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MECHANISMS FOR MIGRATION OF ANADROMOUS HERRING: AN ECOLOGICAL BASIS FOR EFFECTIVE CONSERVATION

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Abstract. Land use planners have the challenge of incorporating biologically sound guidelines into development plans to balance human development with conservation of natural resources. Valued as an important component of the natural heritage of the northeastern United States, anadromous river herring (*Alosa pseudoharengus*, *A. aestivalis*) represent a model system to look at how ecological data can help conserve biological diversity in systems impacted by humans. Juvenile river herring spend 3–7 months in freshwater then migrate to the ocean. However, factors that trigger migration, and consequently influence distribution and abundance, are not well understood. Thus, our objectives in this study were to (1) describe juvenile river herring migration patterns, both ''peak'' (>1000 fish/wk) and ''all'' (>30 fish/wk) migration; (2) identify potential cues for this migration; (3) examine effects of one type of ecosystem alteration, low water levels, on river herring; and (4) suggest how this information can be incorporated into an effective conservation plan. Weekly during June–November 1994, we sampled both migrating and nonmigrating river herring and seven associated abiotic and biotic variables in one continuous and one intermittent flow system on Cape Cod, Massachusetts. We then used multiple logistic regression to predict when juvenile river herring migrate. In the continuous-flow system, juvenile river herring migration primarily occurred during the midday hours from July through early November, with the peaks of migration, comprising >96% of all migrating fish observed in early July and early September. The peaks of migration occurred during the new moon, when *Bosmina* spp. density was low, and all periods of migration occurred when water visibility was low, during decreased amounts of rainfall. In the intermittent-flow system, juvenile river herring migration was frequently inhibited due to low water levels, and herring were on average 25 mm smaller than those in the continuous flow system. Using these results, managers can more effectively monitor river herring populations by identifying factors associated with migration and isolating critical flow periods when fish movement is likely to occur. Thus, we can detect changes in herring population size due to human impacts. Ultimately, these data can be incorporated into an ecologically sound conservation plan for juvenile anadromous herring that may help ensure their survival while balancing human needs for natural resources.

Key words: Alosa aestivalis; Alosa pseudoharengus; *anadromous river herring; balancing conservation with development;* Bosmina *spp.; Cape Cod, Massachusetts (USA); conservation; land use; migration; sustainability; water use.*

INTRODUCTION

In the United States, the human population is growing at a rate of one person every 12 s (U.S. Census Bureau 2000) resulting in development that can radically impact, reshape, and devastate aquatic ecosystems through changes in land use and water allocation. Although a cessation in human development is unrealistic, human impacts on the environment can be influenced. To shape development in a way that balances sustainable human use with the conservation of natural resources, scientists and natural resource managers need to understand how humans and nonhumans use shared resources such that land use planners can incorporate biologically sound guidelines into future development plans.

In Massachusetts, the third most densely populated state in the United States (U.S. Census Bureau 1994, 1996), increased development has resulted in major changes to aquatic ecosystems. On Cape Cod, for example, substantial development since the 1980s has increased the use of lakes and rivers as municipal water supplies and resulted in a higher frequency of ground water diversion. In particular, use of land by cranberry growers who require large quantities of water for maintenance, harvesting, and processing of the berries has impacted flow regimes in coastal systems (U.S. Department of Agriculture 1995, 1996). Despite the high level of urbanization in Massachusetts, one common fish group, the anadromous herring (alewife [*Alosa pseudoharengus*] and blueback herring [*A. aestivalis*])

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is still greatly valued as part of the state's natural heritage. Alewives and blueback herring, collectively termed river herring, are anadromous species found along the Atlantic coast of North America from Labrador, Canada, to Florida, USA (Loesch 1987). Adult river herring ascend coastal rivers to spawn in freshwater systems during late March–early July (Fay et al. 1983). Juvenile river herring remain in freshwater systems for three to seven months, after which they migrate to the ocean in large pulses (Richkus 1975). Anadromous river herring stocks are declining in the Northeast (Boreman 1981, Richkus and DiNardo 1984, Rulifson 1994). The potential negative effects of land use modifications and low water levels on juvenile herring might exacerbate this decline. As a result, anadromous herring in southeastern Massachusetts provide a model system to test if ecological research can provide scientific information on which to base an effective conservation plan that addresses how humans and fish can share natural resources in the face of continued development.

For anadromous fish that move great distances across multiple habitats, maintaining passable migration corridors is crucial. Human development often blocks passage for these fish. To balance conservation and development, it is critical to provide avenues along which fish can move at any time. To adequately manage and conserve important resources like anadromous river herring, it is vital to understand when and why the juvenile fish migrate. In particular, examining proximate cues for juvenile herring migration could help managers to identify critical migration periods and the factors associated with these migration events so that environmentally sound water and land use decisions can be made.

Though critical for effective management, factors that provide proximate cues for migration of anadromous fishes are not well understood. Although high water levels (Kissil 1974, Richkus 1975, Huber 1978), sharp declines in water temperature (Loesch 1969, Richkus 1975, Huber 1978, O'Leary and Kynard 1986), increased water flow due to heavy rainfall (Cooper 1961), and moon phase (O'Leary and Kynard 1986) have been associated with juvenile herring migration, factors that actually trigger migration are unknown. Similarly, for Atlantic salmon (*Salmo salar*), migration timing has been associated with, but not necessarily triggered by, various factors including water flow (Hesthagen and GarnÅs 1986, Hvidsten and Johnsen 1993, Rottiers and Redell 1993, Hvidsten et al. 1995), turbidity (Rottiers and Redell 1993), water temperature (Fried et al. 1978, Solomon 1978, Jonsson and Ruud-Hansen 1985, Hesthagen and GarnÅs 1986, Rottiers and Redell 1993, Hvidsten et al. 1995), and moon phase (Hvidsten et al. 1995). Likewise, downstream migration of other salmonids has also been associated with flow (Berggren and Filardo 1993), moon phase (Mason 1975), and photoperiod (Hartman et al. 1967, Zaugg 1981). In spite of all past research on migrating fish, specific factors that trigger migration, and thus drive an important component of distribution and abundance of anadromous fish, are still unknown.

A management plan that provides effective guidelines for land management and development while promoting conservation must incorporate information on distribution, abundance, and migration patterns. Hence to thoroughly describe migration patterns we quantified diel, seasonal, and species-specific migration patterns for juvenile herring. For seasonal migration, we examined both ''peak'' periods of migration (>1000 fish/wk) and ''all'' periods of migration (>30 fish/wk), because all migration events may be vital to sustain a population. Second, to test whether migration was due to the size or age of the fish, rather than to external factors, we sampled juvenile herring that had not yet migrated (hereafter called nonmigrating herring) within their rearing areas and compared the size and age of these fish to migrating herring. Third, to identify factors that potentially trigger out-migration (i.e., migration out of the freshwater system), we measured seven physical and biological characteristics of the study system that past studies have identified as potentially important in initiating fish migration and built a multivariate model to predict under what conditions juvenile herring will migrate. Next, we examined the relationship between water discharge and its potential effects on the herring population by comparing herring body size in a low flow system where fish are frequently prevented from migrating to those fish from our primary study system, a continuously flowing system. Finally, we speculated how this information might be incorporated into a management plan that balances conservation and development.

