Environmental and Endogenous Factors Influencing Emigration in Juvenile Anadromous Alewives

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[Article]

Environmental and Endogenous Factors Influencing Emigration in Juvenile Anadromous Alewives

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Abstract.—We analyzed migration of juvenile anadromous alewives *Alosa pseudoharengus* at Bride Lake, a coastal lake in Connecticut, during summer 2006 and found that migration on 24-h and seasonal time scales was influenced by conditions of the environment and characteristics of the individual fish. To identify environmental cues of juvenile migration, we continuously video-recorded fish at the lake outflow and employed information-theoretic model selection to identify the best predictors of daily migration rate. More than 80% of the approximately 320,000 juvenile alewives that migrated from mid-June to mid-August departed in three pulses lasting 1 or 2 d. Pulses of migration were associated with precipitation events, transient decreases in water temperature, and transient increases in stream discharge. Diel timing of migration shifted over the summer. Early in the season, most migration occurred around dawn; late in the season, migration occurred at night. To identify individual characteristics associated with migratory behavior, we compared migrating juveniles collected as they were exiting Bride Lake with nonmigrating juveniles collected from the center of the lake. Migrants were a nonrandom subset of the population; they were on average 1–12 mm larger, were 2–14 d older, had grown more rapidly (11% greater length at age), and were in better condition (14% greater mass at length) than nonmigrant fish. We infer that the amount of accumulated energy has a positive effect on the net benefit of migration at any time in the migratory season.

Fish migrations are prompted by combinations of environmental and endogenous factors. Environmental factors that commonly influence migration timing include abiotic factors, such as seasonal changes in temperature and photoperiod, and biotic factors, such as changes in food abundance and the behavior of conspecifics. Endogenous factors influencing migration timing include fish age, sex, size, and the amount of energy reserves. For example, juvenile salmonid migrations are stimulated by temperature and photoperiod (Metcalfe and Thorpe 1990; McCormick et al. 1998; Whalen et al. 1999) and are modified by endogenous factors, such as metabolic rate (Metcalfe et al. 1995; Forseth et al. 1999) and size (Metcalfe and Thorpe 1990; Theriault and Dodson 2003).

We studied the juvenile migration of the alewife *Alosa pseudoharengus*, an anadromous clupeid species that inhabits the western North Atlantic Ocean from North Carolina to the island of Newfoundland. Many populations of alewives spawn in the spring in small coastal ponds or lakes connected to marine systems by small streams; alewives are also known to spawn in large river systems and their tributaries, but relatively little is known about these less-accessible populations. The timing of juvenile alewife migration from nursery grounds to the sea varies within a single location; emigration of young of the year (age 0) is observed throughout the summer and also in the autumn (Loesch 1965; Kosa and Mather 2001). Analysis of this variability in timing should shed light on factors influencing growth and mortality among juvenile alewives. Theory suggests that spawning adult and juvenile migrations have a selective advantage when there are improved opportunities for juvenile growth in habitats other than their spawning habitat (Gross et al. 1988). The benefits realized by migrating should outweigh the costs of migrating, taking into account relative differences in growth opportunity and mortality risk between the environments (Gross 1987). Few data presently exist on alewife growth and mortality rates in nursery areas relative to coastal marine habitats. Survival estimates for anadromous alewives in nursery ponds vary between 0.0001% (Kissil 1974) and 1.0% (Havey 1973).

Because early stage diadromous migrations entail dramatic changes in environment for small, relatively vulnerable organisms, the context in which these migrations occur is of particular interest. The success of a year-class is likely to be shaped in part by the proportion of individuals that complete the first migration. Anthropogenic perturbations to aquatic

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environments that disrupt the associations between exogenous and endogenous factors or that interfere with passage when migration behaviors are underway may have a serious effect on population sustainability (McCormick et al. 2009). Therefore, it is important to investigate the drivers of migration in species for which there is a conservation concern.

Our study of juvenile alewife emigration was stimulated by evidence that native alewife populations have suffered widespread declines in abundance (Hightower et al. 1996; Gibson and Myers 2003; Schmidt et al. 2003). Commercial landings of alewives have dwindled to a small fraction of the peak landings recorded in the 1950–1960s (Davis and Schultz 2009). In response to population declines, the Connecticut Department of Environmental Protection (CDEP) instituted an emergency closure of the state's alewife fishery in 2002. Similar closures were instituted in the neighboring states of Massachusetts and Rhode Island in 2005. Multiple stressors to the populations have been hypothesized, including (1) fishing mortality because of targeted fisheries and bycatch losses and (2) higher levels of natural mortality arising from rebounding stocks of striped bass *Morone saxatilis*. Decadal shifts to younger fish in the age structure of the spawning run and reductions in the proportion of repeat spawners implicate mortality sources acting on alewives at sea or during the spawning migration (Davis and Schultz 2009). There has been minimal research on the possibility that factors acting on alewife juveniles have also played a role in population declines. Survivorship of alewives through the juvenile freshwater stage is low (1.0–1.5 surviving juveniles/adult; Cooper 1961; Kissil 1974) and may be regulated by competition for food resources (Post et al. 2008). High juvenile mortality has adverse effects on the returning numbers of spawning adults from that year-class (Havey 1973; Jessop 1990). Therefore, it seems likely that the relative success or failure of early stages will influence local abundance and eventual recovery of local alewife populations.

One environmental factor that can have a direct effect on juvenile alewife success is the availability of egress to the sea, given seasonal fluctuations in stream water hydrology. Summer flow connecting coastal nursery lakes to salt water is often reduced and during periods of low rainfall can cease entirely. Significant delays of seaward migration incurred by such periods could lead to reduced growth and increased juvenile mortality (Vigerstad and Cobb 1978; Kosa and Mather 2001). This threat may be increasing in magnitude. In the past several decades, coastal landscapes have become more developed and, hence, more affected by human activities, especially increased water usage for residences and recreational activities (Malmqvist and Rundle 2002). This increased demand on coastal water supplies has led to more frequent dewatering of coastal streams that are the paths of alewife migration.

The objectives of this study were to evaluate a set of environmental and endogenous variables that may influence migration timing in juvenile anadromous alewives representing a single, well-studied population in Bride Lake, Connecticut. To test for endogenous factors that govern readiness to migrate, we compared migrating juveniles collected as they were exiting Bride Lake to nonmigrating juveniles collected from the center of the lake. To test for environmental variables that influence migration rate, we monitored juvenile emigration via a nearly continuous video record at Bride Lake's single narrow outflow. The alewife population in Bride Lake has been heavily studied over the past five decades (Kissil 1974; Post et al. 2008; Dalton et al. 2009; Davis and Schultz 2009; Walters et al. 2009), but most of the research has focused on the adult life stage.

