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SPECIAL SECTION: AMERICAN SHAD AND RIVER HERRING

Spatial and Temporal Variability in Instantaneous Growth, Mortality, and Recruitment of Larval River Herring in Tar–Pamlico River, North Carolina

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Abstract

We estimated the variation in the instantaneous rates of growth and mortality between cohorts of larval alewife *Alosa pseudoharengus* and blueback herring *A. aestivalis* in the Tar–Pamlico River, Pamlico Sound, North Carolina. The age of larvae captured by push net was estimated by counting the daily rings on sagittal otoliths. Weight-at-age and abundance-at-age data were used to generate instantaneous daily growth (*G*) and mortality rates (*M*) for 7-d cohorts. The instantaneous daily growth rate was relatively constant between cohorts, ranging from 0.103 to 0.277 for alewives and from 0.105 to 0.200 for blueback herring. The instantaneous daily mortality rate was more variable between cohorts, ranging from 0.064 to 0.270 for alewives and from 0.100 to 0.251 for blueback herring. All but one blueback herring cohort had an *M*/*G* value exceeding 1.0, indicating that these cohorts were losing biomass during the early larval stage. For alewives, *M*/*G* values were more variable, with 50% of the cohorts having values less than 1.0. The effect of habitat was consistent between species, with *M*/*G* values being higher and closer to 1.0 at sites in tributary creeks and backwater areas of Tar River. The overall *M*/*G* values were 0.57 for alewives and 1.60 for blueback herring from both backwater and main-channel sites, indicating that the environmental conditions in the Tar–Pamlico River are more favorable for alewives.

The variability in patterns of recruitment success for fishes that have a protracted spawning season may be due to the habitat type and quality experienced by the early life stages. This is especially the case for anadromous species whose drifting eggs and larvae encounter many different habitats and conditions, ranging from swiftly moving water to estuarine habitats. Quality is defined as the general characteristics in a given area that influence growth and mortality. In temperate zones, these early stages may also experience a wide range of hydrographic conditions that lead to large differences in recruitment between intra-annual cohorts. The factors that influence the growth and mortality of early life stages will vary among these habitat types and conditions, thus controlling recruitment success. There are three main factors that contribute to the failure or

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success of recruitment: (1) feeding success, (2) transport, and (3) predation.

Alewives *Alosa pseudoharengus* and blueback herring *A. aestivalis* are anadromous clupeids found on the East Coast of North America. The range of blueback herring extends from New Brunswick to the St. Johns River in northern Florida. Alewives are found from the coast of Labrador south to southern Georgia (Murdy et al. 1997). These two species are collectively referred to and managed as river herring. They share spawning areas where their distributions overlap (Street et al. 1975; Frankensteen 1976), and spawning can be segregated spatially and temporally (O'Connell and Angermeier 1997). Blueback herring are generally several orders of magnitude more abundant than alewives in the middle and southern portions of their range.

Rulifson (1994) noted that most alewife runs in the United States were declining and that many of the blueback herring runs are undocumented. However, overexploitation has reduced the population size of both species throughout their ranges (Gibson and Myers 2003; Schmidt et al. 2003). Widespread declines in these stocks and those of other alosine species have been attributed to overfishing, degraded water quality, and loss of habitat (Crecco and Savoy 1984; Kosa and Mather 2001). In North Carolina, river herring landings have steadily declined since 1950 (Hightower et al. 1996).

Year-class strength is established during the juvenile stages for many fishes (Sissenwine 1984; Pepin 1993). However, for some fishes, including alosines, the year-class is established prior to the prerecruitment stage (Shepherd and Cushing 1980; Crecco et al. 1983). Minor variability in daily mortality can result in tenfold or greater differences in the early stages of fish development. Spawning overlap is high both spatially and temporally for alewives and blueback herring and can have important effects on survival, growth rates, recruitment, and predator avoidance (Fortier et al. 1995; Gotceitas et al. 1996). Factors such as competition and predation by adults and juveniles play an important role in the spawning and recruitment success of these species (Schmidt et al. 1988).

We propose that there are temporal and spatial differences in the larval growth and mortality of river herring and that these differences are species specific. We compared the growth and mortality rates of alewives and blueback herring between tributary–backwater sites and the main-stem midchannel areas of the Tar River. These two habitat types are differentiated by the fact that the backwater areas (characterized as tributaries) have slower currents than the midchannel areas. Our overall objective was to determine which habitat type and which part of the spawning season contributed most to the survival and production of early life stages of alewives and blueback herring.

METHODS

Study area.—The study was conducted in the lower Tar–Pamlico River between Grimesland and Washington, North Carolina. The Tar River is the largest tributary of Pamlico River Estuary. From its headwaters in Person County, the Tar River flows southeast for 225 km and becomes Pamlico River at sea level near Washington. The Tar–Pamlico River basin encompasses 3,758 km of streams, drains 14,090 km^2, and is the fourth largest river basin in the state. The tributaries of the Tar River in its eastern reaches are influenced by backflow because of fluctuations in the flow of the Tar River (Benton 1972). Many of its streams are slow flowing and have floodplains with extensive swamps, hardwood forests, or marshes. Only about 4% of the total water area in the Pamlico Sound complex of eastern North Carolina is considered primary nursery area for estuarine, marine, and anadromous fishes, and a large portion of this area is located in the Pamlico River Estuary (Copeland et al. 1984).

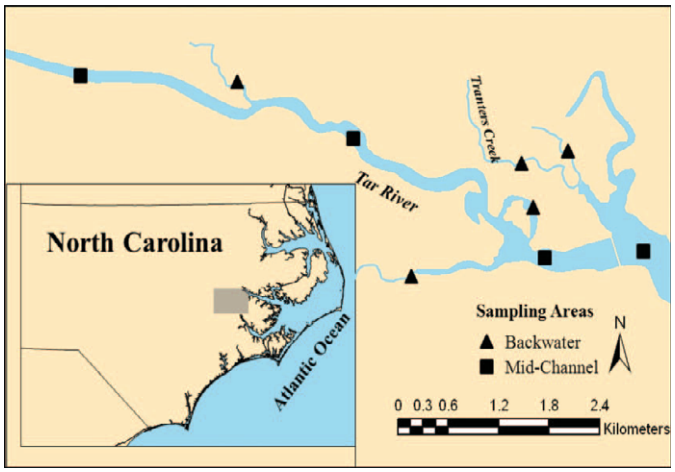


FIGURE 1. Map of ichthyoplankton stations in the Lower Tar River, North Carolina, at which sampling for alewives and blueback herring occurred in 2005. The symbols represent habitat types.