METHODS

Primary study site

Santuit Pond (Mashpee, Massachusetts; Fig. 1) is a 67.7-ha, mesotrophic, unstratified lake with 5.1 km of shoreline and a mean depth of 1.2 m (maximum depth, 3 m). It is bordered by several cranberry bogs, and ~40% of the shoreline contains private homes. This lake is the headwater for the Santuit River, which flows for 3.5 km before emptying into Nantucket Sound. Santuit River is a small, first-order stream with a mean width of 2.8 m and a mean depth of 0.3 m. Despite the cranberry bogs, continuous flows are maintained in the river throughout the year. Santuit Pond serves as the only spawning ground for river herring within this system.

Patterns of migration

To assess diel patterns of migration, we sampled the Santuit River once per week during 3 July–6 November 1994. Using ReBar stakes (ReBar Stakes, Louisville, Kentucky), drift nets (0.6 m wide × 0.4 m high × 1.5 m long, with 0.32-cm mesh) were set across the entire

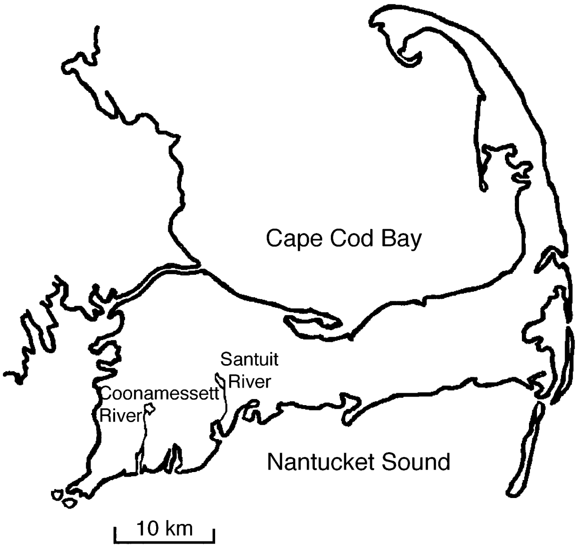

FIG. 1. Map of the study sites used to examine mechanisms for juvenile river herring out-migration. Both the primary study system, the Santuit River, and the secondary study system, the Coonamessett River, are on Cape Cod in southeastern Massachusetts, USA.

width of the stream for 15 min of each hour for 24 h beginning at 0900. All herring were counted, and a subsample was identified to species by examining the color of the peritoneum (Scott and Scott 1988). In addition, ~50 herring/h were measured (total length [TL] ± 1 mm).

To characterize the seasonal pattern of juvenile herring migration from Santuit Pond, migrating herring were collected three times each week during late June–early December 1994 in the Santuit River using drift nets set as described. Drift nets were set for 15 min, in each of three time strata, (a) 1300–1500, (b) 1500–1700, and (c) after dark, in order to intensively sample periods of traditionally high migration (Richkus 1975, Richkus and Winn 1979). All herring were counted, identified to species, and ~60 fish per sample were measured (TL ± 1 mm), masses measured (nearest ±0.1 g), and frozen within two hours of collection. Data from diel samples were combined with these weekly samples to characterize the seasonal pattern of migration. Overall diel and seasonal distributional patterns, alewife, blueback herring, and the combined river herring patterns were analyzed.

Migrating and nonmigrating herring

In any given sampling period during which herring migrate, other herring remain in the nursery area. Consequently, examining differences in biological characteristics of migrants and nonmigrants might provide insight into triggers for migration. Migrating herring were captured as described. To sample nonmigrating herring within Santuit Pond, juvenile herring were collected using one haul of a bag seine (9.1 × 2.4 m, with 6.4-mm mesh) pulled through a 33-m littoral zone transect parallel to shore once per week beginning in July. All seining was done approximately one hour after sunset. Beginning in late August, eight 5-min electrofishing transects (5 inshore, 3 open water) were used to collect juvenile herring once per week. During each electrofishing transect, one netter captured as many herring as possible using a dip net with 6.4-mm mesh and then estimated the proportion of fish captured during each transect. The total number of herring captured during each transect was then counted. Each week, up to 60 herring were identified to species, measured (TL ± 1 mm), masses measured (nearest ±0.1 g), and frozen within two hours of collection. Both collection methods were continued until no further herring were captured in the lake.

To evaluate the impact of herring age on migration timing, we examined sagittal otoliths from a subsample of migrant and nonmigrant herring from all dates on which concurrent lake and river samples were available. In the laboratory, sagittal otoliths were removed, placed in 30% sodium hypochlorite (bleach) followed by distilled water, air dried, mounted on glass slides using Pro-Texx (Sigma Chemical, St. Louis, Missouri, USA) with the sulcus facing up, and assigned a randomly chosen number (Limburg 1994). We next polished one of the two otoliths to approximately the mid-sagittal plane by hand using a series of 1–30-μm lapping films to expose the core. Images of the otoliths were projected on a computer monitor and manipulated using Optimus software (OPTIMAS 1995). Age was determined by tallying increment counts. Otoliths were read two or three times and were discarded if <10% agreement existed between the increment counts (Davis et al. 1985). The formation of daily otolith rings has been validated in the related American shad, *Alosa sapidissma* (Limburg 1994). Because comparing samples collected at the same time was more important than examining differences in trends for the entire data set, we examined differences between migrating and nonmigrating herring by comparing distributions of body size (TL) for five dates, as well as age for two dates, using the Kolmogorov-Smirnov test. Regression lines are shown to indicate trends through time, but were not used to examine differences between migrating and nonmigrating herring.

Physical characteristics

To test whether physical aspects of the Santuit River and Lake system affected herring migration, we measured discharge, water temperature, water visibility, precipitation, lunar cycles, and photoperiod during March–November 1994. Stream velocity (cm/s) was assessed using a Marsh McBirney electronic flow meter (model 2000; Marsh McBirney, Frederick, Maryland, USA) at 0.6 m depth for 10 equidistant points across a single transect located below the outlet of Santuit Pond. Velocity measurements were taken twice during each diel sample and concurrent with the two daytime weekly drift net samples; these were then converted to discharge (m^3/s) (Gordon et al. 1992). Santuit Pond water temperature was recorded hourly using a Ryan thermograph (model J-180; Ryan Instruments, Redmond, Washington, USA) set at a depth of 1 m. Water visibility was quantified weekly using a Secchi disk (model 77912; Forestry Suppliers, Jackson, Mississippi, USA) at one site in Santuit Pond. Precipitation levels were obtained from daily measurements taken at Otis Air Force Base, Mashpee, Massachusetts. Lunar cycles were obtained from published charts. Photoperiod measurements were calculated for the mid-Cape Cod area during 1994 (D. Bristol, *personal communication*).

