Estimating the Food Requirements and Prey Size Spectra of Larval American Shad

Authors: Riley, Kenneth L., and Binion, Samantha M.

Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 4(1) : 228-238

Published By: American Fisheries Society

URL: https://doi.org/10.1080/19425120.2012.675979
Estimating the Food Requirements and Prey Size Spectra of Larval American Shad

Kenneth L. Riley* and Samantha M. Binion
Department of Biology, East Carolina University, 1001 East 5th Street, Greenville, North Carolina 27858, USA

Anthony S. Overton
Department of Biology and North Carolina Center for Biodiversity, East Carolina University, 1001 East 5th Street, Greenville, North Carolina 27858, USA

Abstract

Widespread declines in American shad Alosa sapidissima along the Atlantic coast have been attributed to overfishing, a decrease in water quality, and loss of habitat. Recent surveys along the Roanoke River and Albemarle Sound, North Carolina, suggest that stocks are continuing to decline despite extensive management and stock enhancement efforts. Laboratory experiments were conducted to evaluate the effect of prey density on the growth and survival of American shad and to determine whether larvae can survive and grow in a riverine environment with a limited forage base. Larvae were reared from 11 to 20 d posthatch in one of five treatments: (1) no food; (2) low food (1 prey/L), which simulated the prey densities in the Roanoke River; (3) medium food (50 prey/L), which simulated the prey densities typical of coastal watersheds; (4) high food (500 prey/L); and (5) Artemia spp. (500/L). Larval survival was 35 ± 7% (mean ± SE) and was not significantly different among treatments. Treatments with starved fish had the lowest survival (22 ± 12%), while the highest survival was observed in treatments with high densities of wild zooplankton (46 ± 18%) and Artemia (40 ± 16%). Length-specific growth rates were 0.017 mm/d for the starved treatments and 0.024, 0.029, 0.034, and 0.039 mm/d for the low-prey, medium-prey, high-prey, and Artemia treatments, respectively. Larval growth as a function of length was not significantly different between the Artemia and high-prey treatments; however, growth in these treatments was significantly higher than in those with lower prey densities. Weight-specific growth rates ($G_w$) were significantly higher for the Artemia treatment ($G_w = 0.129$) than for all the other treatments ($G_w = 0.081$). Analysis of stomach contents indicated that American shad were selectively feeding on the smallest zooplankton (80–250 μm) and that larvae exhibited a strong preference for copepod nauplii and rotifers. These results suggest that spatial and temporal overlap between larvae and zooplankton is important for larval growth and survival.

The early life history of fishes is a critical stage that can significantly affect year-class strength and recruitment levels. Relatively small variations in mortality rates, growth rates, or stage duration can cause fluctuations in recruitment that vary by one or two orders of magnitude (Houde 1994). Because recruitment level is primarily determined during early life stages, evaluating the influence of physical and biological conditions on the survival and growth of fish larvae has become a fundamental practice in fishery science (Bergenius et al. 2002; Jenkins and King 2006; Rakocinski et al. 2006).

During the past century, a number of hypotheses have been developed to explain recruitment variability. These hypotheses

---

Subject editor: Karin Limburg, State University of New York College of Environmental Science and Forestry, Syracuse, New York

*Corresponding author: ken.riley@noaa.gov

1Present address: Department of Biology, North Carolina State University, 100 Eugene Brooks Avenue, Raleigh, North Carolina 27695, USA.

Received March 31, 2011; accepted September 12, 2011
largely attribute larval mortality to a lack of food resources that leads to starvation or results in differential growth rates affecting feeding success and predator avoidance (Houde 2008). Hjort’s “critical stage” hypothesis (1914, 1926) suggested that starvation is a serious threat to larval fish and that suitable prey must be available during the first feeding stage to prevent massive mortality and possible recruitment failure. Cushing’s match/mismatch hypothesis (1972, 1990) expanded on Hjort’s original work and proposed that starvation is a threat for the entire larval period, from the onset of exogenous feeding through metamorphosis. Cushing also proposed that larval survival, growth, and variability in year-class strength could be explained by the spatiotemporal overlap between peaks in prey productivity (i.e., using phytoplankton as a proxy for zooplankton) and larval fish abundance. Considerable evidence to support these hypotheses has resulted from field observations of a variety of species from different ecosystems (Fortier et al. 1995; DeVries et al. 1998; Beaugrand et al. 2003; Durant et al. 2007); however, some of the most compelling research supporting these hypotheses has resulted from controlled experiments using hatchery-reared fish in a laboratory setting (Bremigan and Stein 1994; Gotceitas et al. 1996; Chick and Van Den Avyle 1999).