Larval sampling and analysis.—Sampling stations in the lower Tar River were classified into two habitat types: midchannel or backwater. The five backwater sampling stations were located in three primary creeks (Tranters Creek, Bear Creek, and an unnamed creek), a secondary creek (Cherry Creek) that is a tributary of Tranters Creek, and an oxbow (Figure 1). The four midchannel stations were located in the main stem of the river. Samples were collected from a 4-m johnboat with a bow-mounted aluminum frame. Ichthyoplankton were collected using paired surface push nets mounted on the bow of the boat. Each net was housed in an aluminum frame with a 0.5-m-square opening. Each push net had a 5:1 ratio and was constructed from 505-μm nitex mesh. A Sea-Gear Model MF315 flowmeter was mounted in the center of each net to estimate the amount of water filtered during each tow. The nets were pushed into the current for 2 min at a speed of 1.03 ± 0.11 m/s (Overton and Rulifson 2007). Surface (1-m below the surface) and bottom (0.5 m above the bottom) water temperature (°C), salinity (‰), and dissolved oxygen concentration (mg/L), were measured using a YSI Model 85 Multiparameter Water Quality Meter.

Larval samples were funneled through a 295-μm sieve to remove all water, and the contents were then flushed and

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preserved in 95% ethanol. Larvae from each sample were separated from debris, stained with bengal red biological stain, counted, and identified to the lowest taxon possible (Lippson and Moran 1974; Walsh et al. 2005). Standard lengths (SL; postflexion larvae) or notochord lengths (NL; preflexion larvae) were measured to the nearest 0.1 mm; all lengths will henceforth be referred to solely as SL. To determine larval abundance, the catches between the two nets were averaged. We then standardized the abundance to catch per unit effort (CPUE = number/100 m^3). A repeated-measures analysis of variance (ANOVA; Maceina et al. 1994) was used to compare mean larval lengths to determine whether there was a significant habitat effect for each species. The stations were treated as the class variables, and the sampling dates were treated as the time variable (Proc Mixed in SAS; SAS Institute 2000). We used the PROC GENMOD procedure in SAS to test for differences in CPUE (CPUE + 0.001) between habitat types. We assumed a negative binomial distribution because biological data can be influenced by overdispersion when assuming a Poisson distribution (Jones et al. 1978).

Otolith preparation and analysis.—The alewives and blueback herring were divided into 3-mm length-classes. A subsample of each available length-class was randomly selected from each sample for otolith analysis. Otoliths were removed using tweezers and a microprobe under a dissecting microscope and were affixed to a glass slide using Depex mounting medium. Otoliths were examined at 100× magnification under a compound microscope with a video attachment and analyzed with Image Pro Discovery software. Increment counts, radius widths, and increment widths were measured on the left sagitta unless it was lost, broken, or unreadable, in which case measurements were taken using the right sagitta. Increment widths were made along a linear axis from the otolith's core to its edge (Campana 1992). Otolith increments were counted on two separate occasions by a single reader. A third count was made if the first two counts differed by more than two increments. The mean increment of the two increment counts plus 2 d was the estimated age (Sismour 1994a).

Mortality rates.—Four age–length keys were constructed, one for each species and habitat type. This maintained the habitat-specific integrity of the size-at-age data, allowing mortality estimates within each habitat. Larval ages were subtracted from the date of capture to estimate hatch dates. Larvae were then divided into 7-d cohorts beginning with the earliest hatch date for each species (day of the year 77 for blueback herring and day 91 for alewives).

Daily instantaneous mortality rates were estimated by regressing the $\log_e$ transformed abundance-at-age data on age since hatching based on an exponential model of decline, that is,

$$N_t = N_0 \cdot e^{-Zt};$$

N_t = abundance of larvae at age t;
N_0 = estimated abundance at time of hatching;
Z = the instantaneous daily mortality coefficient;
t = age since hatching (d).

Cohort-specific survival (recruitment potential) can be estimated from the M/G ratio, where M is the instantaneous mortality rate and G is the weight-specific growth coefficient. This ratio is an indicator of the production potential of larval cohorts and is often termed the physiological mortality rate (Rilling and Houde 1999; Hoffman and Olney 2005). M/G ratios compare beneficial growth with loss sustained through mortality. Cohorts with M/G ratios less than 1.0 are thought to have good recruitment potential because they are gaining biomass. The M/G ratios were determined for all 7-d cohorts for which growth and mortality estimates were available and compared for each species. These estimates were then grouped by species and the M/G ratios were compared for each species across habitats. We attempted to estimate the cohort mortality for each species in each habitat type. However, too few mortality estimates proved to be significant ($P < 0.05$), so cohort-specific mortality was estimated across habitat types. The same procedures were carried out for instantaneous growth in weight and the M/G ratios.

Growth rates.—Somatic growth rates (mm/d) were calculated from the slopes of a linear regression based on the following equation:

$$L_t = a + gt;$$

L_t = the standard length (mm) at age t (d);
a = the estimated length at hatch;
g = the somatic growth rate (mm/d).

Species-specific dry weights were determined from 50 randomly selected larvae of each species. The larvae were placed in a drying oven for 24 h at 60°C, then weighed. Larval lengths were converted to dry weights from one of the following weight–length relationships:

$$W = (4 \times 10^{-6})L^{2.4323} \quad \text{(alewives)}$$

or

$$W = (2 \times 10^{-6})L^{2.5598} \quad \text{(blueback herring)},$$

where W is dry weight (mg) and L = SL (mm).

Species and habitat-specific growth rates in weight then were estimated from an exponential model fitted by regressing $\log_e$ transformed dry weights on age:

$$W_t = W_0 e^{Gt},$$

where W_t is dry weight (mg) at time t (d), W_0 is dry weight (mg) at hatch, and G is the weight-specific growth coefficient.

Coefficients in growth model regressions for each species were compared between habitats by analysis of covariance

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(ANCOVA). The ANCOVAs tested for differences in slopes (growth rates) and *y*-intercepts in the growth equations.

RESULTS

Hydrology

The mean depth in the study area was 3.03 m, and there were no significant differences between the backwater and midchannel areas. Discharge information was obtained from the U.S. Geological Survey gauging station near Greenville, North Carolina (02084000), 15 rkm upstream from the sampling area. Average discharge was 41 m^3/s. Discharge increased from April to May and then declined rapidly to less than 25 m^3/s (Figure 2). On one sampling date, we observed negative river flow in the midchannel and backwater areas. Riverwide mean daily water temperatures increased from 18.3°C in April to 27.4°C (range, 15.5–28.2°C) by the end of June. There were no significant differences between surface and bottom water temperatures at either the midchannel (*t*-test, $P = 0.105$) or backwater areas (*t*-test, $P = 0.472$; Figure 3). Mean salinity did not vary in any significant pattern and was generally no more than 0.1‰ during the study. Mean dissolved oxygen decreased from 6.32 mg/L in April to hypoxic conditions (1.57 mg/L) in June. Mean dissolved oxygen was significantly higher in the surface water of the midchannel areas (*t*-test, $P = 0.007$), but there were no differences between the bottom water concentrations (Figure 3).