Food availability

To quantify the food resources available to juvenile herring in Santuit Pond, we sampled zooplankton weekly during March–November 1994 with one vertical haul of a 53-μm, 30-cm diameter zooplankton net at three locations. All samples were preserved in 70% ethanol, and zooplankton density and species composition were quantified in the laboratory using a dissecting microscope. Samples were identified based on the dichotomous keys of Balcer et al. (1984) and Pennak (1989), counted, and classified into functional groups as described in Stahl and Stein (1994). These classifications were based on systematics, size, behavior, and other characteristics related to herring feeding ecology. Up to 22 individuals of each taxon were measured (nearest ±0.01 mm) using a digitizer with Sigma Scan (Jandel Scientific 1988) in order that length could be converted to biomass using length–mass regressions (Dumont et al. 1975, Culver et al. 1985).

Migration cues

To ensure that we identified all potentially important periods of migration, we analyzed data for two migration patterns including the ‘‘peaks’’ of migration ($>$1000 fish/wk) and ‘‘all’’ periods of migration ($>$30 fish/wk). Because the response variable (i.e., migration or no migration) was dichotomous and the distribution was non-normal, we used logistic regression. Prior to analysis, we created dummy variables for periods of migration and periods of no migration for each sample week. We performed univariate logistic regression analyses on discharge, water temperature, water visibility, rainfall, lunar cycle, photoperiod, and total zooplankton, calanoid, cyclopoid, and *Bosmina* spp. density and biomass for both peak and all migration periods to test for a relationship between these physical and biological characteristics of the Santuit system and timing of herring migration (seasonal pattern). Physical and biological characteristics were examined primarily as weekly means, change one week prior, or weekly point estimates. Because our goal was to seek patterns that would generate hypotheses rather than rigorously test hypotheses, we used $P = 0.06$ as a guide for whether a variable in each individual test was of potential interest. To maximize our chances of seeing all potentially important interactions, we did not correct the alpha level for use in multiple tests (i.e., do the Bonferronni correction). Given the complex nature of the system, the broad type of question we asked, and the paucity of information available about this type of system, we think this approach to determining comparison-wide alpha is justified.

Next, we examined multivariate relationships that might both describe and predict the timing of herring migration. Our goal was to obtain the most biologically significant model that contained the fewest independent factors. We incorporated all significant single factors ($P < 0.06$) into multiple logistic regression models for both peak and all periods of migration and then examined multivariate models with all possible combinations of these significant factors. To compare between multivariate models and thus identify the most important factors for migration, we used the log-likelihood ratio test (Hosmer and Lemeshow 1989) that compared the difference between model log-likelihoods using G (G = twice the difference between model log-likelihoods). The G value was then compared to a χ^2 distribution with one degree of freedom. Models were compared by sequentially dropping out factors and then comparing each resultant model to the full model. For these comparisons, $P > 0.05$ indicated that the dropped factor added little to the full model, thus allowing us to determine the model with the most parsimonious set of factors. When more than one model was found to be significant, the model with the lowest P value was deemed to be the best (Hosmer and Lemeshow 1989). In our small, alewife-dominated systems, examining species separately did not alter general conclusions. Hence, we only show migration cues for both species combined.

Low-flow comparison

For anadromous fish, discharge is a whole-ecosystem attribute and difficult to manipulate independent of other factors. Thus, to indirectly test how one important aspect of ecosystem alteration, discharge, might affect herring size and migration patterns, we compared herring size in Coonamessett Pond, a low-flow system in which juvenile fish are frequently prevented from outmigration, to our primary study system, Santuit Pond. Coonamessett Pond (Falmouth, Massachusetts) is a 63.9-ha lake with 4.7 km of shoreline, 25% of which is developed (Yako 1998: Fig. 1). Coonamessett Pond is the headwater for the Coonamessett River, yet the water level of Coonamessett Pond frequently is not high enough to provide flow of water into the river. Hence, anadromous herring are often trapped in the lake, unable to migrate to the ocean. Coonamessett Pond is geographically close and physically similar to Santuit Pond (Yako et al. 2000), except for the flow

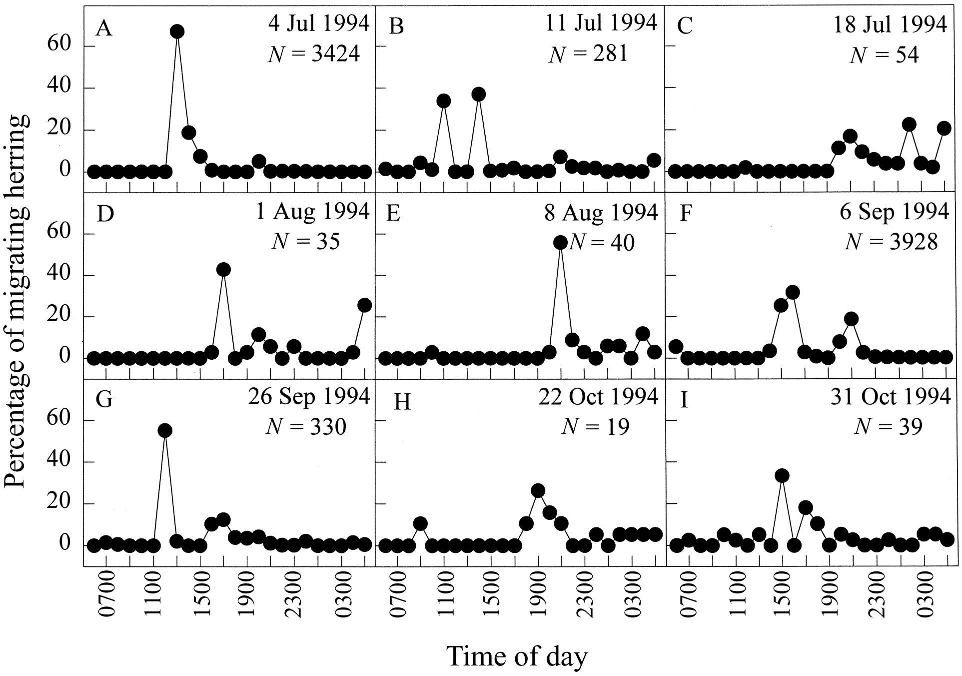

FIG. 2. Diel patterns of migration of juvenile river herring observed in the Santuit River on nine sampling dates during July–October 1994. Dates shown are those in which >10 fish migrated per day. Percentages (y-axis) are of total number of migrating herring per diel sample. N represents the total number of herring captured during each diel sample.

regime. In Coonamessett, like Santuit, both migrating and nonmigrating herring were captured, and flow was measured biweekly as we have described.