Methods

Location and temporal extent of study.—This study was conducted between June and September 2006. Bride Lake is located in East Lyme, Connecticut, and is a 29-ha, coastal lake with a maximum depth of 8 m. More than 50,000 anadromous alewives spawn every year in Bride Lake (Gephard et al. 2006; Davis and Schultz 2009). Bride Lake is connected to Long Island Sound by Bride Brook, a 3.5-km, first-order stream. Bride Brook occasionally dries up in summer months, but this is not an annual occurrence. The lake flows into the stream over a weir approximately 0.5 m high when all removable boards are in place. The weir is the only exit from the lake.

During the spring months (March through May) of every year since 2005, a weir trap and electronic fish counter have been placed upstream from the weir to enumerate and sample adult alewives arriving to spawn (Gephard et al. 2006). For the 2 years before this (i.e., 2003 and 2004), fish arriving to the weir were trapped and counted by hand (Davis and Schultz 2009). Downstream passage is prevented during this time and is typically opened for spent adults in late May. The fish counter is read every weekday; weekend counts are allowed to accumulate and are recorded on the following Monday.

Juvenile alewife sampling began when there was first evidence of migration in June. Before mid-June, there was no evidence of juvenile migration; personnel were regularly on site throughout the spring during both daylight and crepuscular periods. On 18 June 2006, we observed a number of juvenile alewives at the weir and other signs of emigration, such as the presence of piscivorous fish and birds. Migration and sampling continued for 2 months. Migration rate monitoring ended when outflow from the lake had become intermittent. Sampling of migrating juveniles ended at the end of August because of a poor catch rate.

Collection and analysis of data on environmental correlates of migration timing.—To collect a video record of emigration rate, we constructed a 2.0 × 1.5-m raceway immediately downstream from the weir that funneled all migrants from the pond through a viewing area. The camera was mounted above this viewing area to provide an overhead perspective of the water flow and of any migrating fish. We positioned a lamp to illuminate the raceway at night without increasing light at the weir, which might influence emigrating fish. To facilitate fish observation and counting, the viewing area was painted white with black lines spaced 2 cm apart. Video (VHS; Panasonic AGTRT650) was recorded on a 24-h loop and included a time stamp.

We video-recorded the lake outflow for 54 d beginning several days after migration was first observed. Various events (e.g., change of videotape, thunderstorms, failure of lights) caused interruptions in the video record. We regarded interruptions as inconsequential when they were short or when they occurred during time periods in which migration was rarely observed. Because of substantial interruptions, we omitted 12 d from the data set, including the partial first day of recording. Within the remaining video record, there was continuous recording on 27 d; the record for all 42 d that were retained was 93% complete. The video record was terminated on 14 August 2006, when Bride Brook became dry. Flow resumed in the brook on 29 August 2006; however, we did not resume the video record at that time.

Migratory activity was evaluated for each minute of the video record to create a migrant abundance index. The number of fish in the counting area of the ramp was estimated for each second and summed to represent number per minute. Juvenile alewives were not observed swimming upstream or making other efforts to return to the lake. During periods when many fish were migrating, it was not possible to count fish individually, but it was possible to categorize numbers with confidence into orders of magnitude. We therefore quantified migration rate on an ordinal scale based on numbers (N) counted (0: 0 fish; 1: $N = 1$–10 fish; 2: $N = 11$–100 fish; 3: $N = 101$–1,000 fish; 4: $N = 1{,}001$–10,000 fish; 5: $N > 10{,}000$ fish). We used this ordinal scale, the log abundance index, for hypothesis testing. For a rough estimate of the total number of migrants in a time period, we summed counts assuming the minimum value for each interval.

We estimated the hatch date composition of alewife migrants by combining the seasonal record of migrant abundance with the data on daily age of migrants. The hatch date composition of each week's migrants was estimated by subtracting their age from the capture date. The hatch date composition of all migrants was estimated by aggregating the weekly data on hatch date composition and weighting each week by the estimated number of migrants in that week.

Environmental data (temperature, rainfall, stream discharge, and lunar phase) were also collected. Water temperature was recorded hourly using a temperature logger placed at the weir at a depth of 0.5 m and was averaged for each day. Daily rainfall was obtained from a gauge at the Groton, Connecticut, airport. Stream discharge was estimated from daily readings of water level taken at a staff gauge that was calibrated to discharge from a flow curve (M. Poola, Town of East Lyme, personal communication).

The association between the number of migrating juvenile alewives and environmental variables was evaluated via negative binomial regression. The response variable in the regression models was an index of daily migration rate: the sum of migration rate values (i.e., categories 0–5) for each day. Each date was treated as an independent data point. Rainfall data were lagged by 1 d, reflecting the expectation that the previous day's precipitation would have a delayed effect on streamflow. An effect of season was tested by standardizing date to a mean of 0 and including date and date-squared (date^2) as predictors. The effect of moon phase was tested via harmonic regression (Batschelet 1981; Lorda and Saila 1986; Schultz et al. 2003) wherein the 328-h cycle is partitioned into two trigonometric variables that can be used as predictors in linear regression models. Collinearity among the regressors was assessed via correlation tables and eigenanalysis of the design matrix (Belsley et al. 1980). The eigenanalysis was conducted via the COLLIN option in the REG procedure of the Statistical Analysis System version 9. This analysis indicated that the date variables and discharge were correlated but that the effect was not sufficiently strong to influence regression estimates (condition index < 10). All possible combinations of seven regressors were evaluated. The explanatory strength of candidate models was assessed using information-theoretic criteria (small-sample-corrected Akaike's information criterion [AIC$_c$] and related measures of model support; Burnham and Anderson 2002). Because of the intercorrelation, the support for candidate models with one or the other of the correlated regressors will be similar.