Larval Catch Composition, Distribution, and Abundance

Alewife and blueback herring larvae were present in our samples from April through June. A total of 1,894 larvae were captured, of which 46% were identified to the species level. One night of sampling, we collected more than 1,000 newly hatched (<3.3-mm) larvae that could only be identified to genus.

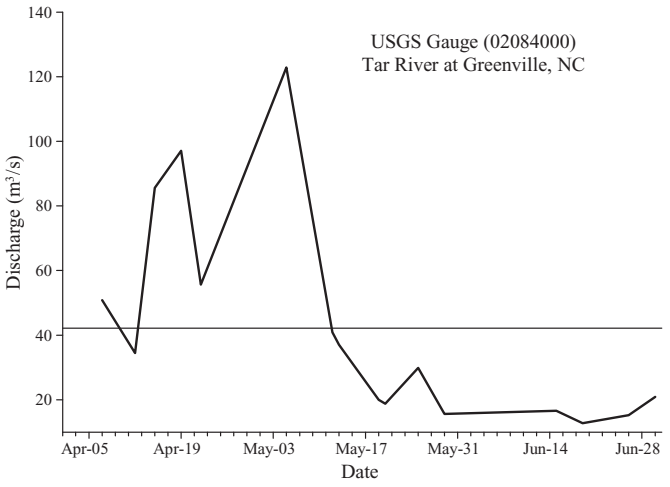


FIGURE 2. Mean daily river discharge for the Tar River in 2005. The USGS gauge from which the data were obtained is located 12 river kilometers above our sampling area. The horizontal line represents the mean (42 m^3/s) Tar River discharge for 2005.

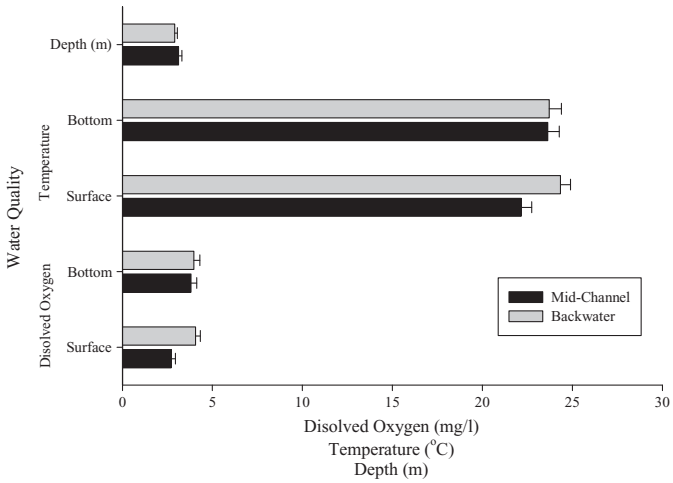


FIGURE 3. Mean depth, temperature, and dissolved oxygen at the collection sites in the backwater and midchannel areas of the lower Tar River. Error bars represent SEs.

Blueback herring collected in the midchannel and backwater sites arrived about 1 week earlier than alewives in the backwater areas. Blueback herring were captured in 37% of backwater samples but in only 24% of midchannel samples. The lengths of the blueback herring ranged from 3.2 to 32.9 mm, and despite larger larvae being captured in the midchannel areas, these differences were not significant (ANOVA; $P = 0.06$; Figure 4).

The mean CPUE for blueback herring was 7.54 (range = 0–218.5), and it was significantly higher in backwater sites (ANOVA; $P < 0.001$; Figure 5). The peak CPUE occurred one week earlier than alewife. The largest differences in CPUE between habitat types occurred during week 16. The overall CPUE was about 10 times greater at the backwater sites than at the midchannel sites.

The lengths of the larval alewives collected ranged from 3.0 to 39.2 mm SL (Table 1). The mean length was significantly (ANOVA, $P < 0.0001$) higher in the midchannel areas (14.1 mm; SD, 7.8) than in the backwater areas (8.8 mm; SD, 6.6). Alewives were captured at 41% of the backwater sites but only 27% of the midchannel sites. Alewives were present almost 1 month later in the midchannel sites (Table 1).

The mean CPUE for alewives was 9.28 (range = 0–289.3). As with blueback herring, mean CPUE was significantly higher at backwater sites (ANOVA; $P < 0.001$; Figure 5). The peak CPUE for alewives occurred during week 19 (in May) almost 3 weeks later than the arrival of blueback herring. The largest differences in CPUE between habitat types occurred during week 19. By that week, alewives was eight times more abundant in the backwater areas (Figure 5).

Growth, Mortality, and *M*/*G* Ratios by Habitat

Alewives.—Seven alewife cohorts were identified (Table 2). The hatch dates for alewives spanned the period from March 31

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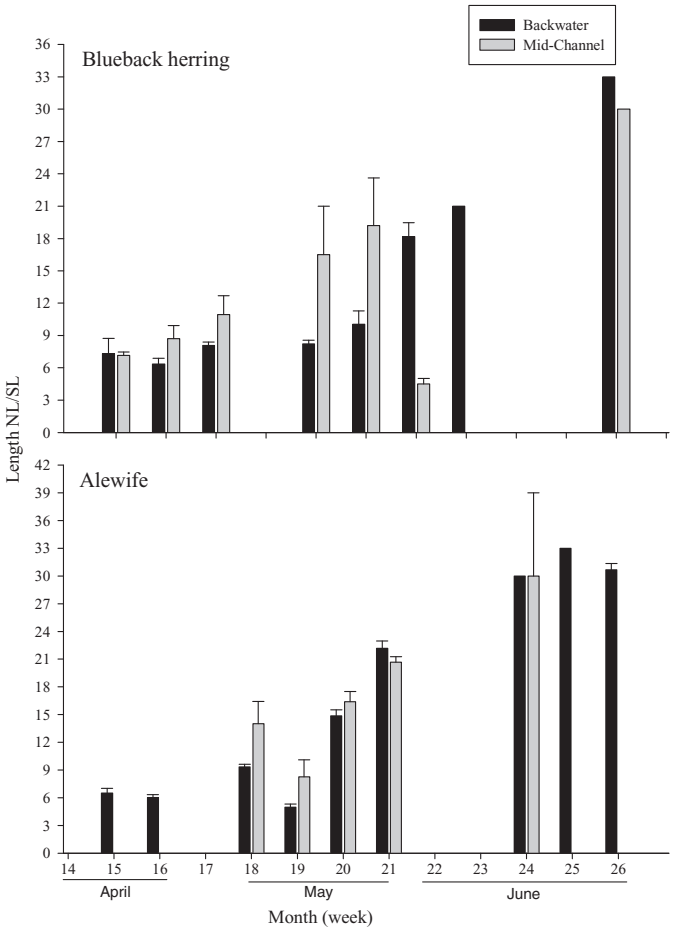


FIGURE 4. Weekly mean lengths of alewives and blueback herring collected in the midchannel and backwater areas of the Tar River in 2004. Error bars represent SEs.