RESULTS

Patterns of migration

In general, migrating fish were patchily distributed through time. Migration did not occur on each day sampled, nor did it occur at each hour of the 24-h diel sampling period (Fig. 2). Overall, migration of >30 fish/d occurred during only eight of the 19 diel samples (Fig. 2A–G, I), with >1000 fish migrating only on two dates, 4 July and 6 September (Fig. 2A, F). During six of the nine weeks, migration peaked during 1100–1700 (Fig. 2A, B, D, F, G, I), while during the other three weeks migration peaked later in the evening, during 1900–2100 (Fig. 2C, E, H). Even when most migration occurred during the afternoon, smaller numbers of fish also migrated after dark, ~2000 (Fig. 2B, D, F, I). Although variation in diel migration occurred, the majority of fish migrated at 1300 on 4 July (Fig. 2A) and 1600 on 6 September (Fig. 2F), producing a less variable migration pattern over the entire season (Fig. 3A). Both alewives (Fig. 3B) and blueback herring (Fig. 3C)

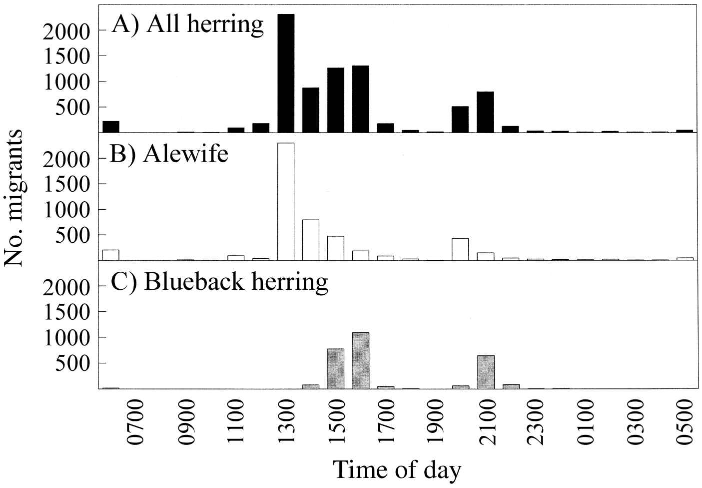

FIG. 3. Overall diel pattern of migration of juvenile (A) river herring, (B) alewives, and (C) blueback herring observed in the Santuit River during 1994. These data represent the sum of diel samples over 19 wk.

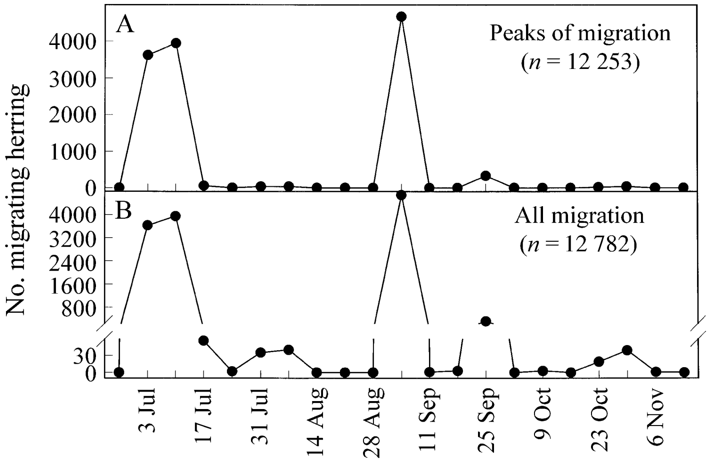

FIG. 4. Seasonal pattern of migration for river herring collected in Santuit River during 1994. Both (A) "peaks" of migration, defined as >1000 fish per week, and (B) "all" periods of migration, defined as >30 fish per week, are shown.

exhibited the same migration pattern as the aggregate of both river herring species (Fig. 3A).

Relative to seasonal patterns, the "peaks" of migration (>1000 fish), which included 96% of all migrating herring, occurred during three weeks, 3 July, 10 July, and 4 September (Fig. 4A). Fish migrating during these three weeks made up our peak migration data set. In addition, smaller numbers of fish (30–1000) migrated during five other weeks, 17 July, 31 July, 7 August, 25 September, and 30 October. These lesser movement events comprised anywhere from 1% to 84% of the remaining migrating fish, but only 4% of the total catch (Fig. 4B). Thus, the "all" migration data set was composed of fish from the three peak migration weeks and the five other smaller migration events. Overall, >97% of all herring captured had migrated by the second week of September, and no herring were captured after the week of 6 November, although sampling continued for several more weeks.

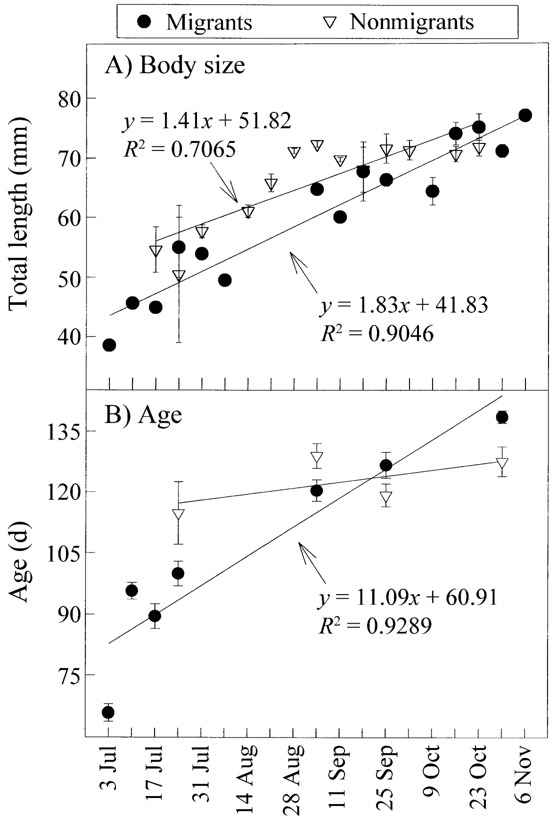

FIG. 5. (A) Body size and (B) age of migrating and nonmigrating juvenile herring collected from the Santuit system during 1994. Age was determined through otolith examination.