The diel pattern of migration was evaluated using circular statistics (Batschelet 1981). The mean time of migration $\bar{\phi}$ was estimated as:

$$\bar{\phi} = \arctan(\bar{y}/\bar{x}) \quad \text{if } \bar{x} > 0, \text{ or}$$

$$\bar{\phi} = 2\Pi + \arctan(\bar{y}/\bar{x}) \quad \text{if } \bar{x} < 0,$$

where ϕ_i is the time of day of migration event i (numbering 1 to n), expressed as an angle within the 24-h cycle,

$$\bar{y} = \frac{\sum_{1}^{n} f_i \sin \bar{\phi}_i}{\sum_{1}^{n} f_i},$$

$$\bar{x} = \frac{\sum_{1}^{n} f_i \cos \bar{\phi}_i}{\sum_{1}^{n} f_i},$$

and f_i is the value of the abundance index ($1 \leq f_i \leq 5$).

The SD of migration time (s) was estimated as:

$$s = \sqrt{2(1 - r)},$$

where

$$r = \sqrt{\bar{x}^2 + \bar{y}^2}.$$

To test whether migration times were randomly distributed over the 24-h cycle, we used the Rayleigh test. To test whether the distribution of migration times varied among dates, we used tests of independence in contingency tables. Contingency table entries were minutes in which migrations occurred, weighted by the abundance index. We aggregated migration times into four different time periods (after rounding minute to the nearest hour: 1700–0400, 0500–0800, 0900–1300, and 1400–1600 hours), aggregated dates into weeks, and conducted a *G*-test. We also further aggregated time into two periods (0500–0800 hours and other), aggregated dates into the first and the second 4-week periods, and then conducted a Fisher's exact test on the resulting 2 × 2 table. For graphical presentation, the mean $\bar{\phi}$ and s were converted from angles into times.

Collection and analysis of data on endogenous influences on migration timing.—Juvenile alewives were collected in two areas of Bride Lake and classified as migrants or nonmigrants (Table 1). Juveniles collected as they passed over the weir into Bride Brook were classified as migrants. Migrants were collected with a dip net weekly as close to the beginning of each week as possible. Juveniles that were collected in the center of the lake were classified as nonmigrant fish; these fish were collected at night on a bimonthly schedule by means of a 100-m^2 purse seine with 3.18-mm mesh. All fish collected were measured for total length (TL) and euthanized. Twenty randomly selected individuals were preserved in 95% ethanol, and an additional 20 randomly selected fish were frozen upon return from the field site.

Age in days since hatching was estimated from the microstructure of sagittal otoliths. Sagittal increments have not been validated as a daily age record in alewives but have been validated in American shad *A. sapidissima* (Limburg 1994). Sagittae were removed from all fish that were preserved in 95% ethanol. Otoliths were rinsed and cleaned in deionized water, dried, and then mounted onto a slide with thermoplastic glue. Otoliths were then ground and polished with silicon-carbide paper (600–1,200 grit). We enumerated daily increments using a compound microscope with oil immersion at 400× magnification. Fish age was estimated as the mean of replicate determinations. Replication and evaluation of replicates followed previously established practices (Schultz et al. 2005). Two readers examined each otolith at least two times independently. Large variability among replicate counts (SD > 8, coefficient of variation [100 × SD/mean] > 10%) was typically the result of a single count that could be attributed to misinterpretation of subdaily increments. In these cases, the divergent count was eliminated and the mean of the replicates was recalculated. In cases where a divergent replicate could not be clearly identified, additional replicate counts were taken. After elimination of divergent replicates, the mean SD among replicates was 3.2 and the mean coefficient of variation was 5.2%.

We estimated condition as residual dry mass (Jakob et al. 1996). Specimens that had been frozen for storage were dried to constant mass at 68°C for 48 h. Residual dry mass is the amount by which an individual's dry mass departs from the dry mass expected based on the fish's length; the expected value is estimated from the pooled data by regressing $\log_{10}$-transformed dry mass against $\log_{10}$-transformed length. In addition to the use of regression to assign individual residual dry mass values, we also tested whether dry mass increased with length in an isometric fashion (slope of the log–log regression = 3). The scaling slope was evaluated against the null hypothesis value of 3 with a *t*-test.

Standard linear models were used to estimate temporal effects and differences in length, age, length at age, and condition between migrant and nonmigrant alewife juveniles. We tested for temporal variability in state variables via one-way analysis of variance (ANOVA), treating week as a categorical variable. Differences in length and age between migrant and

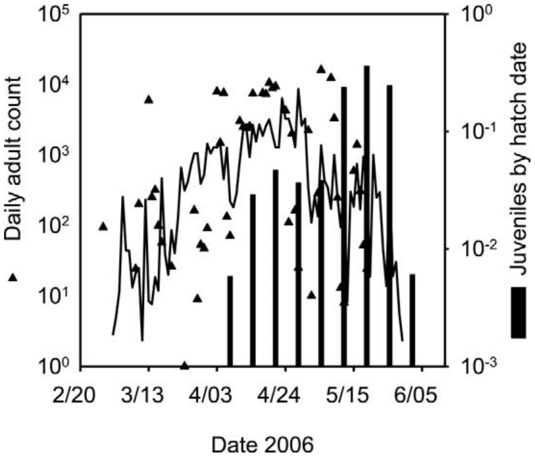

FIGURE 1.—Seasonal timing of adult alewife migration and spawning in Bride Lake, Connecticut. The solid triangles represent daily counts of spawning adults migrating into the lake as recorded by an electronic fish counter during 2006. Missing values occurred because the counter was not read on weekends. The solid line represents the mean daily adult count for 2003–2009, excluding 2006. Vertical bars represent the seasonal distribution of hatching as a proportion. Date on the *x*-axis is month/day.

nonmigrant juveniles were tested with a *t*-test for each week that both classes of juveniles were collected. Condition and size-at-age differences between migrant and nonmigrant juveniles were tested via analysis of covariance (ANCOVA) in which length and age, respectively, were included as covariates. The magnitude of the difference in condition and size at age between migrant and nonmigrant juveniles was estimated as the difference in least-squares (LS) means; the mean dependent variable for each class was adjusted to a common mean value for the independent variable(s). For this comparison, condition (log-transformed residual dry mass) was back-transformed; back-transformed values were corrected for bias according to Sprugel (1983) and Newman (1993).

Results

Environmental Influences on Migration Timing

The first adult alewives returning to Bride Lake to spawn arrived at the end of February 2006 (Figure 1). Over the next few weeks, adults appeared sporadically and there was a substantial pulse lasting several days in mid-March. Adults arrived steadily throughout April and the first half of May; 89% of adults arrived during that 6-week period. The total number of adults migrating into Bride Lake in 2006 was 129,114; the median date of arrival at Bride Lake was 19 April.

