewife condition, growth (during the peak hatching period, 15 Jun–15 Jul 2001 and 2002), and mortality rates in Lake Michigan and Muskegon Lake, Michigan. Length-specific mass values were estimated from fitted regression relationships for small (<9.35 mm) and large (9.35–30.00 mm) alewives (see Figure 5). Statistical procedures are described in the text.

Year and variable	Lake Michigan	Muskegon Lake	Test statistics	P
2001				
Length-specific mass (mg)				
7 mm total length	0.3	0.5	$F_{1,409} = 12.3$	<0.01
20 mm total length	7.5	10.0	$F_{1,515} = 21.3$	<0.01
Growth (mm/d)	0.91 ± 0.03	0.91 ± 0.02	$t_{141} = 0.218$	0.83
Mortality Z (per d)	0.22 ± 0.06	0.14 ± 0.06	$t_{14} = 0.88$	0.40
2002				
Length-specific mass (mg)				
7 mm total length	0.4	0.4	$F_{1,756} = 0.4$	0.52
20 mm total length	6.6	8.8	$F_{1,718} = 55.8$	<0.01
Growth (mm/d)	0.85 ± 0.02	0.93 ± 0.02	$t_{154} = 2.70$	<0.01
Mortality Z (per d)	0.30 ± 0.04	0.16 ± 0.03	$t_{14} = 3.30$	<0.01

ton; thus, young alewives in Muskegon Lake were in better condition (length-specific weight), occasionally grew slightly faster (depending upon the temporal scale of growth comparisons), and survived better than those in Lake Michigan. The combination of a favorable growth environment and early hatching dates in turn allowed age-0 alewives to reach a larger mean size by fall in Muskegon Lake than in Lake Michigan. In addition, the selective process of size-dependent overwinter mortality probably served to exacerbate the relatively high recruitment success of individuals from Muskegon Lake.

Growth and Condition

During the peak hatching period, young alewives occasionally grew slightly faster in Muskegon Lake than in Lake Michigan. However, given the apparent superior growth environment in Muskegon Lake (more favorable temperatures and zooplankton densities), it is somewhat surprising that differences in growth rates between habitats were not more pronounced. Young alewives are partially (if not entirely) visual predators, and low water clarity in drowned river mouth lakes could limit encounter rates with zooplankton prey, thereby constraining consumption and growth rates.

Alternatively, individual alewives may allocate energy resources differentially into various components of growth (length versus girth and mass). It is likely that structural tissues (which set the limit for an individual's length) can grow at some finite rate; evidence suggests that young fish experiencing exceedingly fast growth also incur some performance costs (Billerbeck et al. 2001; Arnott et al. 2006). Thus, at high consumption rates, individuals may approach some maximum rate of growth in length, at which time surplus energy must be invested elsewhere. Our findings of similar growth rates among habitats but greater length-specific mass for young alewives in Muskegon Lake suggest that growth rates of larval alewives are high in both habitats. Consistent with this hypothesis, estimates of larval alewife growth rates from other studies (e.g., Heinrich 1981; Essig and Cole 1986) are generally lower (at least not substantially greater) than our estimates (see below).

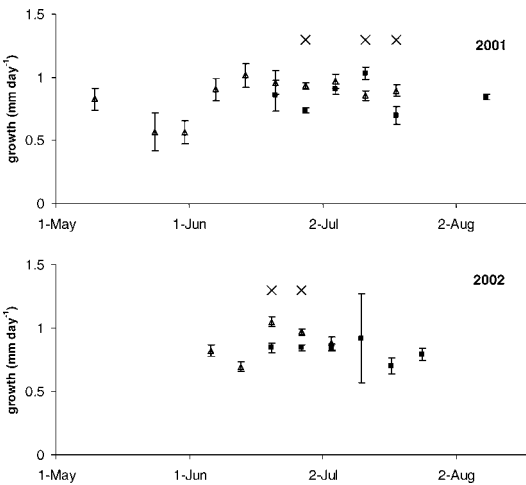


FIGURE 6.—Estimated mean growth rates (mm/d; \pm SE) of weekly alewife cohorts in Muskegon Lake, Michigan (open triangles), and Lake Michigan (closed squares) during 2001 (upper panel) and 2002 (lower panel). Symbols (X) indicate temporally paired cohorts with significantly different mean growth rates.

We assumed that estimates of growth rate reflect average rates for particular cohorts. In general, larval fish mortality rates are thought to be size dependent, such that smaller, slower-growing fish experience higher mortality rates than faster-growing fish (Miller

TABLE 3.—Catches of age-0 (2002) and yearling (2003) alewives with midwater (M) and bottom (B) trawls in Muskegon Lake and Muskegon Channel, Michigan, and Lake Michigan.