Alewives migrated throughout the entire season, whereas blueback herring were not found in any samples until the beginning of September, after which they dominated the catches. During the first week in September, 57% of the migrating fish were blueback herring and 43% were alewives. By the end of September, samples of migrating fish were 75% blueback and 25% alewives. Because these late-migrating fish were a small component of the anadromous herring (3% of the total herring run), blueback herring had a minor impact on migration patterns. Therefore, overall migration patterns did not change when both species were combined, and we examined both alewives and blueback herring together in all subsequent analyses.

Migrating and nonmigrating herring

Mean total lengths of both migrating (Fig. 5A; $R^2 = 0.9046$, $P = 0.0001$) and nonmigrating herring (Fig. 5A; $R^2 = 0.7065$, $P = 0.0020$) increased significantly through time. Based on paired samples, early in the season (July 17, 31), migrating alewives were smaller than nonmigrants (Table 1; $P = 0.03$–0.08). In September, migrating alewives were smaller than nonmigrants, although no size difference existed for the two groups of blueback herring. By the end of the season (October), no difference existed in size between mi-

TABLE 1. Comparison between frequency distributions of total length and age of migrating vs. nonmigrating juvenile alewives and blueblack herring in the Santuit River/Pond system during 1994.

	Total length (mm)			Age (d)†		
Sample week	Migrants‡	Nonmigrants‡	*P*	Migrants‡	Nonmigrants‡	*P*
17 July	45.0 ± 0.6 (56)	54.6 ± 3.8 (5)	0.0891	···	···	···
31 July	53.9 ± 0.6 (37)	57.7 ± 1.1 (9)	0.0322*	···	···	···
4 September						
Alewife	69.9 ± 0.5 (257)	75.5 ± 0.8 (50)	0.0007*	124.2 ± 5.4 (5)	132.4 ± 3.6 (10)	0.1813
Blueblack herring	60.4 ± 0.3 (313)	59.0 ± 2.0 (4)	0.9963	119.1 ± 3.1 (14)	119.7 ± 5.2 (3)	0.9877
25 September						
Alewife	60.7 ± 0.6 (12)	82.3 ± 0.8 (13)	0.0001*	132.0 ± 4.7 (7)	120.8 ± 5.3 (6)	0.3380
Blueback herring	67.7 ± 1.25 (48)	65.1 ± 0.7 (22)	0.3024	123.4 ± 4.5 (9)	117.7 ± 2.4 (6)	0.4756
23 October						
Alewife	81.0 ± 2.9 (7)	80.5 ± 0.5 (2)	0.6900	···	···	···
Blueback herring	69.4 ± 0.9 (7)	70.0 ± 1.3 (10)	0.5253	···	···	···

Notes: Comparisons were made using the Kolmogorov-Smirnov test. Samples from July 1994 contained all alewives.

* $P < 0.05$.

† Paired samples were not available for age analysis at the beginning and end of the season.

‡ Means ± 1 SE (*n*).

grants and nonmigrants for either species (Table 1). Age of both species of migrating herring, determined from otolith analysis, increased significantly through time (Fig. 5B; $R^2 = 0.9289$, $P = 0.0005$), but did not increase significantly for nonmigrating herring (Fig. 5B; $R^2 = 0.2974$, $P = 0.4547$). For dates when paired comparisons were possible, we found no significant difference between age of migrating and nonmigrating alewives nor blueback herring (Table 1).

Physical characteristics

Mean weekly discharge decreased gradually through time in the Santuit River during 1994 (Fig. 6A). Peaks of migration occurred when discharges were at intermediate levels (Fig. 6A) and when weekly discharge decreased (Table 2). However, all periods of migration were not related to any measurement of discharge. Water temperatures in Santuit Pond peaked at 27°C during 1994, never exceeding the upper lethal limit of 30°C for herring (Fig. 6B; McCauley and Binkowski 1982). No clear relationship was evident between water temperature and either peak or all herring migration. Water visibility in Santuit Pond sharply declined from 2.5 m to 0.5 m during the first week of July (Fig. 6C), and this decrease in visibility likely was due to a large bloom of cyanobacteria (L. A. Yako, *unpublished*

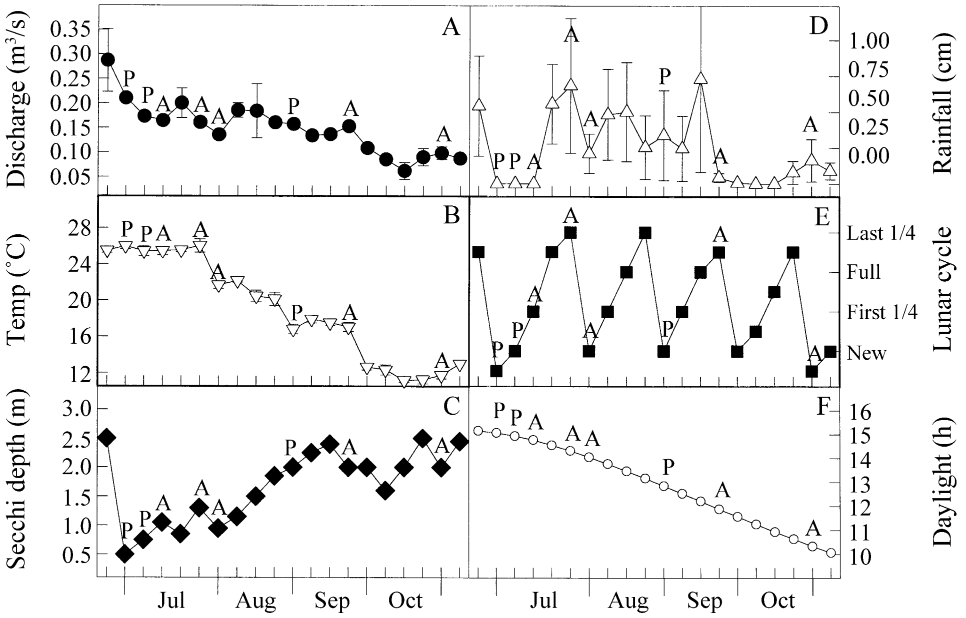

FIG. 6. Physical characteristics of the Santuit system during 1994 including (A) mean discharge, (B) mean water temperature, (C) water visibility, (D) weekly mean rainfall on Cape Cod, (E) 1994 lunar cycles, and (F) photoperiod patterns calculated for the mid-Cape Cod area. P denotes a ''peak'' period of migration; A denotes ''all'' periods of migration observed in the Santuit River during 1994. Note that peak periods of migration are included in the ''all'' periods of migration.

TABLE 2. Results of unvariate logistic regression models for factors possibly associated with the ''peaks'' of migration and ''all'' periods of migration in the Santuit River during 1994.