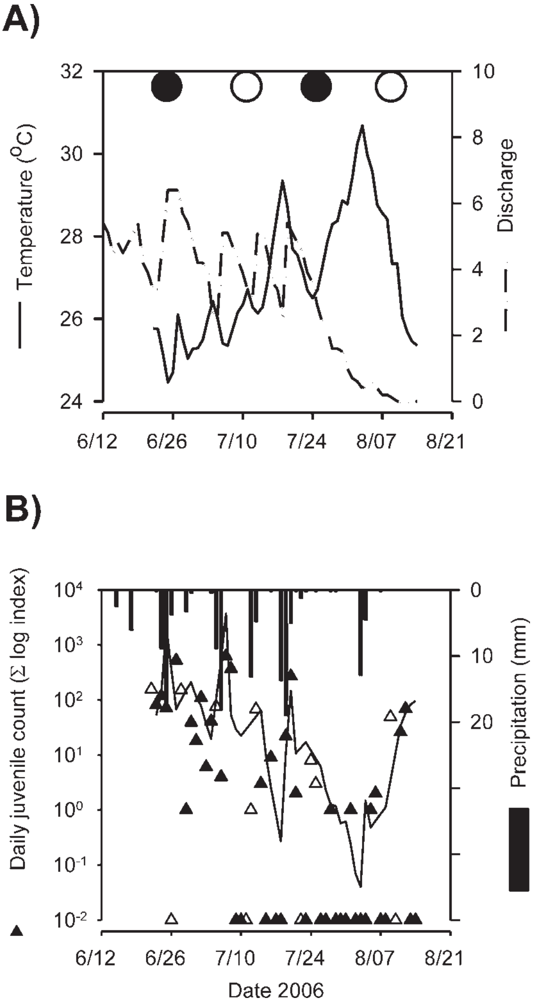

FIGURE 2.—Seasonal timing of juvenile alewife migration in Bride Lake, Connecticut, and associated environmental variables during 2006: **(A)** daily values of temperature (°C) and stream discharge (ft^3s^{-1}), with moon phases represented along the top (solid circles = new moon; open circles = full moon); and **(B)** daily migration rate (solid triangles; ordinal scale of 0–5, with values of 0 plotted as 0.01; see Methods) for each date of the video record (open triangles represent data that were discarded because the video record on these dates was incomplete). Temporal migration pattern predicted by the best regression model (including two predictors: temperature and the previous day's rainfall) is represented by the solid line in (B); precipitation (mm) is represented by vertical bars. Date on both *x*-axes is month/day.

The temporal distribution of the 2006 run was comparable with that of the other annual runs recorded since 2003 (Figure 1), and its magnitude was relatively high. Median dates of arrival have been as early as 16 April (in 2003) and as late as 26 April (in 2008). The overall median arrival date for 2003–2009 (excluding 2006) was 21 April. The number of adults in the run

TABLE 1.—Sample sizes of migrant and nonmigrant juvenile alewives in Bride Lake, Connecticut, by week of collection during 2006. The sample sizes used in dry mass and age analyses are given in parentheses (dry mass *n*, age sample *n*). In all but 2 weeks, all migrant or nonmigrant fish were collected on a single date.

Week	Migrants	Nonmigrants
16 Jun	47 (0[a], 20)	50 (20, 20)
30 Jun	40 (20, 19)	0
7 Jul	60 (20, 20)	30 (20, 20)
14 Jul	40 (20, 19)	0
21 Jul	40 (20, 20)	0
28 Jul	0	50 (20, 20)
11 Aug	40 (20, 20)	0
1 Sep	20 (0, 21)	50 (0, 20)

[a] Samples for dry mass determination were inadvertently destroyed.

TABLE 2.—Regression models that best predicted the daily migration rate of juvenile alewives from Bride Lake, Connecticut, in 2006. Table entries for each model include regressors (d = date; d^2 = date squared; z = one of two terms for lunar phase; t = temperature, °C; q = stream discharge, $\mathrm{ft}^3\mathrm{s}^{-1}$; r_{-1} = rainfall, mm, lagged by 1 d), Akaike's information criterion corrected for small sample size (AIC_c), difference in AIC_c between the given model and the best model (Δ_i), Akaike weight (w_i), and evidence ratio (which is equal to w_1/w_i, where w_1 is the Akaike weight of the best model). Models are listed in order of lowest to highest AIC_c. Table displays the five most predictive models (those for which evidence ratio <3; evidence ratio > 3 indicates low model support; Burnham and Anderson 2002). Regressors with a positive slope are indicated in bold text.

Regressors	AIC_c	Δ_i	w_i	Evidence ratio
t, $\boldsymbol{r}_{-1}$	281.25	0.00	0.0317	
t, $\boldsymbol{q}$, $\boldsymbol{r}_{-1}$	281.67	0.42	0.0257	1.23
d, t, $\boldsymbol{r}_{-1}$	281.82	0.57	0.0238	1.33
z, t, $\boldsymbol{r}_{-1}$	281.92	0.67	0.0227	1.39
z, t, $\boldsymbol{q}$, $\boldsymbol{r}_{-1}$	283.42	2.17	0.0107	2.96

has been as low as 68,757 (2005). The number migrating into Bride Lake in 2006 was the highest observed since 2003. The mean run size for 2003–2009 (excluding 2006) was 80,840 fish.

The hatch date distribution of alewife offspring was estimated via age analysis of the migrant juveniles. The earliest hatching occurred about 1 month after the first adults arrived on the spawning ground; the latest hatching occurred about 2 weeks after the last adults arrived (Figure 1).

Most of the juveniles that migrated from mid-June to mid-August 2006 departed in several 1- or 2-d pulses. During mid-June to mid-August, we video-recorded 360,000 migrating juveniles. Within the 42 d of video record that were retained for further analysis, we recorded approximately 320,000 migrants. Our methods resulted in a conservative estimate of the number of fish that migrated in 2006. We estimated that 84% of these migrants departed Bride Lake in three episodes: late June, early July, and late July (Figure 2B).

The results of the regression analysis indicated that temperature, the previous day's rainfall, date, and discharge were the best predictors of migration rate (Table 2). No single-regressor model yielded a measure of fit comparable with that of models having two or more regressors. For most of the season, pulses of migration were associated with precipitation events, transient decreases in water temperature, and transient increases in stream discharge (Figure 2A, B). The decrease in migration rate as the season progressed was accompanied by a seasonal decrease in stream discharge; date and stream discharge were roughly interchangeable as regression predictors (Table 2). Rainfall in early August did not reverse the decline in discharge, but migration rate recovered somewhat and increased as temperature fell from peak values. Moon phase appeared as a predictor in two of the supported models because of the occurrence of a new moon during the first migration peak and a full moon during the late-season recovery (Figure 2A).