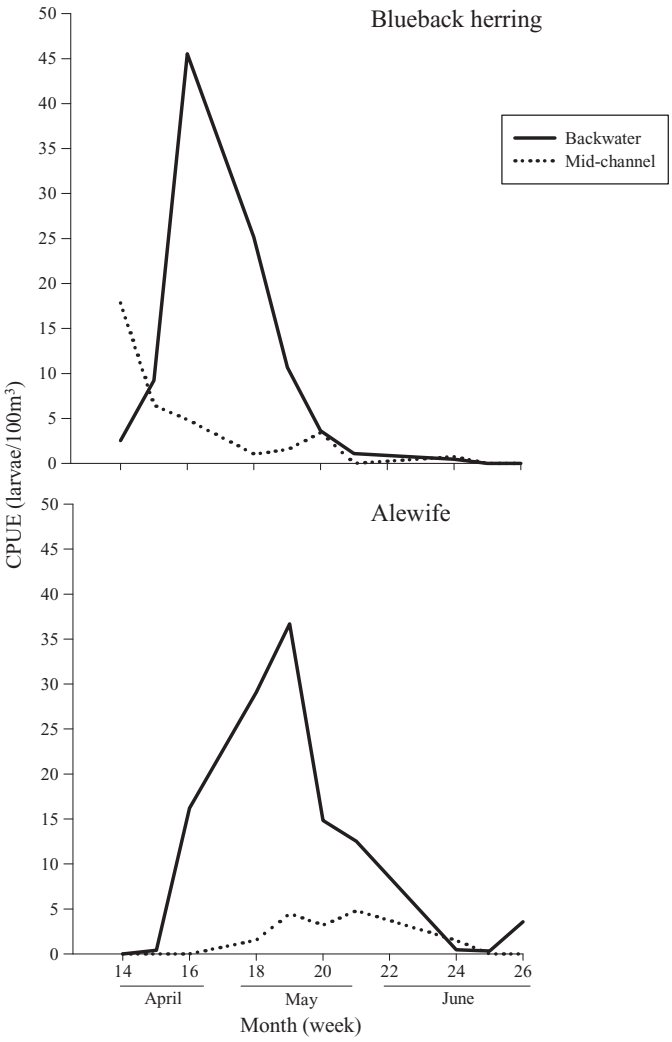


FIGURE 5. Larval blueback herring and alewife concentrations from the backwater and midchannel areas of the lower Tar River in 2004.

(day of the year 91) to May 16 (day 141). There were two peaks in hatch day frequency for alewives. The first peak occurred from day 111 to day 120 and is represented by cohorts 3 and 4. The second peak occurred from day 131 to day 133, and it primarily consisted of individuals from cohort 6 (Figure 6). Cohorts 4 and 5 were most abundant and were captured on five separate sampling dates. Mortality rates were only obtained for cohorts 3–6 (the mortality rates for the remaining cohorts were not significant; $P > 0.05$); cohort 3 had the lowest mortality rate (0.064), while cohort 6 had the highest (0.270) (Table 2). Each successive cohort had a higher mortality rate than the preceding cohort, but the nonsignificant ($P < 0.10$) mortality rate of cohort 5 was an exception to this pattern. Cohorts with larger sample sizes (cohorts 4 and 6) generally had higher mortality rates. Cohort 1 had the lowest growth rate (0.103), while cohort 6

TABLE 1. Date range of capture, proportion of tows with captures, and range and mean (SD) standard length and catch per unit effort (CPUE; larvae/100 m^3) for blueback herring and alewives in habitats sampled in the lower Tar River in 2004.

					Length						CPUE			
	Dates of capture		% Tows with capture		Blueback herring			Alewife			Blueback herring		Alewife	
Habitat	Blueback herring	Alewife	Blueback herring	Alewife	Range	Mean	*N*	Range	Mean	*N*	Range	Mean	Range	Mean
Backwater	Apr 7–Jun15	Apr 15–Jun27	37	41	3.2–32.9	8.35 (5.42)	628	3.1–33.2	8.89 (6.60)	642	0–218.5	10.12 (30.4)	0–289.3	13.5 (38.6)
Midchannel	Apr 7–Jun15	May 5–Jun 10	24	27	3.5–30.2	8.88 (6.68)	123	3.0–39.2	14.21 (7.89)	52	0–56.3	3.2 (9.1)	0–18.77	2.02 (4.13)

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TABLE 2. Summary of 7-d cohort data for alewives, including hatch date ranges (days of the year), first and last days of capture, the total number of trips in which the cohort was captured, instantaneous growth per day (G), mortality rates per day (M), M/G ratios, and associated SEs. The growth and mortality estimates are significant at $\alpha = 0.05$ unless there is an asterisk, in which case the estimate is significant at $\alpha = 0.10$; ns represents estimates for which the slope of the regression was not significant.

Alewife cohort	Hatch date range	First day captured	Last day captured	Number captured	Number of trips	G	M	M/G
1	91–97	106	113	13	2	0.103 (0.023)	ns	ns
2	98–105	106	126	45	3	0.128 (0.010)	ns	ns
3	106–112	113	133	111	3	0.177 (0.017)	0.064 (0.021)	0.36 (0.23)
4	113–119	126	141	113	5	0.134 (0.008)	0.175 (0.019)	1.30 (0.52)
5	120–126	126	147	43	5	0.231 (0.019)	0.086 (0.041)*	0.37 (0.21)
6	127–133	133	141	198	4	0.277 (0.019)	0.270 (0.062)	0.97 (0.51)
7	134–141	141	141	11	1			

experienced faster growth (0.277). Except for cohort 4, the later cohorts experienced faster growth.