Food availability is a product of the prey size spectrum, prey mobility, the patchiness of prey distribution, and prey density (Kamler 1992; Horn and Ferry-Graham 2006). Spending energy searching for and capturing prey can have severe consequences if a larva is not successful at feeding. At first feeding, most larvae have limited ability to detect, capture, and consume prey, and feeding success is often low (<10%; Rosenthal and Hempel 1970). Feeding success increases exponentially with growth, age, and experience (Hunter 1972; Gerkling 1994). With an abundance of food, larval feeding rates increase asymptotically until maximum consumption or satiation is achieved (Eldridge et al. 1981).

While an adequate quantity of prey is important to avoid starvation, optimal foraging theory suggests that for any size fish there exists a restricted range of optimal prey sizes (Miller et al. 1988). Prey size dominates prey selection patterns, and the size of the mouth limits what size prey can be ingested. Prey body width (BW) is the critical dimension limiting consumption (Hunter 1981; Krebs and Turingan 2003). Studies supporting this finding propose that the optimal prey width ranges from 30% to 50% of mouth gape (Shirota 1970; Cunha and Planas 1999; Riley et al. 2009). Thus, as larvae grow their preference for larger prey sizes increases proportionately (Puvanendran et al. 2004). Fish larvae are opportunistic, and those capable of feeding on large prey items can attain satiation with lower densities of prey (Munk 1992).

The aim of the present study was to conduct laboratory trials to evaluate the effect of food availability on the growth, survival, and feeding success of larval American shad Alosa sapidissima. This species has gained considerable attention because recent surveys suggest that stocks are continuing to decline despite management efforts, stock enhancement, and measures to restore habitat for adults (Greene et al. 2009). The results of this study are used to infer whether shad larvae can obtain enough food at experimental prey densities to survive and grow in a riverine environment with a limited forage base of zooplankton.

**METHODS**

**Sources of larvae.**—American shad larvae were obtained from the U.S. Fish and Wildlife Service’s Edenton National Fish Hatchery. The fish used in the experiments were cohorts of the same age that had undergone the same treatments as American shad larvae stocked into the Roanoke River, North Carolina. Wild-caught broodstock that were of Roanoke River origin were spawned on 4 May 2008. The larvae obtained for use in the experiments were of the same age but mixed progeny.

Within the hatchery, larvae were reared using standard production methods with brine shrimp Artemia spp. as the primary live feed (Howey 1985). Fish were marked by immersion in a bath of oxytetracycline hydrochloride (Hendricks et al. 1991). Incubation and rearing temperatures at the Edenton hatchery ranged from 17.0°C to 22.0°C, salinity was 2.0 practical salinity units (psu), and pH levels were greater than 7.5.

**General experimental conditions.**—Fish were obtained 9 d after hatching (DAH) and approximately 5 d after transitioning to live feeds. They were transported to East Carolina University’s Aquatic Animal Research Laboratory in an insulated cooler with supplemental oxygen. Upon arrival at the laboratory, the fish were allowed to equilibrate to the temperature and salinity prior to transfer into two large (80-L) holding tanks. The fish were held for 24 h and fed Artemia spp. nauplii before being stocked into the experimental systems. The experiments were conducted in a temperature-controlled laboratory under cyclic photoperiod conditions (14 h light : 10 h dark).

The larvae were reared in freshwater to simulate the water quality characteristics of the Roanoke River. To produce freshwater for the experiments and holding tanks, sterilized water was conditioned within an aerated reservoir. Salinity was adjusted to 1.0 psu with artificial sea salt (Instant Ocean, Cincinnati, Ohio). Total hardness was adjusted to 140 mg/L with calcium carbonate, and total alkalinity was adjusted to 220 mg/L with sodium bicarbonate.

The experiments were conducted using 21-L cylindrical plastic tanks (N = 35) that were transparent and colorless. The tanks were wrapped in black plastic to simulate downwelling light (a more natural condition) and to provide sufficient contrast between prey and background for feeding. The tanks were gently aerated, and surface lighting was maintained under a photon fluence rate of 3.63–4.84 μmol photons·s⁻¹·m⁻² provided by overhead fluorescent light fixtures. Each tank was stocked with a total of 84 larvae at 10 DAH. The goal of stocking was to select a low enough density (4 larvae/L) to accurately project growth and survival while not masking the effects of treatment.
variables (Chesney 1989). Larvae that died within the first 24 h were replaced.

The larvae were reared from 11 to 20 DAH in five treatments: (1) no food; (2) low food (1 prey/L), which simulated the prey densities in the Roanoke River; (3) medium food (50 prey/L), which simulated the prey densities typical of coastal watersheds; (4) high food (500 prey/L); and (5) Artemia (500 prey/L), which served as an experimental control. The latter treatments also simulated the prey densities typically used in hatchery operations. Treatments were randomly assigned to tanks, and each treatment was replicated seven times. To obtain estimates of larval growth and survival, we harvested one tank from each treatment at 12 DAH and three tanks from each treatment at 16 and 20 DAH. Fish were harvested from the tanks by siphoning the water and concentrating the fish on a 53-μm-mesh Nitex sieve.