The diel distribution of migration had two distinct peaks (Figure 3). The earlier peak coincided with a period around dawn, and the second peak occurred in mid-day. Migration times were distributed nonrandomly over the day (Rayleigh test: $P < 0.001$).

The time of day that migration occurred was not constant over the season (Figure 4). The null hypothesis that migration time was independent of week was rejected ($G = 1{,}400$, df = 21, $P < 0.0001$). In the first 4 weeks of the season, migration was usually observed in the hours around dawn; 57% of the minutes in which migrants were observed were within this 4-h period. In the latter 4 weeks of the season, less than 9% of the minutes in which migrants were observed were within this time period (Fisher's exact test: $P < 0.0001$).

Endogenous Influences on Migration Timing

The length of migrating juvenile alewives varied over the season. The smallest migrant collected at the weir was 28 mm TL, and the largest was 75 mm (mean ± SE = 41 ± 0.4 mm). Length varied significantly among weeks (one-way ANOVA: $F = 105$; df = 6, 280; $P < 0.0001$). Migrant length varied in a complex fashion over the season; migrants were relatively large in mid-June, were smallest in late June, and progressively increased in length thereafter (Figure 5).

Migrants were longer than nonmigrants during all sample weeks. The smallest nonmigrant fish collected by purse seine was 22 mm TL, and the largest was 57

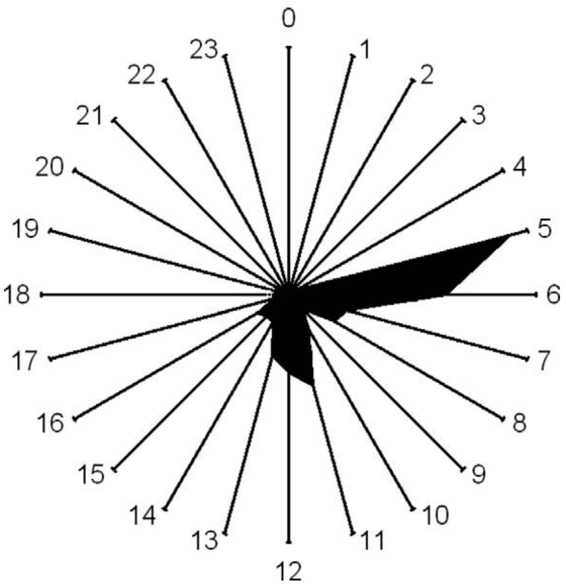

FIGURE 3.—Diel timing of juvenile alewife migration from Bride Lake, Connecticut, during 2006. The time distribution was derived by aggregating the 42 d with near-complete video records and summing the log abundance index (see Methods) for each hour. Each radius in the radar plot represents an hour in the 24-h cycle. Abundance is represented as distance along the radius. Scale is omitted for clarity; the maximum value for each radius is sum (log abundance index) = 600.

mm (mean = 38 ± 0.6 mm). The mean length of nonmigrant fish progressively increased over the season (one-way ANOVA: $F = 440$; df = 3, 176; $P < 0.0001$; Figure 5). In every week that both migrant and nonmigrant fish were collected, there was a significant difference in length between the two groups (week of 16 June: $t = 15$, df = 95, $P < 0.0001$; week of 7 July: $t = 3.3$, df = 88, $P = 0.002$; week of 1 September: $t = 6$, df = 68, $P < 0.0001$). The difference in mean TL between migrant and nonmigrant fish was higher in mid-June (12 mm) than later in the season (1–4 mm).

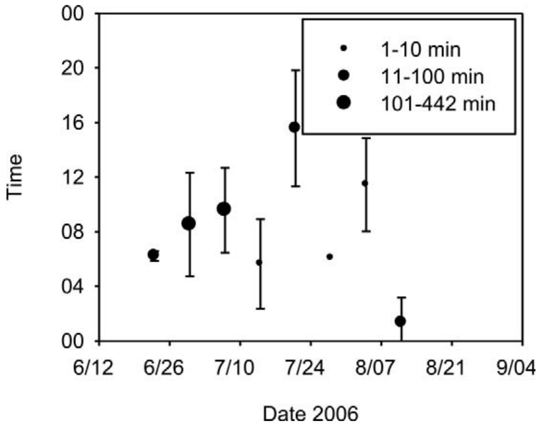

FIGURE 4.—Seasonal variability in daily time (00 = 2400 hours, 04 = 0400 hours, 08 = 0800 hours, etc.) of juvenile alewife migration from Bride Lake, Connecticut, during 2006. Mean (±SD) time of migration was estimated for 8 weeks, which included 42 d with near-complete video records. Symbol size varies with sample size (number of minutes in which migrants were observed). Date on the *x*-axis is month/day.

Migrants had a higher condition index than nonmigrants. There was a strong relationship between dry mass and length (Figure 6A) that deviated significantly

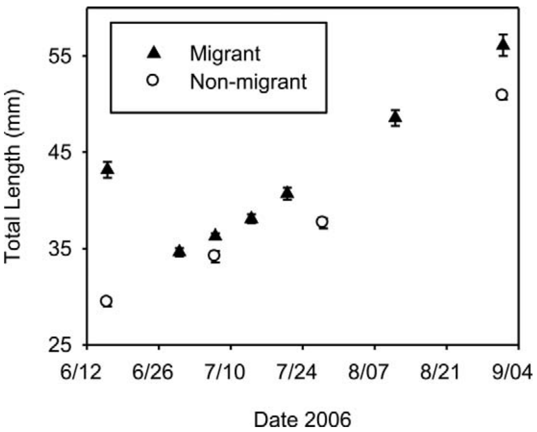

FIGURE 5.—Mean total length (±SE) of migrant and nonmigrant juvenile alewives in Bride Lake, Connecticut, estimated for each week of collection during 2006. Date on the *x*-axis is month/day.