The mean somatic growth rates for alewives were 0.457 and 0.460 mm/d (ANCOVA, $P < 0.001$) at backwater and mid-channel sites, respectively, and 0.464 mm/d overall (Figure 7). The weight-specific instantaneous growth rates followed a similar pattern, with growth in backwater areas being lower (0.161) than that in the midchannel (0.174). The overall

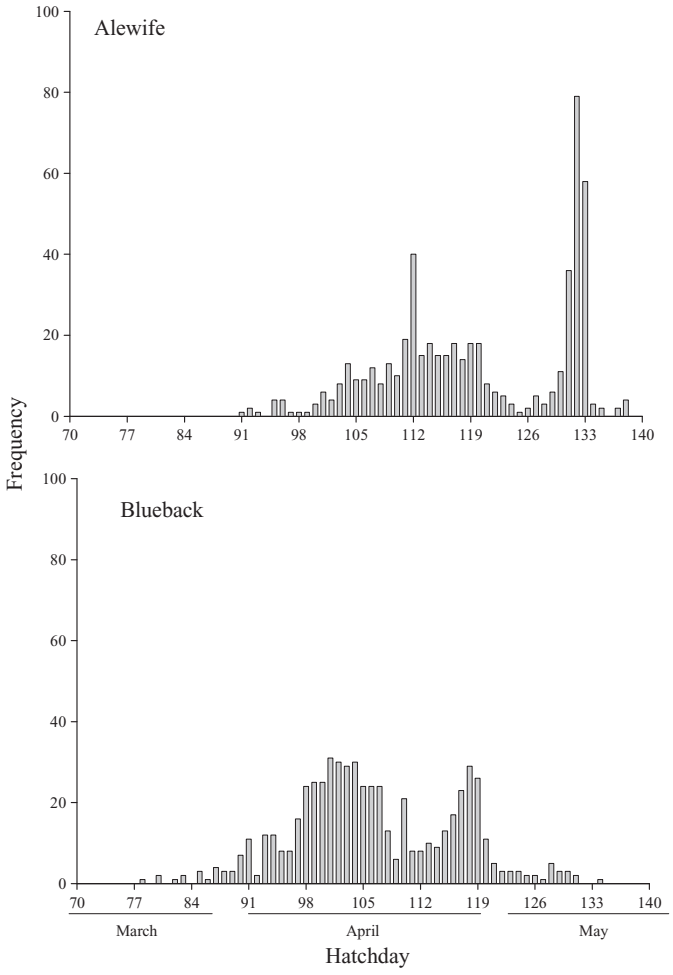


FIGURE 6. Estimated age frequency distributions for larval alewives and blueback herring in the lower Tar River from otolith increment analysis.

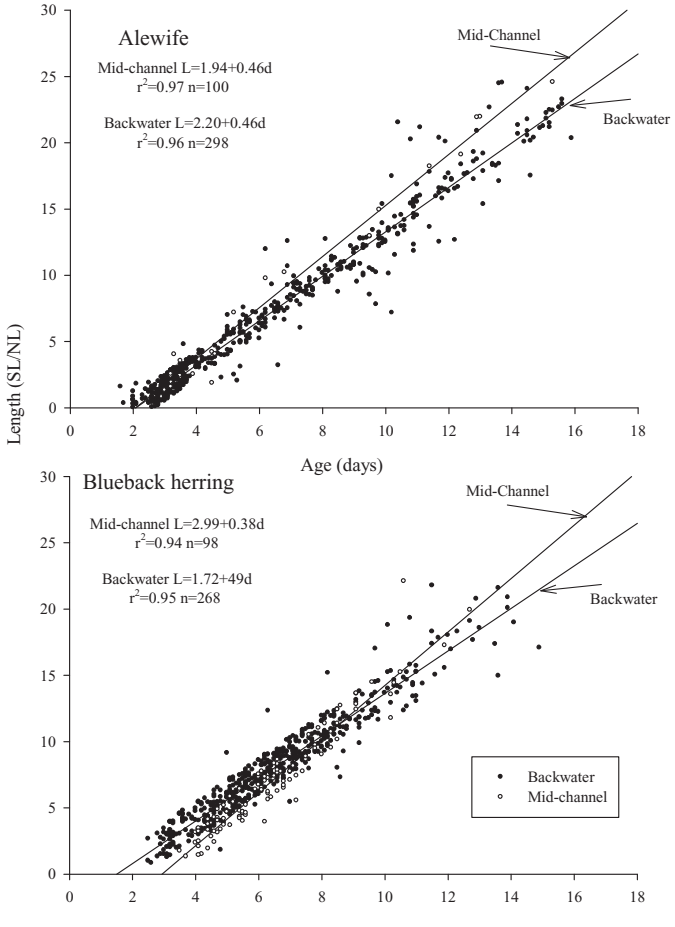


FIGURE 7. Habitat specific linear growth models for alewives and blueback herring in the lower Tar River, North Carolina in 2004. Abbreviations are as follows: L = standard length (mm), d = age in days (estimated from otolith-increment analysis).

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TABLE 3. Systemwide and habitat-specific mean (SE) somatic growth rates, weight-specific instantaneous growth per day (G) and mortality rates per day (M), and M/G ratios for alewives and blueback herring in the Tar River in 2004. An M/G ratio less than 1.0 indicates that the group is gaining weight.

	Species							
	Blueback herring				Alewives			
Habitat	Somatic	G	M	M/G	Somatic	G	M	M/G
Backwater	0.495 (0.028)	0.156 (0.013)	0.270 (0.023)	1.73 (0.71)	0.457 (0.027)	0.161 (0.011)	0.127 (0.013)	0.79 (0.36)
Midchannel	0.383 (0.053)	0.129 (0.015)	0.186 (0.024)	1.47 (0.34)	0.460 (0.101)	0.174 (0.013)	0.035 (0.017)	0.20 (0.28)
Overall	0.480 (0.024)	0.165 (0.013)	0.269 (0.022)	1.63 (0.57)	0.464 (0.027)	0.166 (0.10)	0.120 (0.012)	0.72 (0.39)

mortality estimate for alewives (0.120) was slightly lower than the backwater estimate. For alewives, the physiological rate among cohorts was variable and showed no consistent patterns (Table 3).

The M/G ratios ranged from 0.36 to 1.30 but were less than 1.0 for 75% of the identified cohorts, indicating that most of the cohorts were gaining biomass. There was no correlation between mortality and growth (Pearson correlation: $r = 0.436$, $P = 0.53$). The mortality rate for all alewives in the Backwater sites was 0.127, which was higher than the mortality rate experienced in the midchannel sites (0.035) (Table 3). Growth rates were also lower in the backwater areas (0.161) than in the midchannel areas (0.174). The M/G ratios were less than 1.0 for alewives in both habitats, indicating that this group of larvae was gaining biomass.