	P			
	''Peaks'' of migration		''All'' migration	
Factor (weekly)	Mean	Change	Mean	Change
Discharge	0.2396	0.0504†	0.4831	0.1672
Water temperature‡	0.1779	0.5223	0.1088	0.4307
Water visibility	0.0671§	0.1649	0.0248†§	0.7800
Rainfall	0.3120	0.3683	0.4104	0.0300†
Lunar cycle	0.0119†	···	0.1387	···
Photoperiod	0.0811	0.1232	0.1251	0.2902
Total zooplankton density	0.4215	0.5385	0.6503	0.1055
Calanoid density	0.7875	0.6105	0.9629	0.0737
Cyclopoid density	0.6289	0.2720	0.8389	0.3926
Bosmina density	0.0296†	0.4733	0.3709	0.7059
Total biomass	0.6972	0.5761	0.6124	0.0557†
Calanoid biomass	0.9293	0.4392	0.8948	0.1718
Cyclopoid biomass	0.3028	0.1480	0.9192	0.1478
Bosmina biomass	0.0929	0.0788	0.4365	0.1060

† Factors with $P < 0.06$ were considered significant and included in multiple logistic regression models.
‡ P value for optimum temperatures: peak, 0.2874; all, 0.7387.
§ These P values are for ''measurements'' rather than means.

data). Water visibility was significantly related to ''all'' periods of migration (Table 2) and marginally related to ''peaks'' of migration. During July–early November 1994, mean weekly rainfall never exceeded 0.8 cm (Fig. 6D), and increased rainfall did not correspond to increased discharge in the Santuit River. No clear trends relative to rainfall and peaks of migration were apparent, but all periods of migration generally occurred when rainfall was low (Table 2). Relative to lunar cycles, migration took place at all moon phases except the full moon (Fig. 6E). Specifically, peaks of migration occurred near the new moon, whereas no distinct trends were evident between lunar cycle and all periods of migration (Table 2). Photoperiod decreased predictably through time with most migration events occurring when there was >14 h of daylight (Fig. 6F), yet no clear patterns relative to photoperiod and herring migration were observed.

Food availability

Zooplankton density and wet biomass were high (>50 zooplankters/L and >600 μg/L, respectively) prior to the first migration event (Fig. 7A, B). Total zooplankton density (Fig. 7A) and total biomass (Fig. 7B) in Santuit Pond remained low (<40 zooplankters/L and <325 μg/L, respectively) during July–mid-October, but increased thereafter when nearly 99% of all herring had migrated. No clear patterns between herring migration and total zooplankton density were observed. Nor did a clear trend exist between migration peaks and total zooplankton biomass. But all periods of migration generally occurred when biomass declined to low levels (Table 2). Density of the preferred prey of herring (e.g., adult copepods, both calanoids and cyclopoids, and *Bosmina* spp.; Vigerstad and Cobb 1978), generally were low at <10 individuals/L. Specifically, densities of calanoids and cyclopoids did not increase through time (Fig. 7C), yet *Bosmina* spp. density increased above 10 individuals/L in late September (Fig. 7D). No clear relationships between herring migration and copepod density and biomass were observed. Peaks of migration occurred when *Bosmina* spp. density was low (Table 2) but no pattern was detected between *Bosmina* spp. density and all periods of migration, nor between *Bosmina* spp. biomass and any period of migration.

Migration cues

For the peaks of migration, changes in weekly discharge, lunar cycle, and *Bosmina* spp. density were significant in univariate logistic regressions (Table 2). We incorporated all combinations of these three factors into multiple logistic regression models. All the multiple logistic regression models were significant at the $P < 0.05$ level (Table 3); hence, we compared models using the log-likelihood ratio test. Overall, the single best model contained lunar cycle and *Bosmina* spp. mean density (Table 3).

For all periods of migration, results of univariate logistic regression analysis indicated weekly water visibility, change in rainfall, and change in zooplankton biomass were significant (Table 2). Hence, we incorporated all combinations of these three factors into multiple logistic regression models. Because all of the multiple logistic regression models were significant at the $P < 0.05$ level (Table 4), we again compared models using the log-likelihood ratio test. The best single model included water visibility and change in rainfall (Table 4).

Low-flow comparison

To examine the role of low discharge levels on herring populations, we sampled the Coonamessett river

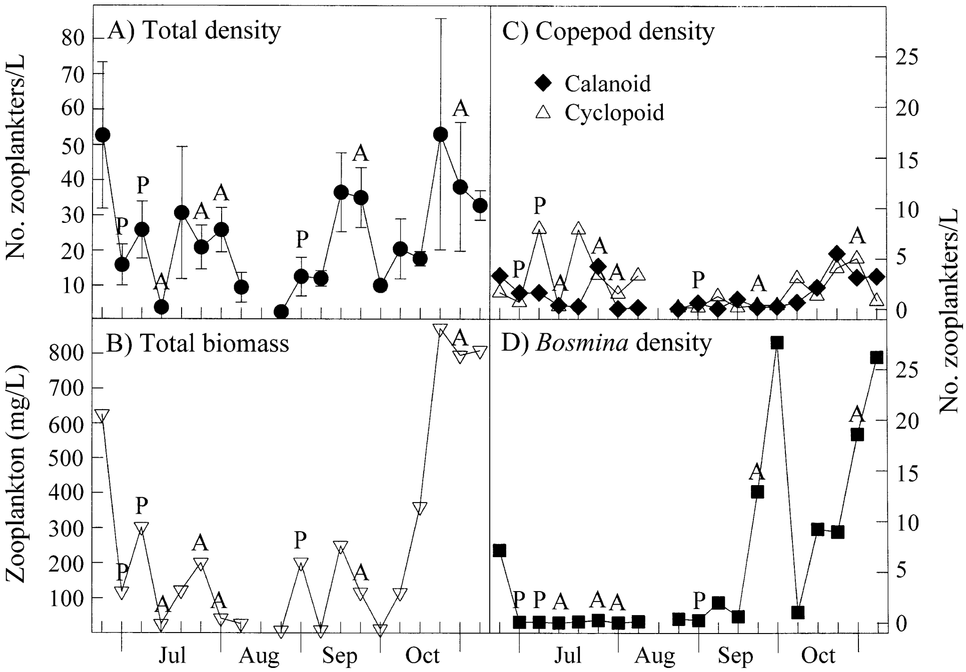

FIG. 7. Mean estimates of (A) total zooplankton density, (B) total zooplankton biomass, (C) copepod density, and (D) *Bosmina* density measured in Santuit Pond during 1994. P denotes a "peak" period of migration; A denotes "all" periods of migration observed in the Santuit River during 1994. Note that peak periods of migration are included in the "all" periods of migration for analyses.

and pond system during June–December 1994. Juvenile herring migrated during two weeks, 26 June and 20 November 1994 (Fig. 8A). Discharge levels were quite low throughout the season (Fig. 8B). Size of nonmigrating herring increased significantly through time (Fig. 8C; $R^2 = 0.6218$, $P = 0.0001$). On average, nonmigrating herring, which were confined to Coonamessett Pond due to low water levels, were 25 mm smaller than those in Santuit Pond (Figs. 4A and 8C).