With exception of the treatments in which the fish were fed no food and 24-h-old Artemia nauplii, the food consisted of size-sorted wild zooplankton (53–800 μm) collected from a series of oxbow lakes adjoining the Tar River in Greenville, North Carolina (35°37′33″N, 77°21′42″W). Zooplankton were collected at irregular intervals ranging from 24 to 48 h to provide the quantities of prey needed for experiments. We frequently collected zooplankton throughout the experiment to ensure zooplankton were alive at the time of feeding, actively swimming in the water column, and did not lose nutritional quality. After collection, all samples were filtered through an 800-μm-mesh Nitex sieve to prevent the introduction of ichthyoplankton, insects, and other predatory species. Reference samples of plankton were preserved in a 5% solution of formalin for species identification and evaluation of their size frequency distribution. The body length and width of the zooplankton were measured on up to 25 individuals per taxon.

Fish were observed at least twice daily at 0900 and 1500 hours, and mortalities were counted, removed, and preserved. General observations of fish behavior were recorded. Prey densities were monitored within each tank by sampling background densities using a 3-mL Hensen-Stempel pipette, plankton counting wheel, and dissecting microscope to enumerate prey. Food was added as needed to individual tanks to maintain a consistent prey density for each treatment. Tank aeration kept live feeds evenly distributed.

Tanks were siphoned as needed to remove wastes. Water quality was maintained with 50% daily water changes. Water quality was monitored daily by measuring temperature, dissolved oxygen, salinity, pH, and total ammonia nitrogen. There was no significant difference in any of the water quality parameters among tanks or treatments. Water temperature was 24.0 ± 0.2°C, salinity was 1.1 ± 0.1 psu, dissolved oxygen was 5.8 ± 0.8 mg/L, pH was 8.0 ± 0.2, and ammonia was less than 0.2 mg/L.

Larval survival and growth.—Larvae harvested from tanks were euthanized via immersion in a clove oil solution and photographed using a dissecting microscope at 40× magnification. All larvae were photographed on their left sides in the sagittal plane. The microscope was equipped with a high-resolution video camera, and still images were recorded as uncompressed files in Tagged Image File Format (TIFF) at 6 megapixels.

Larvae and selected anatomical features were measured and analyzed using SigmaScan Pro 5.0 image analysis software (SPSS Science, Chicago, Illinois). All morphometric measurements were recorded to the nearest 0.001 mm, and calibration errors were maintained less than 1 μm (<0.1% of 1 mm). The total length (TL) and notochord length (NL) of larvae was measured along lines parallel to the longitudinal axis of the fish (Snyder 1983). The length of the upper jaw was measured from the premaxillae and maxillae to the point of articulation with the dorsal process of the dentary. The length of the lower jaw was measured from the dentary to the point of articulation with the angular and maxillae.

The mouth gape was determined using length measurements of the upper and lower jaws and the law of cosines equation for a triangle with two known sides and an angle between them, that is,

\[ a^2 = b^2 + c^2 - 2bc \cos \alpha, \]  

where \( a \) is the mouth gape, \( b \) is the upper jaw length, \( c \) is the lower jaw length, and \( \alpha \) is a measure of the angle that forms the degree of mouth opening. The calculations were based on the assumption that during active feeding the mouth of a larva opens to an angle ranging from 90° to 120° in order to capture prey (Shirota 1970; Krebs and Turingan 2003). Optimal prey sizes were estimated at 30% and 50% of the mouth gape for larvae (Yasuda 1960; Shirota 1970; Hunter 1981; Cunha and Planas 1999). Linear regression analysis was used to model optimal prey size based on the TL and NL measurements. Using the regression model, optimal prey dimensions were estimated at 50% of mouth gape.

Linear regression was used to examine larval growth and mortality rates. Mortalities were tallied by the daily removal of dead larvae from each experimental tank and comparison of that number with the number of larvae surviving to the time of harvest. The relationships between TL and age, NL and age, and mouth gape and age were plotted separately. Data for the TL, NL, and mouth gape of larvae were fitted to a simple linear equation. Comparison of these plots allowed assessment of somatic growth patterns through time. Length-specific growth rates were calculated using the equation

\[ G = \frac{\log_e X_2 - \log_e X_1}{t_2 - t_1}, \]  

where \( G \) is the growth rate, \( t_1 \) is larval age at the start of the experiment, \( t_2 \) is larval age at the end of the experiment, \( X_1 \) is measured length at the start of the experiment, and \( X_2 \) is measured length at the end of the experiment.

Weight-specific growth was measured as dry weight. Samples of 10 larvae from each tank were individually weighed.
Fish were rinsed with distilled water, placed in aluminum pans, and dried at 60°C to a constant weight (24 h). Weight-specific growth rates were calculated using equation (2) with dry-weight measurements replacing length measurements.