Blueback herring.—Nine cohorts were identified for blueback herring (Table 4). The hatch dates for blueback herring occurred from 18 March (day 78) to 17 May (day 139). There were two peaks in hatch day frequency. The first occurred from day 98 to day 107 and is represented mostly by cohorts 4 and 5 (Figure 6). The second peak occurred from day 116 to day 119 and is represented by cohort 6. Cohort 4 was the most abundant ($n = 218$) and was captured on five separate sampling trips. Weight-specific growth rates for blueback herring were obtained for all cohorts except cohort 1. Cohort 2 had the slowest growth rate (0.105), while cohort 9 had the fastest (0.391). As with alewives, the later cohorts experienced faster growth rates. Mortality rates for blueback herring were only obtained for cohorts 2–6; cohort 2 had the lowest mortality rate (0.100), while cohort 6 had the highest (0.251). We observed that each successive cohort had a higher mortality rate than the preceding cohort. Mortality rates among blueback herring cohorts were not related to sample size (Pearson correlation: $r = 0.83$, $P = 0.16$).

The M/G ratios ranged from 0.64 to 1.85 with no consistent pattern. These ratios were near or above 1 except for cohort 3 (0.65; Table 4). There was no correlation between mortality and growth (Pearson correlation: $r = 0.222$, $P = 0.71$). The mean somatic growth rates for blueback herring were 0.495 and 0.460 mm/d (ANCOVA, $P < 0.001$) at backwater and midchannel sites, respectively, and 0.464 mm/d overall (Figure 7). The instantaneous growth rate was lower in the midchannel areas (0.129) than in the backwater areas (0.156). The instantaneous mortality rates for blueback herring were 0.270 in the backwater areas and 0.186 in the midchannel areas. The M/G ratios were more than 1.4 in both areas, indicating that this group of larvae was losing biomass.

DISCUSSION

Our data show that the general spawning period for the two species is consistent with the spawning seasons reported

TABLE 4. Summary of 7-d cohort data of blueback herring. See Table 2 for additional information.

Blueback herring cohort	Hatch date range	First day captured	Last day captured	Number captured	Number of trips collected	G	M	M/G
1	77–83	98	98	6	1			
2	84–90	98	113	21	3	0.105 (0.027)	0.100 (0.029)	0.95 (0.58)
3	91–97	98	113	69	4	0.198 (0.018)	0.126 (0.053)	0.64 (0.42)
4	98–105	103	126	218	5	0.200 (0.015)	0.214 (0.038)	1.07 (0.61)
5	106–112	110	126	104	3	0.170 (0.019)	0.221 (0.048)	1.30 (0.73)
6	113–119	126	134	127	3	0.136 (0.008)	0.251 (0.021)	1.85 (0.75)
7	120–126	126	141	29	4	0.234 (0.013)	ns	ns
8	127–133	133	141	14	3	0.273 (0.033)	ns	ns
9	134–141	141	141	11	1	0.391 (0.084)	ns	ns

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in North Carolina (Walsh et al. 2005; Binion 2011). Several studies have reported little evidence for the differential timing of spawning between the two species (Street et al. 1975; O'Connell and Angermeier 1997; Walsh et al. 2005), but some studies suggest that alewives spawn before blueback herring (Jones et al. 1978; Loesch 1987). Our data do not support either spawning theme. The back-calculated hatch day frequency data showed that spawning extended from mid-March through mid-May for blueback herring and from early April through June for alewives. Additionally, our data show that blueback herring began to hatch about 14 d earlier than alewives.

The hatch day frequency data suggest that blueback herring spawn earlier than alewives in the Tar–Pamlico River. However, the difference may be explained by the differential spawning migration patterns between blueback herring and alewives and our sampling locations. The spawning location of blueback herring within a river varies greatly and blueback herring may not swim as far upstream as alewives to spawn (Jones et al. 1978). However, O'Connell and Angermeier (1997) showed that upstream areas of rivers may also be used for spawning by blueback herring. We sampled in the lower reaches of both the Tar River and the tributary backwater creeks. Blueback herring occurred first in our samples. There is some evidence that spawning by alewives and blueback herring in the Tar River is very limited upstream of our sample sites. Smith (2006) sampled ichthyoplankton from February through June 2004–2005 48 river kilometers upstream of our sampling area. In 2004, the mean density of alewife larvae in his study was 0.009/100 m^3, many orders of magnitude lower than our estimate of 9.28/100 m^3. He only collected one blueback herring larva during this same period. This is evidence that our sampling area represents the spawning area for alewives and blueback herring; the observed differences in hatch date frequencies may represent true differences in spawn timing between the two species.

Alewife and blueback herring larvae were present in both habitat types but the abundance of both species was consistently higher at the backwater sampling sites. This suggests that the spawning area of both species is located in the backwater areas. Alewives and blueback herring will spawn in a variety of habitats, including shallow and deep streams, ponds, swamps, and oxbows (Jones et al. 1978; Johnston and Cheverie 1988; Walsh et al. 2005). Backwater and tributary areas are also important spawning areas for blueback herring (Meador et al. 1984). Although we did not quantify the speed of the current, the currents in the midchannel areas were always swifter than those at the backwater sites. This difference in current velocities may mean that the currents in the midchannel areas are too swift for them to function as spawning habitat (Street et al. 1975).

Our data suggest a shift in relative growth between habitats for blueback herring. At age 9 d (10–12 mm SL/NL), the relative growth rates increased in the midchannel areas. Walsh et al. (2005) reported that blueback herring larger than 10 mm SL undergo a habitat shift away from their spawning areas. The size-specific habitat segregation of larvae has also been reported in the Santee River, South Carolina; Meador et al. (1984) reported that larger (>12 mm SL) blueback herring larvae were more abundant in the main river channel than in backwater tributaries. Our results differ from those reported for the Pamunkey River, Virginia, where Sismour (1994b) found that alewife and blueback herring larvae grew faster in creeks than in the main channel of the river. He attributed these differences to the prey field of river herring larvae. The abundance of zooplankton prey in the backwater (3,953/m^3) and midchannel (3,782/m^3) areas were very similar to that in the Tar–Pamlico River ($z = 0.0858$, $P = 0.932$; A. Overton, unpublished data). For alewives, there was no increase in growth rates in the midchannel. However, alewife larvae were significantly larger in the midchannel areas. These size distribution data suggest that habitat use changes with age. The midchannel areas may be serving as secondary nursery habitat for larger alewife and blueback herring larvae.