DISCUSSION

Patterns of migration

Juvenile river herring migration varied through time, with migrating herring being patchily distributed both within a diel cycle and throughout the summer and fall. In the Santuit River, most migration events occurred during the mid to late afternoon, a pattern consistent with that seen in other systems (Cooper 1961, Kissil 1974, Richkus 1975, Richkus and Winn 1979, Kosa and Mather 2001). The "peaks" of movement in the Santuit River occurred within 1300–1600, with some movement also occurring after dark, which is a pattern not commonly observed by others (e.g., Richkus 1975, Kosa and Mather 2001). Diel patterns also differed across seasons, perhaps because of seasonal differences in abiotic and biotic factors within Santuit Pond. Identifying these differences in timing is critical for effective monitoring.

TABLE 3. Results of multiple logistic regression models associated with peaks of migration.

Model	P	Log-likelihood	G Value	G P†
DC × LC × BD	0.005	1.939	···	···
DC × LC	0.025	4.585	5.292	0.021
DC × BD	0.027	4.676	5.473	0.035
LC × BD	0.002	1.990	0.102	0.750

Notes: Factors included in the models are those with $P < 0.06$ in univariate logistic regression models. Statistics associated with all two-variable models are based on comparisons with the three-variable model. Model comparisons are based on the log-likelihood ratio test (G = twice the difference between model log-likelihoods) and then compared to a χ^2 distribution with df = 1. Model abbreviations are: DC, discharge change; LC, lunar cycle; BD, *Bosmina* spp. density.

† A value of $P > 0.05$ corresponding to G demonstrates that the dropped factor adds little to the model containing the other factors.

TABLE 4. Results of multiple logistic regression models associated with all periods of migration.

Model	P	Log-likelihood	G	
			Value	P†
WV × RC × TBC	0.023	8.175	⋯	⋯
WV × RC	0.009	8.176	0.001	0.980
WV × TBC	0.040	9.715	3.080	0.075
RC × TBC	0.071	10.287	4.224	0.040

Notes: See Table 3 *Notes.* Model abbreviations are: WV, water visibility; RC, rainfall change, TBC = total zooplankton biomass change.

† A value of $P > 0.05$ indicates that the dropped factor adds little to the model containing the other factors.

Migration occurred over a four-month period (Kissil 1974, Richkus 1975) and was variable through time. Anadromous juvenile herring out-migration generally had a bimodal distribution (also see Kosa and Mather 2001), with the first peak of migration occurring in early July and the second peak occurring in early September in the Santuit River. Alewives migrated throughout the entire migration season and constituted >75% of all migrating fish in the Santuit River during 1994. Blueback herring began migrating later in the season, but are known to commence spawning (Fay et al. 1983) and downstream migration (O'Leary and Kynard 1986) later than alewives. Despite small differences in seasonal migration patterns, blueback herring represented only a small proportion of the total fish captured in the Santuit River.

Understanding overall patterns of variation in migration is essential for accurate monitoring. Most herring (>96%) migrated during the peak periods of migration; therefore, these peaks are of paramount importance for management of these species. However, herring also migrated on several other, nonpeak days. Ultimately, examining the overall picture of herring migration (i.e., ''all'' migration events and both species) is essential, because it may provide insight into factors driving the overall abundance and distribution of these fish. Specifically, we do not know which group of juveniles (i.e., early or late migrators) has the highest adult return rate, and survival and recruitment may be different for fish migrating during peaks vs. nonpeak migration events. Therefore, if we are to build a predictive model to help manage land, water, development, and herring populations, we need to understand cues for herring migration during all periods to effectively monitor progress.

Migration cues

Herring migration was influenced by a wide array of physical and biological factors. However, because all herring >20 mm total length (TL) were physiologically tolerant to saltwater (Yako 1998), osmoregulatory physiology was likely not an important factor controlling migration timing. Despite the fact that mean size of migrating fish increased significantly through time (Cooper 1961, Kissil 1974, Richkus 1975), migrating fish were consistently smaller than nonmigrating fish throughout most of the migration season. Examining body size at age for both groups suggests that alewives migrating in early and midsummer were smaller for the same age than those fish that remained in the nursery area and thus had reduced growth. If juvenile fish use the nursery area to grow because it is a safer environ-

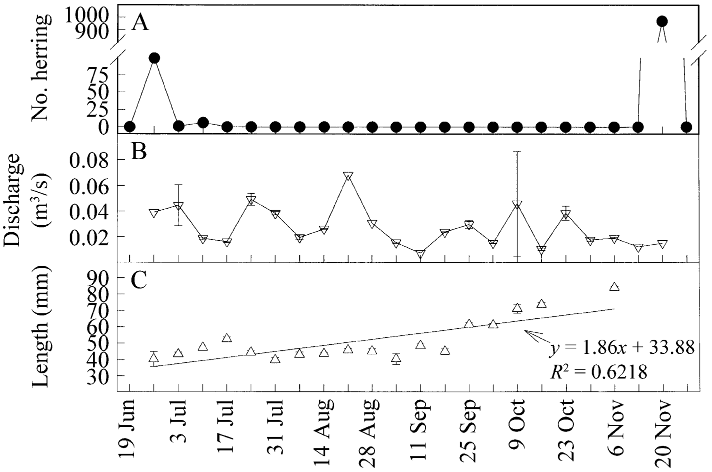

FIG. 8. (A) Seasonal pattern of migration of juvenile river herring, (B) seasonal pattern of discharge, and (C) mean total lengths of nonmigrating juvenile river herring, for the Coonamesset system in 1994.

ment than the ocean (Gross 1987), migration may be the best strategy for fish that are not growing well in the rearing habitat. During July–September 1994, Santuit Pond zooplankton density was quite low (<40 zooplankters/L) relative to densities required for recruitment of fishes with zooplanktivorous larvae (>100 zooplankters/L; Werner and Blaxter 1980, Eldridge et al. 1981, Li and Mathias 1982). Hence, it is possible that competition for limited zooplankton could have been intense. In a related study, migrating herring had a much higher incidence of empty stomachs than did nonmigrating herring (R. B. Heun, L. A. Yako, M. E. Mather, and F. Juanes, *unpublished data*), suggesting that migrating fish may not have competed for food as well as nonmigrants, thus leading to slower growth.