Water body	Year	Date	Trawl type	Number of tows	Fish per 10-min of trawling (mean \pm SD)		
Muskegon Lake	2002	29 Jul	M	1	4.5		
		27 Aug	M	2	6.0 \pm 2.8		
		10 Sep	M	2	17.7 \pm 15.6		
		23 Sep	M	2	32.0 \pm 32.5		
		24 Sep	M	2	34.5 \pm 7.8		
		07 Oct	M	3	9.0 \pm 11.3		
		21 Oct	M	3	11.2 \pm 7.1		
		06 Nov	M	3	23.1 \pm 30.1		
		18 Nov	M	2	10.7 \pm 15.1		
		22 Apr	M	4	0.0		
		Muskegon Channel	2002	27 Aug	M	1	0.0
09 Sep	M			1	3.0		
10 Sep	M			1	0.0		
23 Sep	M			1	48.0		
07 Oct	M			1	0.0		
21 Oct	M			1	0.0		
06 Nov	M			1	4.7		
18 Nov	M			1	0.0		
22 Apr	M			1	0.0		
Lake Michigan	2002			19 May	M	1	0.0
				29 Jul	M	1	0.0
		27 Aug	M	2	0 \pm 0		
		09 Sep	M	2	0.5 \pm 0.7		
		24 Sep	M	4	0 \pm 0		
		25 Sep	B	4	0 \pm 0		
		07 Oct	M	2	0.8 \pm 1.1		
		09 Oct	B	3	19.8 \pm 33.7		
		21 Oct	M	2	0 \pm 0		
		22 Oct	B	2	0 \pm 0		
		07 Nov	B	3	12.3 \pm 6.0		
Lake Michigan	2003	18 Nov	M	1	0.0		
		19 Nov	B	2	0.6 \pm 0.8		
		21 Apr	B	5	0.0		
		22 Apr	B	3	0.0		
		19 May	B	2	0.0		
		21 May	B	10	0.0		
		11 Jun	B	6	0.7 \pm 1.2		
		12 Jun	B	14	4.4 \pm 12.7		

et al. 1988). Indeed, there is evidence that larval alewives in Lake Michigan experience such size-dependent mortality (Mansfield and Jude 1986). Thus, our estimates of growth rates may not be indicative of mean rates for entire cohorts but rather may be biased to reflect growth of faster-growing individuals that are more likely to survive initial life.

Our growth rate estimates deviated somewhat from those of past studies. Heinrich (1981) monitored growth of larval alewives in the laboratory and estimated that during the first 50 d of life, larval alewives grew 0.63 ± 0.03 mm/d (mean \pm SE). During 1989–1992, larval alewives were collected in Lake Michigan and growth rates estimated based on otolith increments were 0.8–0.9 mm/d (D. Jude, unpublished data). Essig and Cole (1986) collected anadromous larval alewives in a coastal Massachusetts pond; although these authors did not directly estimate growth rate, they derived a linear relationship between

number of otolith increments and total length. From this relationship, we calculated an average growth rate of 0.73 mm/d for anadromous larval alewives between 6.0 and 13.9 mm. Discrepancies in observed larval alewife growth rates among these studies are probably attributable to different ambient conditions (including different temperatures). The lower average growth rate estimated by Heinrich (1981), as compared with estimates from our study, may partially reflect the absence of size-dependent mortality in the laboratory. Also, there may be processes unaccounted for under laboratory conditions (e.g., prey patchiness and turbulence-induced higher contact rates between alewife predators and zooplankton prey) that consistently lead to higher larval fish ingestion and growth rates in the wild (e.g., Mackenzie et al. 1990; Mackenzie 2000).

We identified a biphasic length–weight relationship for young alewives, whereas other authors have