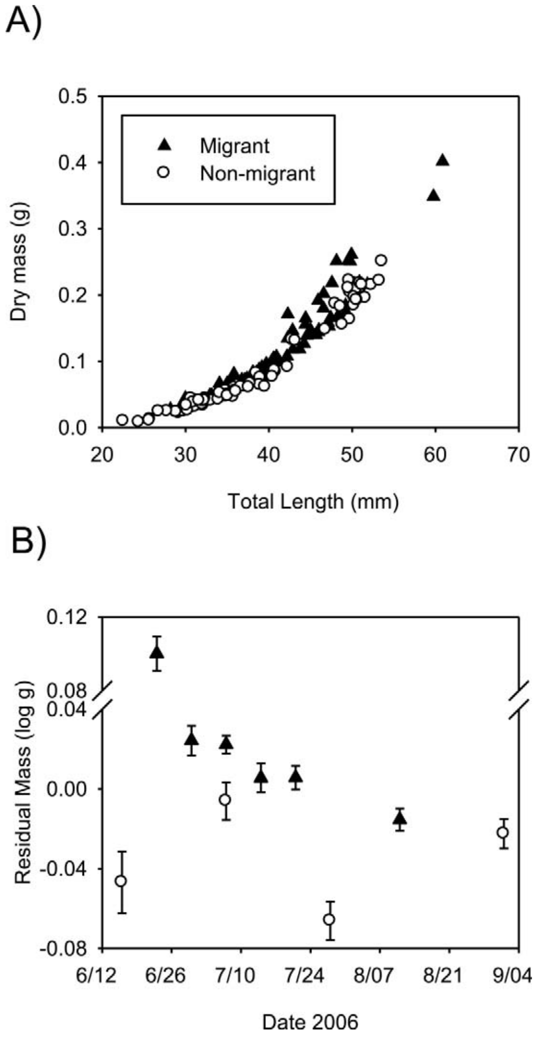

FIGURE 6.—Condition of juvenile alewives in Bride Lake, Connecticut, during 2006: **(A)** dry mass plotted against total length of migrant and nonmigrant juveniles and **(B)** mean (±SE) residual dry mass (log transformed) of migrant and nonmigrant juveniles, estimated for each week of collection (a break in the *y*-axis was necessary because of the higher residual dry mass of the early migrants; date on the *x*-axis is month/day).

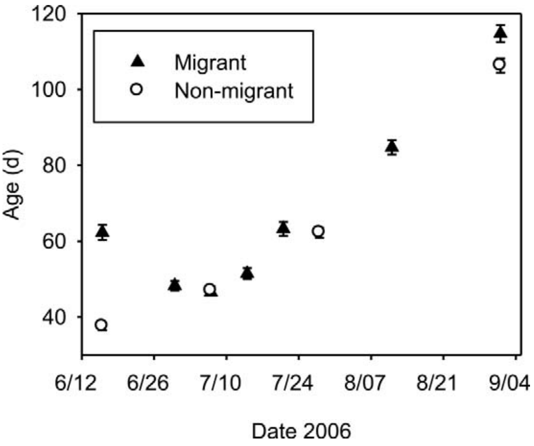

FIGURE 7.—Mean (±SE) age of migrant and nonmigrant juvenile alewives in Bride Lake, Connecticut, estimated by week of collection in 2006. Date on the *x*-axis is month/day.

from isometric scaling (regression of $\log_{10}$[dry mass] versus $\log_{10}$[TL]: $r^2 = 0.96$, slope = 3.7, SE = 0.05; *t*-test of null hypothesis that slope = 3.0: $t = 13$, $P < 0.0001$). Migrants had greater mass at length than did nonmigrants (ANCOVA, migrant versus nonmigrant difference after elimination of nonsignificant interaction: $F = 66$; df = 1, 191; $P < 0.0001$). Migrant dry mass at length was about 14% greater than nonmigrant dry mass at length (back-transformed LS mean dry mass at 39 mm: 85 mg for migrants, 74 mg for nonmigrants). Mass at length varied over the season among both migrants and nonmigrants (ANCOVA, week effect after elimination of the nonsignificant interaction; migrants: $F = 32.91$, df = 5, 111, $P < 0.0001$; nonmigrants: $F = 6.9$, df = 3, 71, $P = 0.0004$; Figure 6B).

Migrant alewives were the same age or older than nonmigrants. The age of both migrating and nonmigrant fish varied among dates (one-way ANOVA; migrants: $F = 209$, df = 6, 132, $P < 0.0001$; nonmigrants: $F = 491$, df = 3, 76, $P < 0.0001$). Mean migrant age was relatively high early in the season, declined to a minimum of 42 d in early July, and then progressively increased for the remainder of the season (Figure 7). Mean age of nonmigrants increased progressively over the season (Figure 7). Migrants were older than nonmigrants in mid-June and late in the season but not in early July (week of 16 June: $t = 21$, df = 38, $P < 0.0001$; week of 7 July: $t = 1.0$, df = 38, $P = 0.32$; week of 1 September: $t = 3.5$, df = 39, $P = 0.001$). The difference in mean age between migrants and nonmigrants was higher in mid-June (16 d) than later in the season (1.8 d during the week of 1 September).

Migrants were larger at age than nonmigrants. There was a strong linear relationship between length and age in an analysis combining migrants and nonmigrants (Figure 8A; bivariate regression: TL = 22.1 + [0.294 × age]; $r^2 = 0.72$). The slope of the length–age relationship did not differ between migrants and nonmigrants (ANCOVA, length × migration type interaction: $F = 1.6$; df = 1, 215; $P = 0.20$). The length of migrants at mean age was 11% greater than the corresponding length of nonmigrants (ANCOVA,