In this study, the peaks of herring migration correlated to lunar phases and changes in food availability. Specifically, peak migration occurred near the new moon when density of *Bosmina* spp., a preferred prey item of herring, was low. Changes in moon phase frequently control patterns of animal behavior, perhaps because the cycles of the moon provide a seasonal clock upon which animals may cue for aggregation or movement (Smith 1985). For example, at the new moon, increases in spawning activity (Reimer et al. 1974, Hay 1990) and seaward migration (O'Leary and Kynard 1986, Stokesbury and Dadswell 1989, Hvidsten et al. 1995) have been observed for various species. The bright phases of the moon, especially the full moon, may increase the vulnerability of prey to a predator due to increased visibility, thus resulting in decreased activity levels of the prey during these periods (Pearson 1960, Longland and Price 1991, Hughes et al. 1994).

Food availability, specifically *Bosmina* spp. density, was the second factor influencing peak migration. Both daily and seasonal patterns of animal behavior may be influenced by food. Changes in both diel (Ogden and Buckman 1973, Baumann and Kitchell 1974, Hall et al. 1979, Janssen and Brandt 1980, Arkett 1984, Bevelhimer and Adams 1993) and seasonal (Sergeant 1973, Erman 1981, Buckley and Kynard 1985, West et al. 1992) distributions have been observed in foraging animals. In addition, changes in distribution have been observed in response to competition (Peterson and Andre 1980, Metcalfe 1991). Though no study has documented fish migrating as a response to competition, a change in food availability has been suggested as a migration cue for juvenile anadromous herring (Vigerstad and Cobb 1978, O'Neill 1980). Food may have provided a cue for herring migration in this study. Thus, low densities of preferred zooplankton prey and the potential inability of the herring that migrated to forage effectively in their nursery pond may have driven these herring to migrate.

For all periods of migration, juvenile herring migrated during periods of low water visibility and decreased amounts of rainfall. Low water visibility may correspond to decreased foraging ability for herring. Juvenile alewives are primarily visual particulate feeders, but can use nonselective feeding modes such as filter feeding when prey densities are high (Janssen 1978, 1980). In Santuit Pond, water visibility was frequently low, likely decreasing the ability of herring to see, orient toward, and capture their prey when particulate feeding. At the same time, zooplankton levels were not high enough to elicit filter feeding. Thus, low water visibility probably adversely affected herring growth and may have triggered herring migration. In addition, Kosa and Mather (2001) found a relationship between water visibility and herring abundance across 11 small, coastal systems (including Santuit Pond), suggesting that water visibility and factors that affect foraging contribute to the success of a herring population.

Changes in rainfall provided the second cue for all periods of migration. Rainfall may signal predictable changes in discharge levels. Past researchers have found that herring migration occurred after periods of heavy rainfall (Cooper 1961, Richkus 1975, Huber 1978) resulting in high discharge levels (Kissil 1974, Richkus 1975). Other animals including salamanders (Douglas 1979) and American eel elvers (Sorenson and Bianchini 1986) respond to increased levels of rainfall by increasing their movements. Unlike these other studies, herring migration in the Santuit River occurred during periods of decreased levels of rainfall. Further investigation into the relationship between rainfall and herring migration is needed, but under some conditions herring may be responding to predictable future patterns of discharge, as evidenced by the absence of rainfall rather than the more proximate cue of high levels of discharge at a given time.

In Coonamessett River, the low-flow system, juvenile herring migration was often restricted due to low water levels in the lake. Frequently, small amounts of water flowed from the lake, but water was soon absorbed into the ground below the lake outlet. Even when discharge increased, migration did not always occur. Juvenile herring in Coonamessett Pond were smaller than those in Santuit Pond. This suggests that the inability of Coonamessett Pond herring to migrate might have adverse consequences, such as increasing intraspecific competition and making herring more vulnerable to predation by largemouth bass (*Micropterus salmoides*) in Coonamessett Pond relative to Santuit Pond (Yako et al. 2000). In addition to the effects of low water levels observed in Coonamessett Pond, low water levels have been found to decrease passage efficiency at dams (Taylor and Kynard 1985, Cooke and Eversole 1994), delay or prevent migration (Park 1969, Berggren and Filardo 1993, Achord et al. 1996, Blackwell et al. 1998), reduce useable habitat (Glova and Duncan 1985), increase mortality (Becker et al. 1983, Blackwell et al. 1998), and decrease population size (Martin et al. 1981, Deacon 1988). Though discharge did not provide an apparent direct cue for herring migration in this study, adequate water must be present for herring to migrate and to maintain a viable population (Kosa and Mather 2001).

This study demonstrates that herring migration is not controlled by any single factor, and this complexity adds to the difficulty of successfully managing these species. Herring migration is a complex natural occurrence that does not easily lend itself to manipulation. The results from this study may be widely applicable to similar systems that experience many of the same external influences as Santuit Pond. Future research on juvenile herring migration should focus on more broad-scale patterns of herring migration across systems and incorporate manipulative experiments to lend mechanistic insights towards understanding how factors work together to trigger herring migration.

Implications for management

Urban development associated with a rapidly growing human population can radically affect aquatic ecosystems and impact the fish that inhabit these altered systems. Land use planners have the challenge of incorporating biologically sound guidelines into development plans to balance human development with conservation of natural resources. The goal of a successful conservation plan should be to restore or maintain a sustainable natural ecosystem while upholding the services society requires (Wear et al. 1996, Harwell 1997, Wilzbach et al. 1998, Shin 1999). A successful conservation plan should be based on sound science, related to management goals (Risser 1993, Parrish et al. 1995), involve the cooperation of many groups at the local, state, and federal level (Rasband 1999), and incorporate real data concerning the ecosystem in question and the needs of the community, both real and perceived (Christensen et al. 1996, Harwell 1997).

For river herring, an effective conservation plan should strive to maintain current stocks and preserve or restore watershed health in order to facilitate successful restoration. In addition, water should be budgeted to ensure that adequate water is in stream channels throughout the entire freshwater residence of juvenile herring or at least during potential peak periods of migration. For river herring, understanding mechanisms that drive fish distributions and abundance can aid in the effective development and orchestration of a sound conservation plan for small, coastal systems in which water diversion is a highly debated topic. This study has increased our understanding of herring migration and has provided managers with some level of predictability of migration patterns based on the factors that we identified as important. Specifically, new moon, density of preferred prey, water visibility, and low rainfall were all predictors of migration.

Based on the data presented here, we can better monitor juvenile river herring such that we can adjust magnitude and timing of water diversion. As a result, it may be possible to recognize the indirect effects of low water levels on herring populations, manage water resources in such a way that facilitates herring migration, and help direct discharge at hydropower dams and other points of water diversion to facilitate safe passage for juvenile river herring. Although river-specific differences exist, periods of no migration will exist during which flow regulations could be flexible. Because we now have a better understanding of which factors cue migration, testing the generality of these factors in other similar systems is a logical next step to help strengthen these relationships. Ultimately, we may be able to build a model that tracks conditions for anadromous herring migration based on changes in physical and biological factors.

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