Relative preference for prey species, size, and gut fullness.— At the conclusion of the experiments, 10 larvae were randomly selected from each tank with food to evaluate stomach contents and gut fullness. The larvae were dissected on glass slides using forceps and a fine-point needle. A dissecting microscope at 40× magnification was used to identify ingested prey removed from the foreguts of the larvae. Because histological techniques were not practical and digested prey could not be easily identified in the midgut and hindgut, gut fullness was used as a proportional measure of the gut with food present.

The Manly-Chesson index (Chesson 1978, 1983) was used to measure prey selectivity in the experiments with wild zooplankton. This index is one of the most widely accepted mathematical indexes for prey selectivity (Manly et al. 2002; Chipps and Garvey 2007) because it is possible to test the apparent selectivity against a random model (Manly 1974). Selectivity was defined as the difference between the proportion of a prey type in the diet and its proportion in the culture tank. We used a derivation of the Manly-Chesson index (Chesson 1983) for controlled laboratory experiments with constant prey abundance, namely,

$$\alpha_i = \frac{r_i}{\sum\frac{1}{n_i}} \, \frac{1}{\sum\frac{1}{n_j}} \quad i = 1, \ldots, m$$

where $\alpha_i$ is Manly’s alpha for prey type $i$; $r_i$ and $r_j$ are the proportion of prey type $i$ or $j$ in the diet; $n_i$ and $n_j$ are the proportion of prey type $i$ or $j$ in the environment, and $m$ is the number of prey types. The index $\alpha_i$ ranges from 0 to 1, and selectivity is indicated when $\alpha_i$ values are greater than $1/m$.

Statistical analysis.—Analysis of variance (ANOVA) was used to statistically compare survival, growth, gut fullness, and indices of larval condition among rearing treatments. Water quality variables, including temperature, dissolved oxygen, salinity, pH, and total ammonia nitrogen, were assessed using ANOVA. The general linear model function in SAS (SAS 9.2; SAS Institute, Cary, North Carolina) was used for all analyses. Data were evaluated for normality using the Levene nonparametric test, and the plot of the residuals was analyzed to ensure that assumptions of ANOVAs were satisfied. When necessary, data were logarithmically transformed before statistical analysis to normalize the observations and stabilize the variance. Similarly, percentage or proportion data for larval survival and gut fullness were arcsine-square-root transformed prior to statistical analysis. Tukey’s honestly significant difference post hoc multiple-range tests were used to determine whether there were significant differences among treatment means. Differences were considered significant at $P \leq 0.05$. The results are expressed as the means ± SEs of the data except where indicated differently.

RESULTS

Larval Survival and Growth

Survival within the first 24 h was high (92 ± 5%) and was similar within all tanks. The overall survival of American shad larvae reared through 20 DAH was 35 ± 7% and was not significantly different among treatments. The highest survival occurred among fish fed high densities of zooplankton (46 ± 18%), followed by those fed Artemia (40 ± 16%) and medium densities of zooplankton (37 ± 22%). The lowest survival was observed in fish fed low densities of zooplankton (31 ± 18%) and those that were starved (22 ± 12%).

With high densities of live food such as Artemia or zooplankton, American shad larvae grew 0.45 ± 0.03 mm/d. Length-specific growth rates based on total length measurements were 0.039 ± 0.003 for the Artemia treatments, 0.034 ± 0.003 for the high-prey treatments, 0.029 ± 0.005 for the medium-prey treatments, 0.024 ± 0.002 for the low-prey treatments, and 0.017 ± 0.001 for the treatments with no food. Length-specific growth rates were calculated using equation (2) with dry-weight measurements replacing length measurements.



### Table 1

| Treatment  | $N$ | Size range (mm) | Equation | Coefficient of determination ($r^2$) | Standard error of intercept |
|------------|-----|----------------|----------|--------------------------------------|----------------------------|
| Artemia    | 133 | 9.7–20.0       | $G_{TL} = 0.5 \text{ Age} + 10.9$ | 0.57                                 | 0.20                       |
|            |     | 8.1–13.9       | $G_{NL} = 0.4 \text{ Age} + 9.4$  | 0.72                                 | 0.13                       |
| High prey  | 136 | 9.7–17.2       | $G_{TL} = 0.4 \text{ Age} + 10.9$ | 0.62                                 | 0.15                       |
|            |     | 8.1–12.8       | $G_{NL} = 0.4 \text{ Age} + 9.2$  | 0.78                                 | 0.10                       |
| Medium prey| 110 | 9.7–16.6       | $G_{TL} = 0.3 \text{ Age} + 10.7$ | 0.38                                 | 0.18                       |
|            |     | 8.1–12.7       | $G_{NL} = 0.4 \text{ Age} + 9.2$  | 0.63                                 | 0.15                       |
| Low prey   | 121 | 9.7–16.6       | $G_{TL} = 0.3 \text{ Age} + 10.7$ | 0.29                                 | 0.20                       |
|            |     | 8.1–12.7       | $G_{NL} = 0.3 \text{ Age} + 9.3$  | 0.42                                 | 0.16                       |
| No food    | 125 | 9.7–16.6       | $G_{TL} = 0.2 \text{ Age} + 10.9$ | 0.17                                 | 0.22                       |
|            |     | 8.1–12.0       | $G_{NL} = 0.2 \text{ Age} + 9.3$  | 0.44                                 | 0.14                       |
growth rates based on notochord length measurements were 0.036 ± 0.002 for the Artemia treatments, 0.034 ± 0.001 for the high-prey treatments, 0.034 ± 0.001 for the medium-prey treatments, 0.025 ± 0.001 for the low-prey treatments, and 0.022 ± 0.001 for the treatments with no food. Separate growth equations were developed for each treatment because of significant differences in growth (Table 1). Larval growth as a function of length was not significantly different between the Artemia and high-prey treatments (Figure 1); however, growth in these treatments was significantly higher than in the treatments with lower prey densities at 16 and 20 DAH (ANOVA; df = 4, 45; P < 0.0001). In contrast, at 20 DAH dry weights were not significantly different among the Artemia, high-prey, and medium-prey treatments (Figure 1); however, weights in these treatments were significantly higher than those in the low-prey and starvation treatments (ANOVA; df = 4, 41; P < 0.0001).