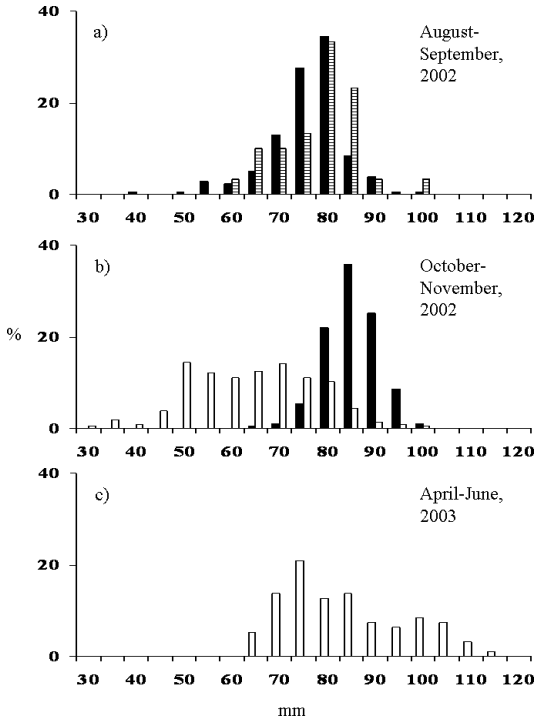


FIGURE 7.—Relative frequencies (%) of age-0 and yearling alewives (grouped into 5-mm length bins) that were captured with midwater and bottom trawls in Lake Michigan (open bars), Muskegon Lake (filled bars), and Muskegon Channel (striped bars), Michigan, during 2002 and 2003: (a) age-0 fish captured during Aug–Sep 2002 in Muskegon Lake (sample sizes: 12 on 27 Aug; 53 on 10 Sep; 112 on 23–24 Sep) and Muskegon Channel (30 on 23–24 Sep); (b) age-0 fish captured during Oct–Nov 2002 in Muskegon Lake (27 on 7 and 9 Oct; 69 on 21 Oct; 58 on 6 Nov; 32 on 18–19 Nov), nearshore Lake Michigan (75 on 7 and 9 Oct; 66 on 7 Nov), and Lake Michigan near Sturgeon Bay (66 on 15 Oct; U.S. Geological Survey collection); and (c) age-1 fish captured during Apr–Jun 2003 in nearshore Lake Michigan (20 on 13 Apr; 75 on 11–12 Jun).

assumed a single-phase relationship (e.g., Klumb et al. 2003a). Given that growth rates of young fish are not necessarily consistently proportional along different dimensions, young fish do not inevitably maintain a constant allometric relationship between body mass and length throughout early ontogeny. For instance, morphologies of young alewives change dramatically from hatch to the end of the larval period (Auer et al. 1982); thus, a multiphase growth model seems appropriate.

Condition measures of individual alewives were highly variable. Both measurement error and tangible differences among individuals may cause such variability. Due to rapid desiccation, it is difficult to

measure wet weights of very small fish larvae. Also, note that Figure 5 (upper panel) depicts a log–log relationship; minor errors of measurement for small larvae thus appear more dramatic than errors of measurement for large larvae. Regardless of potential measurement errors, however, it is not surprising that condition is more variable for smaller larvae. Larval fish experience very high mortality during early life, and only the most robust individuals are likely to survive. Starvation mortality rates may be particularly high during the transition from the yolk sac stage to the exogenous feeding stage (Houde 2002); thus, during this transition, several larvae (which ultimately die) may exhibit very poor condition. For instance, Pepin et al. (1999) quantified ratios of RNA to DNA (another measure of condition) for individual marine larvae and found that while mean values increased, variation in RNA : DNA ratios declined with increasing larval size. Such a pattern is likely to be most dramatic for species that produce small eggs with limited yolk reserves (e.g., alewives). While the degree to which small differences in alewife condition translate to habitat-specific differences in survival is unclear, limited energy reserves and high mass-specific metabolic rates suggest that starvation can occur rapidly and that even marginal increases in energy stores will impart a survival advantage.

Mortality during the Growing Season

Differences in mortality rates among habitats during summer and early fall could dramatically alter the relative number of recruits contributed by various habitats. Our data suggest that during 2002, larval alewife mortality rates were significantly higher in Lake Michigan than in Muskegon Lake. This is somewhat surprising, as acoustic (D.M.M. and D. Kruger, NOAA Great Lakes Environmental Research Laboratory, unpublished data) and trawling (T.O.H., unpublished data) surveys suggest that densities of potential alewife predators are much higher in Muskegon Lake than in the nearshore Lake Michigan study area. Higher predator densities coupled with high temperatures (i.e., increased predator metabolism and swimming speed) will generally result in higher mortality rates. On the other hand, low water clarity (low Secchi depth) may provide a refuge for young alewives from visual predators in Muskegon Lake. In addition, because densities of small-bodied zooplankton were lower in nearshore Lake Michigan, mortality as a result of starvation may be more common in this habitat. Höök (2005) reported that larval alewives exhibited a higher frequency of empty digestive tracts when captured in nearshore Lake Michigan than when captured in Muskegon Lake during 2001. Similarly,

other researchers examining larval alewife digestive tract contents during 2001 and 2002 in nearshore Lake Michigan in the vicinity of Portage Lake found that a high proportion of digestive tracts were devoid of food (2001: 87% empty, $n = 82$; 2002: 66% empty, $n = 53$; J. O'Keefe, Central Michigan University, Mount Pleasant, personal communication). Finally, upwelling events that cause rapid changes in nearshore Lake Michigan temperatures and advect alewife larvae to unfavorable offshore areas have been proposed as an additional source of mortality (Heufelder et al. 1982). Our measures of surface and epilimnetic temperatures suggest that at least two upwelling events occurred within our nearshore Lake Michigan study area during 2001 (Figure 2). No such events were apparent in the drowned river mouth lakes.