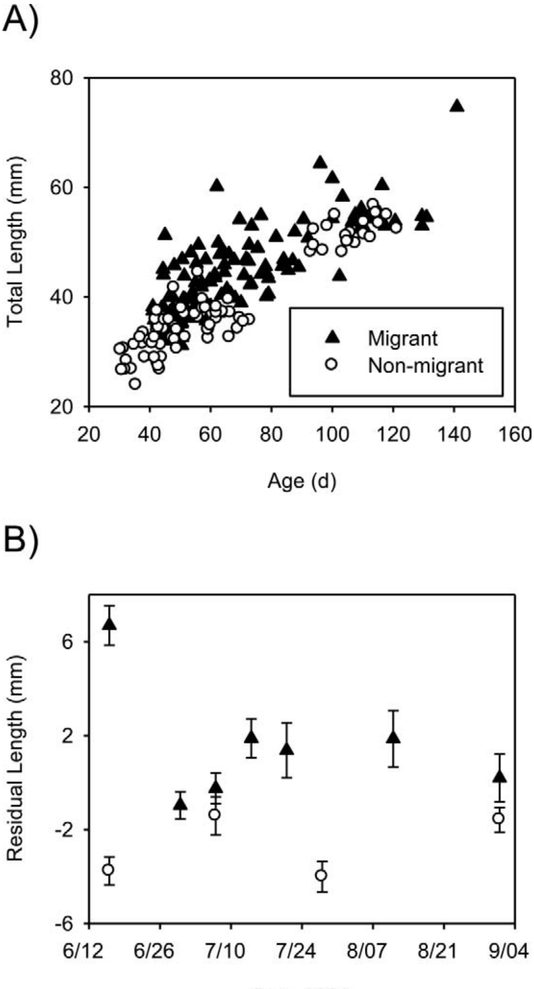

FIGURE 8.—Length–age relationships for migrant and nonmigrant juvenile alewives in Bride Lake, Connecticut, during 2006: **(A)** total length plotted against age and **(B)** mean (±SE) residual length estimated as the mean for each week of collection of individual deviations from expected values based on bivariate regression of length and age.

test of migrant versus nonmigrant difference after elimination of nonsignificant interaction: $F = 52.4$, df = 1, 216, $P < 0.0001$; LS mean TL at 68 d: 43 mm for migrants, 39 mm for nonmigrants). The length-at-age difference between migrants and nonmigrants was most pronounced early in the season (Figure 8B).

Discussion

Migratory behavior of juvenile anadromous alewives in Bride Lake was affected by a combination of individual endogenous factors and environmental factors. Endogenous factors related to an individual's growth and feeding success determined whether the fish exhibited migratory behavior, as indicated by the differences between migrant and nonmigrant fish. Exogenous abiotic factors also influenced migratory behavior, as indicated by the association of daily migration rate with variables such as rainfall and stream discharge and by the significant diel variability in migration rate. Predictors of migration, which may contribute to year-class strength, should be considered for monitoring and management in recovery plans for this species of concern.

Spawning began well after the first adult alewives migrated into the lake. The earliest hatch dates we estimated from the daily age record were one full month after the earliest migrating adults were recorded at the electronic fish counters. The reproductive condition of migrating adults provided an indication of a lag between migration and spawning: "running-ripe" females are uncommon until May at the Bride Lake weir and are almost never collected among the earliest arriving fish. This lag is further supported by the life history of the species. Anadromous alewives begin spawning when water temperatures reach 12–15°C (Collette and Klein-MacPhee 2002). In 2006, the water temperature in Bride Lake reached this temperature range between 12 and 16 April. At this temperature, the egg development time from spawning to hatch is 6 d (Bigelow and Welsh 1925).

Multiple endogenous factors were associated with readiness to migrate in juvenile anadromous alewives. Migrants were generally older, larger in both absolute and relative (size at age) terms, and in better condition (greater mass at length) than nonmigrant fish. This suggests that the amount of accumulated energy has a positive effect on the net benefit of migration at any time in the migratory season. Few researchers of anadromous alewives (Cooper 1961; Kissil 1974; Richkus 1975a; Yako et al. 2002; Iafrate and Oliveira 2008) have examined endogenous factors, and fewer still (Yako et al. 2002; Iafrate and Oliveira 2008) have collected mensural data other than length. In contrast to our findings, previous studies of anadromous alewives have indicated that migrants were a random subset of the fish remaining in the nursery (Cooper 1961; Richkus 1975a; Yako et al. 2002). Hatch date also influenced migration readiness. Analysis of age at migration revealed that mid-June migrants were April hatchlings, whereas fish that migrated in late June and thereafter were predominantly May hatchlings. In agreement with our results, migrating age-0 American shad in the Hudson River were larger and older than nonmigrant American shad (Limburg 1996). There are many possible benefits to migrating in relatively good condition, such as improved locomotory performance, greater ability to avoid predators, and better ability to osmoregulate in seawater. These possibilities remain untested, with the exception of a single experiment on salinity tolerance of Bride Lake alewife juveniles in July; migrants were substantially more tolerant of direct transfer to salt water for 60 h than were nonmigrants (33% versus 95% mortality; E. T. Schultz, unpublished data).

The age at which an individual alewife in Bride Lake accumulates sufficient mass and condition to be migratory may be influenced by maternal investment and by success in feeding after hatching. Maternal investment (i.e., egg size, yolk reserves, or both) is consistently predictive of size at hatch, early growth, and survival (Einum and Fleming 1999; Heath et al. 1999; Berkeley et al. 2004). Therefore, it is likely that a large size at hatch has a pronounced effect on the development of migratory readiness. Size at hatch may be influenced by parental female size; in mature females captured upon entry into Bride Lake, oocyte size was significantly affected by female size but not by date of female migration (E.T.S., unpublished data).

The energetic state at which migratory readiness developed in alewives was not seasonally constant. Mid-June migrants grew to a larger size, were in better condition, and were larger at age than migrants in late June and early July, indicating that April hatchlings had accumulated energy more rapidly than the May hatchlings. Earlier studies have suggested that juvenile alewife production in coastal lakes is determined by planktonic food resources (Havey 1973; Walton 1987), and the temporal changes in food resources within Bride Lake are consistent with this conclusion. By late June and early July, anadromous alewife juveniles have consumed essentially all cladocerans and large copepods available in their lake (Post et al. 2008); in lakes without alewives, large zooplankton remain abundant throughout the summer. Hence, the largest waves of migration occurred when preferred zooplankton had become scarce. Alewives that further delayed migration from Bride Lake migrated at a greater age and length but a lower condition. Seasonal decline in condition of alewives has been observed in previous studies (Vigerstad and Cobb 1978; Iafrate and Oliveira 2008).

During summer 2006, juvenile alewives migrated from Bride Lake on a majority of the days when streamflow was adequate for emigration to take place. The departure of individuals from the lake before mid-July was typically characterized by large pulses of emigration occurring over 1–2 d, a pattern that has been observed in many other systems (Cooper 1961; Kissil 1974; Richkus 1975a; Huber 1978; Kosa and Mather 2001). These large pulses accounted for over 80% of the observed migrants. Analysis of returning adults should be undertaken to assess whether some classes of migrants contribute disproportionately to the spawning stock (Yako et al. 2002).