There were no significant differences in larval mouth gape size among rearing trials at 12 or 16 DAH (ANOVA; df = 4, 45; P = 0.28). The mouth gape of larvae was 0.821 ± 0.076 mm at 12 DAH and 0.963 ± 0.063 mm at 16 DAH (Table 3). The mouth gapes of larvae at 20 DAH were not significantly different among the Artemia, high-prey, and medium-prey treatments; however, the mouth gapes in these treatments were significantly higher than those in the low-prey and starvation treatments (ANOVA; df = 4, 45; P = 0.0003). Predicted values for optimal prey sizes increased linearly with age and length (Figure 2).

Prey Composition and Size Spectra

The zooplankton samples collected during this study were uniform in composition and primarily consisted of cladocerans, copepods, and rotifers (Figure 3). Cladocerans and adult copepods were among the largest prey types, while copepod nauplii and rotifers were the smallest. With the exception of chironomid larvae, insects were absent from samples as a result of significant differences in growth (Table 2). At 16 DAH, larval growth as a function of dry weight was significantly different between the Artemia treatments and all other treatments (ANOVA; df = 4, 95; P < 0.0001). In contrast, at 20 DAH dry weights were not significantly different among the Artemia, high-prey, and medium-prey treatments (Figure 1); however, weights in these treatments were significantly higher than those in the low-prey and starvation treatments (ANOVA; df = 4, 41; P < 0.0001).

The variability in length was less pronounced with notochord measurements (coefficient of variation [CV; SE/mean × 100] = 6%) than with total length measurements (CV = 12%). Because freshly killed larvae were used for measurements, this variability was not the result of sample storage or shrinkage; rather, it was most likely an indicator of larval condition and stage of development. The presence of intact fins and fin rays indicated that the variability was not a result of abrasions from tank surfaces, encounters with other fish (e.g., fin nipping), or harvest methods.

American shad larvae gained 26.6 ± 6.8 μg/d when high densities of Artemia or zooplankton were maintained in tanks. Fish in the treatments with low prey densities and no food lost 9.0 ± 5.4 μg/d. Weight-specific growth rates were 0.128 ± 0.011 for the Artemia treatments, 0.082 ± 0.018 for the high-prey treatments, 0.025 ± 0.006 for the medium-prey treatments, −0.016 ± 0.004 for the low-prey treatments, and −0.020 ± 0.027 for the treatments with no food. Separate growth equations were developed for each treatment because significant differences in growth were observed (Table 2). At 16 DAH, larval

### Table 2

Linear relationships between growth in terms of dry weight ($G_w$) and age for American shad larvae reared at 24°C under various dietary conditions.

| Treatment       | N   | Size range (μg) | Equation                | Coefficient of determination ($r^2$) | Standard error of intercept |
|-----------------|-----|----------------|-------------------------|--------------------------------------|----------------------------|
| Artemia         | 43  | 110–890        | $G_w = 34.6 \text{ Age} + 168.2$ | 0.32                                 | 40.6                       |
| High prey       | 41  | 229–592        | $G_w = 18.8 \text{ Age} + 103.9$ | 0.26                                 | 25.6                       |
| Medium prey     | 37  | 157–277        | $G_w = 3.8 \text{ Age} + 145.8$ | 0.51                                 | 26.0                       |
| Low prey        | 34  | 129–143        | $G_w = -4.0 \text{ Age} + 147.3$ | 0.20                                 | 23.7                       |
| No food         | 41  | 5–88           | $G_w = -15.7 \text{ Age} + 165.7$ | 0.37                                 | 16.3                       |