Survival and recruitment potential were responsive to the growth and mortality rates experienced by alewives and blueback herring. The *M*/*G* ratio is generally an indicator of survival potential during early life stages (Houde 1997). The cohort-specific *M*/*G* ratio for alewives had no consistent pattern; 25% of the cohorts had ratios exceeding 1.0, representing low cohort production potential. This pattern could not be explained, but the increasing growth rates of cohort 5 were coincident with a decreasing mortality rate. In contrast, the increasing growth rate for cohort 6 was coincident with an increasing mortality rate. For blueback herring, the *M*/*G* ratios increased throughout the sampling season, with 80% of the cohorts having ratios exceeding 1.0. This increase is a reflection of increasing mortality rates and decreasing growth rates. The *M*/*G* ratios for the three youngest cohorts (cohorts 7–9) were not estimated, but all three cohorts experienced the highest growth rates, which were most likely a function of increasing water temperature. The same seasonal pattern in growth was observed for alewives. Although there were no clear patterns in cohort-specific *M*/*G* ratios, differential cohort survival has been reported in other alosines. Younger cohorts of American shad *A. sapidissima* were responsible for establishing the year-class in the Hudson River (Limburg 1996). Limburg attributed these patterns to high river flow and low water temperatures that resulted in low survivorship of the larvae that hatched early in the season.

The midchannel areas of the Tar River were used by both alewives and blueback herring, but these areas were particularly well suited for alewife larvae based on their lower *M*/*G* ratios. The *M*/*G* ratios for blueback herring in the midchannel areas were still greater than 1.0, whereas the ratio was 0.20 for alewives. The overall *M*/*G* followed the same pattern, being higher for blueback herring (1.63) than for alewives (0.72). This represents a higher survival potential through the larval stage for alewives. The differences in *M*/*G* ratios may be the result of differences in the times at which larvae arrived at our sampling areas. The majority of blueback herring larvae arrived in April, whereas the highest density for alewives occurred during May. The lower *M*/*G* ratio for alewives in the midchannel area was

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probably influenced by the size of the larvae. The mean length of alewife larvae in the midchannel was 1.6 times greater than that of larvae collected in other areas. Alewives in the midchannel also experienced the lowest mortality rate. Size-selective mortality or the transport of larvae into the midchannel areas (Fortier and Leggett 1985) could have been responsible for the relative abundance of larger larvae and the low *M*/*G* ratios for alewives. Whereas alewives had faster overall growth in the midchannel sites, the faster growth rate for blueback herring at backwater sites did not equate to increased survival. Both species experienced higher survival in the midchannel areas, a phenomenon that is probably explained by the differences in size.

Blueback herring are generally more abundant than alewives in the southern Atlantic, primarily because North and South Carolina are the most southern part of the range for alewives (Berry 1964; Scott and Scott 1988). In the Rappahannock River, Virginia, blueback herring larvae were more abundant than alewife larvae (O'Connell and Angermeier 1997). In our study, however, although the mean CPUE for alewives was slightly higher, there were no significant differences in the abundance of the two species. Smith (2006) noted that larval alewives were more abundant than blueback herring in the Tar River and that alewives were more abundant in the Roanoke River, North Carolina (Walsh et al. 2005). The differences in the abundance of both species may be more of a function of the present abundance of adults. Both species are considered overfished, and the status of their stocks is listed as declining and unknown (Rulifson 1994).

It is difficult to determine the origin of the larvae collected in the midchannel areas of the Tar River. It is possible that some larvae were spawned along the riverbanks in the midchannel or that they were present because they had drifted from backwater areas. Regardless of the origin of the larvae, instantaneous daily mortality was consistently lower in the midchannel areas for both species. For alewives, this decline was coincident with an increasing growth rate, suggesting that rapidly growing larvae in the midchannel areas are less vulnerable to size-selective or growth-rate dependent predation. The vulnerability to predators is dependent on the time it takes to grow to a particular size (Miller et al. 1988; Claessen et al. 2002). For blueback herring, growth and mortality rates were higher in the backwater areas. The growth rates of larvae are dependent on the amount of food per larvae (Shepherd and Cushing 1980; Byström and García-Berthou 1999; Stritzel Thomson et al. 2011).

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REFERENCES

Benton, S. B. 1972. Bed forms and stream loads on several Tar River tributaries on the coastal plain of North Carolina. Journal of the Elisha Mitchell Science Society 88:199–200.

Berry, F. 1964. Review and emendation of: family Clupeidae. Copeia 1964: 720–730.

Binion, S. A. 2011. Evaluating spatial and temporal overlap between larval alosines and potential zooplankton prey in lower Roanoke River and Albemarle Sound, North Carolina. Master's thesis. East Carolina University, Greenville, North Carolina.

Byström, P., and E. García-Berthou. 1999. Density dependent growth and size specific competitive interactions in young fish. Oikos 86:217–232.

Campana, S. E. 1992. Measurement and interpretation of the microstructure of fish otoliths. Canadian Special Publications in Fisheries and Aquatic Sciences 117.

Claessen, D., C. Van Oss, A. M. de Roos, and L. Persson. 2002. The impact of size-dependent predation on popultion dynamics and individual life history. Ecology 83:1660–1675.

Copeland, B., R. G. Hodson, and S. R. Riggs. 1984. Ecology of the Pamlico River, North Carolina: an estuarine profile. North Carolina State University, Raleigh and East Carolina University, Greenville, North Carolina.

Crecco, V., T. Savoy, and L. Gunn. 1983. Daily mortality rates of larval and juvenile American shad (*Alosa sapidissima*) in the Connecticut River with changes in year-class strength. Canadian Journal of Fisheries and Aquatic Sciences 40:1719–1728.

Crecco, V. A., and T. F. Savoy. 1984. Effects of fluctuations in hydrographic conditions on year-class strength of American shad (*Alosa sapidissima*) in the Connecticut River. Canadian Journal of Fisheries and Aquatic Sciences 41:1216–1223.

Fortier, L., and W. C. Leggett. 1985. A drift study of larval fish survival. Marine Ecology Progress Series 25:245–257.

Fortier, L., D. Ponton, and M. Gilbert. 1995. The match/mismatch hypothesis and the feeding success of fish larvae in ice-covered southeastern Hudson Bay. Marine Ecology Progress Series 120:11–27.

Frankensteen, E. D. 1976. Genus *Alosa* in a channelized and an unchannelized creek of the Tar River basin, North Carolina. Master's thesis. East Carolina University, Greenville, North Carolina.

Gibson, A. J. F., and R. A. Myers. 2003. A statistical, age-structured, life-history-based stock assessment model for anadromous *Alosa*. Pages 275–284 *in* K. E. Limburg and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society, Symposium 35, Bethesda, Maryland.