In short, there are several processes (turbidity-mediated refuge from predation, low starvation rate, and lack of upwelling events) that could favor relatively high survival in Muskegon Lake, despite high predator densities. Nonetheless, we acknowledge that our method for estimating mortality rates (i.e., catch curve analysis) assumes that changes in density with size and age of fish are attributable solely to mortality. This is a difficult assumption to evaluate. Water currents rapidly advect larval alewives throughout Lake Michigan proper (Höök et al. 2006), suggesting that both emigration and immigration are significant fluxes (however, it is unknown whether these two processes truly balance).

Our mortality estimates were similar to past estimates for young alewives. Mansfield and Jude (1986) collected larval alewives in nearshore Lake Michigan during 1974–1982 and estimated daily instantaneous mortality rates of 0.02–0.31. In addition, they found that mortality rates tended to change with size, such that smaller larvae exhibited higher mortality than larger larvae (Mansfield and Jude 1986). Essig and Cole (1986) estimated an average daily instantaneous mortality rate of 0.12 for anadromous larval alewives between 6.0 and 13.9 mm. Not surprisingly, Heinrich (1981) estimated a much lower mortality rate ($Z = 0.02$) for laboratory-reared larval alewives.

Overwinter Mortality

If individual alewives are to survive to contribute to the adult spawning stock, then they must overcome potential starvation and predation mortality during the growing season and survive subsequent winters with limited foraging opportunities. Early life processes are bound to influence future survival and ultimate recruitment success (e.g., Ludsin and DeVries 1997). In particular, growth rates during the first year of life should directly influence overwinter survival probabil-

ities. In general, smaller fish tend to have lower energy stores and higher mass-specific respiration rates; therefore, relatively small fish are less likely to survive an extended period of limited feeding. Alewives in the Great Lakes probably feed very little during winter, as evidenced by large decreases in energy densities of somatic tissue from late fall to spring (Flath and Diana 1985; Stewart and Binkowski 1986; Madenjian et al. 2006). Thus, several authors have suggested that age-0 alewives in the Great Lakes must reach some minimum size to survive winter (Brown 1972; Flath and Diana 1985; O'Gorman and Schneider 1986; Bergstedt and O'Gorman 1989). In addition, there is evidence that alewives cannot survive in freshwater at temperatures below 3°C (Otto et al. 1976), thereby suggesting the possibility of extremely high mortality rates during particularly severe winters.

Our data support the notion of high overwinter mortality rates for small age-0 alewives in Lake Michigan. Comparison of size distributions of age-0 alewives caught in trawls during October and November 2002 with size distributions of yearling alewives caught during April and June 2003 suggests that small age-0 alewives did not survive the winter. The smallest fish caught during spring 2003 was 65 mm, whereas several age-0 alewives caught during late fall 2002 were well below this length. Even if one assumes that alewives grow nominally over the winter (e.g., 5 mm), alewives would nonetheless have to achieve a minimum size of 60 mm by the end of the growing season to survive the winter in Lake Michigan.

Juvenile alewives in Muskegon Lake were larger than those in Lake Michigan during fall and thus probably experienced higher overwinter survival. This expectation is partially based upon the notion that young alewives from different habitats experience similar overwintering conditions. There are landlocked alewife populations that are able to complete their entire life cycle within small lacustrine systems (Brooks and Dodson 1965; Scott and Crossman 1973; Lindenberg 1976), and it would therefore seem plausible that Muskegon Lake alewives constitute a resident population. However, we caught no alewives in Muskegon Lake during spring trawling, and no age-1 or older alewives were captured during spring–fall in Muskegon Lake (we did capture several adults in Lake Michigan). Thus, alewives appear to use Muskegon Lake exclusively as spawning and rearing habitat.

Recruitment Success

Integration of our data suggests that during 2001 and 2002, alewives hatching in Muskegon Lake (and perhaps other drowned river mouth lakes) had a recruitment advantage over those in nearshore Lake

Michigan. During 2002, Muskegon Lake alewives experienced higher survival rates during early life. Because of earlier hatching dates and a better growth environment (leading to slightly higher growth rates and mean individual condition), young alewives that spent early life in Muskegon Lake reached a larger size by the end of the growing season and were therefore more likely to survive winter and ultimately recruit to the adult population. We do not suggest, however, that most of the lakewide alewife recruits come from drowned river mouth lakes. In fact, Dufour et al. (2005) found that 42 of 43 yearling alewives captured in Lake Michigan during spring 2003 contained otolith core chemical signatures indicative of early life in Lake Michigan. Thus, while drowned river mouth lakes can probably be classified as nursery habitats (which contribute disproportionate numbers of alewife recruits to the adult population; Beck et al. 2001), they may not constitute effective juvenile habitats (i.e., those that in total, independent of area, contribute large numbers of individuals to the adult population; Dahlgren et al. 2006).

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