### Table 3

Mouth gape size of American shad larvae. The length measurements are means ± SEs for larvae sampled from the Artemia and high-density treatments. The mouth gape estimates are based on calculations assuming that fish mouths open 90° (minimum) to 120° (maximum) during feeding and prey capture.

| Days after hatching | Lower jaw length (mm) | Upper jaw length (mm) | Minimum mouth gape (mm) | Maximum mouth gape (mm) |
|---------------------|-----------------------|-----------------------|-------------------------|-------------------------|
| 12                  | 0.50 ± 0.06           | 0.69 ± 0.05           | 0.763                   | 1.170                   |
| 16                  | 0.51 ± 0.06           | 0.76 ± 0.06           | 0.826                   | 1.174                   |
| 20                  | 0.54 ± 0.05           | 0.86 ± 0.05           | 0.902                   | 1.211                   |
of the sieving process. Minimal overlap in size was observed among the different prey types (Table 4). The variation of prey densities within each treatment was not pronounced, with coefficients of variation ranging from 49% to 68% among treatment replicates.

Larval Behavior
Larvae were observed actively searching for prey in all treatments at the initiation of the experiments. Their search and feeding behavior was typical of larval American shad and other
clupeids, with larvae assuming the S-flex position in anticipation of capturing prey (Blaxter and Hunter 1982; Ross and Backman 1992; Ross et al. 1996). Larvae that were not feeding or that had recently fed oriented themselves in a horizontal position in the upper portion of the water column. Although not measured, search times were shorter and feeding success was more frequently observed in treatments with high levels of prey. During the first 4 d of the experiment, larvae in treatments with no food, low prey densities, and medium prey densities spent a significant amount of time actively swimming. During this period, the larvae were photopositive, oriented their heads upward, and rarely settled on the bottom. Swimming was characterized as a quick dart-and-glide motion followed by long periods of rest (∼10 s). During the last 4 d of the experiment, larvae in treatments with no food or low prey densities rarely swam and settled on or near the bottom of the tank with their heads oriented upward. Larval behavior in tanks with *Artemia* and high densities of prey did not vary during the course of the experiments.

**TABLE 4.** Sizes (means ± SDs) of zooplankton used in feeding experiments with American shad larvae.

| Prey type        | Body length (μm) | Body width (μm) |
|------------------|-----------------|-----------------|
| Daphniidae       | 1,406 ± 198     | 655 ± 179       |
| Bosminidae       | 287 ± 49        | 142 ± 10        |
| Cyclopoida, adult| 1,031 ± 96      | 530 ± 20        |
| Cyclopoida, copepodite | 593 ± 44       | 236 ± 48        |
| Copepod nauplii  | 160 ± 23        | 87 ± 18         |
| Rotifera         | 273 ± 43        | 145 ± 32        |
| *Artemia* spp.   | 506 ± 38        | 232 ± 33        |

**DISCUSSION**

The abundance and distribution of food is critically important for the growth of fish larvae, and the results from this study suggest that aquatic ecosystems with sparse or patchy zooplankton distributions could result in food limitation, starvation, and reduced growth for early larval stages of American shad. Laboratory experiments were conducted to simulate the feeding conditions typical of coastal rivers in North Carolina and more specifically those observed in the Roanoke River and its estuary, Albemarle Sound. This coastal system has been extensively studied over the past 60 years to characterize the ecology of the region and document fluctuations in the populations of anadromous fish species (Hassler et al. 1981; Rulifson et al. 1993).

While it is well known that rivers are not highly productive systems for zooplankton (Hynes 1970; Chick and Van Den Avyle 1999), the abundance and distribution of zooplankton...
in Roanoke River are the lowest among coastal rivers in the southeastern United States. A long-term study (1984–1991) conducted by Rulifson et al. (1993) and a study by Coggins (2005) documented that zooplankton abundances in the Roanoke River are historically low and often 1–2 orders of magnitude lower than those in adjacent watersheds (Table 6). In these studies, zooplankton abundances never exceeded 1,000 individuals/m³ during the critical period (March–June) for larval production. American shad, hickory shad *A. mediocris*, alewife *A. pseudoharengus*, and blueback herring *A. aestivalis* spawn in the Roanoke River and their larvae use this system as nursery habitat (Greene et al. 2009; Harris and Hightower 2010). Low zooplankton abundance in this system is alarming because it increases the probability of a temporal disconnect between zooplankton and larval alosines. Thus, we tested the hypothesis that a temporal asynchrony of predators and prey results in the starvation of fish larvae.

In laboratory experiments, increases in growth (in terms of length and dry weight) were positively correlated with increasing densities of prey. These findings are consistent with studies suggesting that American shad larvae exhibit high rates of growth when *Artemia* spp., a proxy for naturally occurring plankton, are fed at densities of 500 nauplii/L or more (Johnson and Dropkin 1995; Leach and Houde 1999). In contrast with this previous work, we used wild zooplankton as a food source for laboratory experiments. Filtering and sieving plankton samples were useful for preventing the introduction of competitive or predatory ichthyoplankton and insects. Wild zooplankton offered larvae a variety of prey types and sizes similar to the zooplankton found in the Roanoke River and Albemarle Sound (Rulifson and Manooch 1993; Binion 2011). Using discrete methods for feeding larvae, we found that growth was highest when larvae were fed at densities ranging from 50 to 500 prey/L and when they were able to forage on the smallest species of zooplankton.