Gotceitas, V., V. Puvanendran, L. L. Leader, and J. A. Brown. 1996. An experimental investigation of the 'match/mismatch' hypothesis using larval Atlantic cod. Marine Ecology Progress Series 130:29–37.

Hightower, J. E., A. M. Wicker, and K. M. Endres. 1996. Historical trends in abundance of American shad and river herring in Albemarle Sound, North Carolina. North American Journal of Fisheries Management 16:257–271.

Hoffman, J. C., and J. E. Olney. 2005. Cohort-specific growth and mortality of juvenile American shad in the Pamunkey River, Virginia. Transactions of the American Fisheries Society 134:1–18.

Houde, E. 1997. Patterns and consequences of selective processes in teleost early life histories. Pages 173–196 *in* R. C. Chambers, and E. A. Trippel, editors. Early life history and recruitment of fish populations. Chapmen and Hall, London.

Johnston, C., and J. Cheverie. 1988. Observations on the diel and seasonal drift of eggs and larvae of anadromous rainbow smelt, *Osmerus mordax*, and blueback herring, *Alosa aestivalis*, in a coastal stream on Prince Edward Island. Canadian Field-Naturalist 102:508–514.

Jones, P. W., F. D. Martin, and J. D. Hardy Jr. 1978. Development of fishes of the Mid-Atlantic Bight. U.S. Fish and Wildlife Service Biological Services Program FWS/OBS-78/12.

Kosa, J. T., and M. E. Mather. 2001. Processes contributing to variability in regional patterns of juvenile river herring abundance across small

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coastal systems. Transactions of the American Fisheries Society 130: 600–619.

Limburg, K. E. 1996. Modelling the ecological constraints on growth and movement of juvenile American shad (*Alosa sapidissima*) in the Hudson River Estuary. Estuaries 19:794–813.

Lippson, A. J., and R. L. Moran. 1974. Manual for identification of early developmental stages of fishes of the Potomac River estuary. Environmental Technology Center, Baltimore, Maryland.

Loesch, J. G. 1987. Overview of life history aspects of anadromous alewife and blueback herring in freshwater habitats. Pages 89–103 *in* M. J. Dadswell, R. J. Klauda, C. M. Moffitt, R. L. Saunders, R. A. Rulifson, and J. E. Cooper, editors. Common strategies of anadromous and catadromous fishes. American Fisheries Society, Symposium 1, Bethesda, Maryland.

Maceina, M. J., P. W. Bettoli, and D. R. DeVries. 1994. Use of a split-plot ANOVA design for repeated-measures fishery data. Fisheries 19(3):14–20.

Meador, M. R., A. G. Eversole, and J. S. Bulak. 1984. Utilization of portions of the Santee River system by spawning blueback herring. North American Journal of Fisheries Management 4:155–163.

Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences 45:1657–1670.

Murdy, E. O., R. S. Birdsong, and J. A. Musick. 1997. Fishes of Chesapeake Bay. Smithsonian Institution Press, Washington, D.C.

O'Connell, A. M., and P. L. Angermeier. 1997. Spawning location and distribution of early life stages of alewife and blueback herring in a Virginia stream. Estuaries 20:779–791.

Overton, A. S., and R. A. Rulifson. 2007. Evaluation of plankton surface pushnets and oblique tows for comparing the catch of diadromous larval fish. Fisheries Research 86:99–104.

Pepin, P. 1993. Application of empirical size-dependent models of larval fish vital rates to the study of production: accuracy and association with adult stock dynamics in a comparison among species. Canadian Journal of Fisheries and Aquatic Sciences 50:53–59.

Rilling, G., and E. Houde. 1999. Regional and temporal variability in growth and mortality of bay anchovy, *Anchoa mitchilli*, larvae in Chesapeake Bay. U.S. National Marine Fisheries Service Fishery Bulletin 97: 555–569.

Rulifson, R. 1994. Status of anadromous *Alosa* along the East Coast of North America. Pages 108–112 *in* J. E. Cooper, R. T. Eades, R. J. Klauda, and J. G. Loesch, editors. Anadromous *Alosa* symposium. American Fisheries Society, Tidewater Chapter, Virginia Beach, Virginia.

SAS Institute. 2000. SAS user's guide, version 8.01. SAS Institute, Cary, North Carolina.

Schmidt, R., R. Klauda, and J. Bartels. 1988. Distributions and movements of the early life stages of three species of *Alosa* in the Hudson River, with comments on mechanisms to reduce interspecific competition. Pages 141–168 *in* C. L. Smith, editor. Fisheries research in the Hudson River. State University of New York Press Albany, Albany.

Schmidt, R. E., B. M. Jessop, and J. E. Hightower. 2003. Status of river herring stocks in large rivers. Pages 171–182 *in* K. E. Limburg and J. R. Waldman, editors. American Fisheries Society, Symposium 35, Bethesda, Maryland.

Scott, W. B., and M. G. Scott. 1988. Atlantic fishes of Canada. University of Toronto Press, Toronto.

Shepherd, J., and D. Cushing. 1980. A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. Journal du Conseil Conseil International pour l'Exploration de al Mer 39:160–167.

Sismour, E. N., editor. 1994a. Characteristics of the early life stages of cultured alewife and blueback herring emphasizing identification of larvae. American Fisheries Society, Tidewater Chapter, Virginia Beach, Virginia.

Sismour, E. N. 1994b. Contributions to the early life histories of alewife (*Alosa pseudoharengus*) and blueback herring (A. aestivalis): rearing, identification, aging, and ecology. Doctorial dissertation. Virginia Institute of Marine Science, College of William and Mary, Glouster Point.

Sissenwine, M. 1984. Why do fish populations vary. Life Sciences Research Report 32:59–94.

Smith, M. C. 2006. Habitat use of early *Alosa* spp. and striped bass, *Morone saxatilis*, in the Lower Tar River, North Carolina. Master's thesis. East Carolina University, Greenville, North Carolina.

Street, M. W., P. P. J. Pate, B. F. Holland, and A. B. Powell. 1975. Anadromous fisheries research program: north coastal region. North Carolina Division of Marine Fisheries, Completion Report for Project AFCS-8, Morehead City.

Stritzel Thomson, J. L., D. L. Parrish, S. L. Parker-Stetter, L. G. Rudstam, and P. J. Sullivan. 2011. Growth rates of rainbow smelt in Lake Champlain: effects of density and diet. Ecology of Freshwater Fish 20:503–512.

Walsh, H. J., L. R. Settle, and D. S. Peters. 2005. Early life history of blueback herring and alewife in the lower Roanoke River, North Carolina. Transactions of the American Fisheries Society 134:910–926.

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