The near-continuous record of migration allowed us to model juvenile migration in response to environmental stimuli. Possible environmental cues to alewife emigration in coastal systems have been identified in previous studies (Cooper 1961; Kissil 1974; Richkus 1975a; Stokesbury and Dadswell 1989; Yako et al. 2002). Our analysis of the emigration record and environmental data supports cues identified in these previous studies. The results specifically indicated that low water temperature, elevated discharge, and episodes of rainfall were the most predictive environmental prompts for migration. The information-theoretic assessment of models (Table 2) did not decisively identify a single model with best support but instead identified a group of models with one to four regressors. High migration rates occurred on the day after a rainfall event. Rainfall has often been identified as a stimulus to juvenile alewife migration (Cooper 1961; Richkus 1975a; Huber 1978; Stokesbury and Dadswell 1989). Similarly, stream discharge was a positive predictor of migration rate. We observed that during the course of migration, juvenile alewives were attracted to areas of high flow and sought such areas as the optimal channels for downstream migration, as has been reported previously (Cooper 1961; Richkus 1975b). The association between migration and precipitation, with resulting increases in stream discharge, suggests the possibility of energetic benefits to migrating downstream in faster flows or survival benefits due to reduced predation during the migration. Lower water temperature appears to have been associated with increasing migration near the end of the time series, when there was little rainfall and when stream discharge was minimal. Coincidence of this late migration with a full moon may also explain the appearance of a periodic lunar phase variable. Previous research has indicated that alewives migrate in conjunction with new moons (Stokesbury and Dadswell 1989; Yako et al. 2002) but never with full moons.

Our analysis of diel migration patterns indicated that migration was largely isolated to two portions of the day. The more consistently observed daily pulse was associated with sunrise, especially during the first half of the migration season. On days when greater numbers of fish departed the lake, an additional pulse was observed during mid-day hours. The preference for early morning departure contrasts with previous studies, which have all indicated that migration predominately occurred in the afternoon. In some of the earlier studies, the diel timing recorded was the time of passage nearly 1 km downstream from the nursery area (Kosa and Mather 2001; Yako et al.

2002), so migration must have begun earlier in the day and may have been more consistent with the times we observed. However, in one case alewives were exclusively observed migrating at the outflow in the afternoon (Richkus 1975a). The difference in results may also stem from our continuous monitoring of migration. Earlier studies addressing this question have relied on periodic sampling that may have missed significant portions of alewife migration. The variability in reported migration times may also reflect regional differences in migratory behavior within the species.

Diel timing of migration changed later in the season, when stream discharge was low; migrants departed from the lake at night instead of during the day. Two previous studies reported that juvenile alewives migrated at night (Stokesbury and Dadswell 1989; Yako et al. 2002), but all others observed migratory activity solely during the day. Small fish tend to behave differently during periods of low streamflow and water levels because they are more vulnerable to avian predators during these conditions (Allouche and Gaudin 2001; Steinmetz et al. 2003). It is possible that as water flow decreases and predation risk during transit to the ocean increases, fish realize a greater benefit by migrating at night when they would be less visible and when some predators would be less active. In any case, the variability in diel migration timing signifies that developmental stage or seasonally varying environmental conditions have some influence on migration behavior over short time scales.

We were unable to extend the study to the fall months; therefore, we cannot provide a complete analysis of migration or the physical state of the fish that migrated during the final 3 months of 2006. It is nearly certain that most fish migrated during the portion of the season we analyzed. Annual sampling on Bride Lake repeatedly shows that the juvenile alewife population decreases by two orders of magnitude between June and August (D. Post, Yale University, personal communication). Our emigration data mirrored these findings since more than 80% of the alewives observed leaving the lake had done so by 10 July. Consequently, our results remain pertinent to a more complete understanding of juvenile alewife migration dynamics.

Juveniles that delay migration can be subject to the risk of entrapment in nursery habitat when surface outflow ceases. During the course of the study, alewives were unable to migrate between 14 and 29 August 2006. We agree with earlier researchers (Kosa and Mather 2001; Yako et al. 2002) that prolonged entrapment would probably be harmful to fish that would otherwise migrate because they would be subject to a chronically depleted food supply and eventually to winter conditions (Kircheis and Stanley 1981; Loesch 1987; Jessop 1994; Yako et al. 2000, 2002; Kosa and Mather 2001; Post et al. 2008). Anadromous alewives do not appear to be capable of surviving overwinter in their natal lakes, and challenge with cold (5°C) freshwater induces mortality in alewives (McCormick et al. 1997). The addition of large-scale water extraction for human use lowers water tables and exacerbates the risk of entrapment (Nadim et al. 2007). Such anthropogenic alterations to aquatic ecosystems will only increase over the next few decades as coastal development continues; furthermore, global climate change in the northeastern region of the United States is expected to raise summer temperatures and decrease summer precipitation (Moore et al. 1997; Hayhoe et al. 2008; Nelson et al. 2009). The effect of these changes on alewife populations will require analysis of the relative contribution of early versus late juvenile out-migrants to the returning adult breeders.

Several limitations of this study are apparent. Because this study was focused on a single year-class of juvenile alewives in a single location, the applicability of our findings to other settings must be carefully judged. There are several indications that our findings may in fact be broadly applicable. The seasonal timing of adult and juvenile migrations we observed was comparable with reports from other locations in the region and from other years at Bride Lake (Kissil 1974; Ellis and Vokoun 2009). Other similarities to previously published studies include the seasonal decline in condition of migrants and the seasonally varying factors that cue migration. On the other hand, some of our findings differ from those of other studies, such as the reports that migration in juvenile alewives is undertaken by a random subset of the population (Cooper 1961; Richkus 1975b; Yako et al. 2002) and that juveniles primarily migrate during the afternoon (Richkus 1975a; Kosa and Mather 2001; Yako et al. 2002). Additional studies should reveal whether these differences arose because of differences in methods, functional differences among populations, or interannual sampling variability. If regional differences in juvenile emigration exist, they may result from adaptation of local alewife populations to differences in nursery conditions in conjunction with the natal fidelity exhibited by returning adults. Particular attention to juvenile growth and migratory behavior in larger riverine settings is needed to complement the historical emphasis on small coastal ponds. Because of workforce limitations, our sampling and video-recording ended before migration was complete, and nonmigrant sampling was conducted only on a monthly schedule. More frequent and prolonged sampling will be needed for a detailed and complete picture of factors that predict migratory behavior. While limited in scope, this study provides an improved understanding of the factors shaping juvenile anadromous alewife emigration patterns. Future research should include experimental trials that manipulate feeding conditions and use behavioral assays of migration to more directly determine the cues that stimulate migration of anadromous alewives.

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