The results of this study suggest that there is an optimal prey size for larval American shad and that prey size is a function of mouth gape (Figure 2). Fish larvae are generally gape-limited predators (Houde 2008). Larvae with large mouth gapes are less susceptible to starvation, and with growth and increased mouth gape the size spectra of suitable prey expands (Schael et al. 1991; Munk 1997; Bremigan and Stein 1994). The development of models for mouth gape and feeding ability was useful for evaluating the size of zooplankton that larvae can capture and consume. We observed that 20-DAH larvae consumed the smallest zooplankton available, and selectivity measures indicated a strong preference for copepod nauplii and rotifers for all treatments with wild zooplankton. This evidence supports the hypothesis that optimal prey sizes are less than 50% of mouth gape. American shad larvae are dependent on vision for prey detection (Blaxter 1986) and possibly other nonvisual senses (chemoreception or mechanoreception) for prey selectivity (Batty and Hoyt 1986; Salgado and Hoyt 1996).

Although the fish in all treatments demonstrated a preference for small zooplankton (80–250 μm), prey size was correlated with growth rate, suggesting that fish behavior or experience ensures a high rate of success for prey capture and feeding. Our work differs from other published findings about American shad because our fish showed a strong preference for small

---

**TABLE 6.** Comparison of mean zooplankton abundances for coastal rivers and estuaries in North Carolina (NC), South Carolina (SC), and Virginia (VA).

| Study           | System       | State | Mesh size (μm) | Abundance (number/m³) |
|-----------------|--------------|-------|----------------|-----------------------|
| Mallin (1991)   | Neuse River  | NC    | 76             | 32,877                |
| Fulton (1984)   | Newport River| NC    | 76             | 21,900                |
| Lonsdale and Coull (1977) | North Inlet | SC    | 156            | 9,257                 |
| Birkhead et al. (1979) | Cape Fear River | NC    | 156            | 7,450                 |
| Thayer et al. (1974) | Newport River | NC    | 156            | 6,200                 |
| Carpenter and Lane (1998) | Chesapeake Bay | VA    | 202            | 5,798                 |
| Winslow et al. (1985) | Chowan River | NC    | 70             | 3,423                 |
| Rulifson et al. (1993) | Roanoke River | NC    | 250            | 532                   |
| Rulifson et al. (1993) | Albemarle Sound | NC    | 250            | 327                   |
| Coggins (2005)  | Roanoke River| NC    | 90             | 892                   |

---

**TABLE 5.** Mean preference index ($\alpha_i$) values (Chesson 1983) for American shad larvae reared from 11 to 20 d after hatching under various dietary conditions. Values greater than 0.25 indicate a preference for that food type.

| Treatment       | Copepod nauplii (≤100 μm) | Copepodites and copepods (≥100 μm) | Cladocerans | Rotifers |
|-----------------|----------------------------|----------------------------------|-------------|----------|
| High density    | 0.50                       | 0.08                             | 0.10        | 0.31     |
| Medium density  | 0.29                       | 0.09                             | 0.06        | 0.56     |
| Low density     | 0.56                       | 0.00                             | 0.00        | 0.39     |
copepod nauplii and rotifers rather than larger cladocerans (Johnson and Dropkin 1996) or insects (Crecco and Blake 1983). Larval feeding and consumption were related to prey size and not necessarily dependent on prey availability because cladocerans were the most abundant taxa in zooplankton samples. It remains unclear whether large prey were not vulnerable to predation because of larval feeding peculiarities or because of escape and avoidance tactics. Selectively feeding on small prey could alter the size structure of zooplankton assemblages and contribute to interspecific competition with coexisting larvae (Crecco and Blake 1983; Bremigan and Stein 1994; Makrakis et al. 2008). Furthermore, as a result of selectively feeding on smaller prey items, American shad must consume more prey to reach satiation, which could have bioenergetic consequences and affect growth.

Our results show that dry weight is a more appropriate measure of growth than length. While the fish in the treatments with low densities of prey and no food continued to grow in length (0.25 ± 0.06 mm/d), they lost weight (9.0 ± 5.4 μg/d). We observed marginal weight gain in fish reared with a medium density of prey (4.3 ± 1.9 μg/d). The bioenergetic consequences of food deprivation and starvation were reflected in larval condition. Fish in treatments with less than 50 prey/L were undergoing a loss of body condition and the onset of starvation and lagged their cohorts in development as evidenced by weight loss and appearance. These results build on Johnson and Dropkin’s (1995) conclusion that American shad larval growth is sensitive to prey availability and that food deprivation for as little as 2 d can severely affect growth and development. Because prey densities remained constant within experimental treatments, weight loss coupled with gut fullness could be a good predictor of feeding history.

For all treatments with wild zooplankton, significant differences in growth using weight measurements were not detected during the first 4 d of the experiment. This suggests that larvae undergo a transitional period from feeding on Artemia nauplii to feeding on wild zooplankton. This finding has important implications for hatcheries and stock enhancement programs that release larvae into ponds, rivers, and reservoirs. While additional research is needed, we believe that a temporal overlap or weaning period is required in transitioning fish from an environment with the relatively uniform live feeds used in hatchery operations to aquaculture ponds or natural systems with highly variable zooplankton distributions.

Although not significantly different among treatments, larval survival generally increased with prey density. The survival of fish among tanks and treatments (35.3%) was similar to that in previous studies of the early life history of American shad (Limburg and Ross 1995; Ross et al. 1996; Leach and Houde 1999). Unlike in Johnson and Dropkin’s (1995) work with shad larvae at 18 DAH, food deprivation did not elicit a high rate of mortality during the course of this study. The ability of larvae to withstand food deprivation and starvation varies widely among species and has not been studied for American shad (May 1974).

Striped bass Morone saxatilis larvae can survive in a totally starved condition for 30 d (Eldridge et al. 1981; Rogers and Westin 1981), and Atlantic herring larvae can survive for 50 d (Werner and Blaxter 1980). In nature, fish survival after food deprivation is dependent on a number of factors, including fish size, body condition, energy storage, metabolic rate, swimming ability, predation, and temperature (Miller et al. 1988; Fuiman 2002).

Widespread declines in the stocks of American shad along the Atlantic coast have been attributed to overfishing, a decrease in water quality, and loss of habitat. Recent surveys suggest that stocks are continuing to decline despite management efforts to reduce fishing mortality (Boreman and Friedland 2003). Although not a new concept for American shad, stock enhancement has been implemented as a tool to support the recovery of diminished stocks in several watersheds along the East Coast of the United States (Greene et al. 2009). In North Carolina, the rationale for stock enhancement has been based on studies indicating that (1) migration and spawning are restricted because of dam construction and habitat alteration, (2) eggs and larvae experience high rates of mortality in nursery habitats, and (3) juvenile recruitment is driven by strong environmental and density-independent factors (Rulifson 1994; Hightower and Sparks 2003; Walsh et al. 2005). Cultured fish are released to supplement natural recruitment and assist in the recovery of populations to historical levels.

Since 1998, approximately 26.4 million American shad larvae have been stocked into the Roanoke River (NCWRC 2009). Larval fish (12–18 DAH; 8–16 mm TL) are used in shad restoration programs because of the high mortality related to stress from handling, transporting, and stocking juveniles (≥80 mm TL; Johnson and Dropkin 1992; Ross et al. 1993). Hatchery-reared shad larvae are released at riverine sites where river flow rates are controlled for striped bass production (Rulifson and Manooch 1990) and when zooplankton densities are historically low (≤1,000 prey/m³; Rulifson and Manooch 1993). The results from this study are insufficient to suggest the direct causes of larval mortality or the overall effectiveness of a stock enhancement program in the Roanoke River; however, our findings indicate that the distribution of appropriately sized zooplankton prey is a key factor governing the survival of recently released American shad larvae.

Active monitoring should be required as part of any restoration program to evaluate the efficacy of restoration methods and status of recovery. It is critically important that releases of hatchery-reared fish be timed to coincide with peaks in zooplankton production. Zooplankton composition and size distribution vary with season, temperature, water quality, primary productivity, and predation. The presence of adequate densities of suitable prey is essential for the optimal growth and survival of American shad. Furthermore, complex interactions among food abundance, predation, competition, disease, and environmental variability can all affect the success of natural recruitment and an effective stock enhancement program.
ACKNOWLEDGMENTS
This research was supported by the North Carolina Sea Grant College Program (project R/MRD-55). We thank T. Williams for valuable assistance in the field and laboratory. Appreciation is extended to S. Jackson and the staff of the U.S. Fish and Wildlife Service’s Edenton National Fish Hatchery, who cultured and marked the American shad larvae used in our experiments. We also thank J. Govoni, R. Rulifson, and J. Luczkovich for their helpful review of this work.

REFERENCES
Batty, R. S., and R. D. Hoyt. 1995. The role of sense organs in the feeding behaviour of juvenile sole and plaice. Journal of Fish Biology 47:931–939.

Beauchamp, G., K. M. Brander, J. A. Lindley, S. Souissi, and P. C. Reid. 2003. Plankton effect on cod recruitment in the North Sea. Nature (London) 426:661–664.

Bergenius, M. A. J., M. G. Meekan, D. R. Robertson, and M. I. McCormick. 2002. Larval growth predicts the recruitment success of a coral reef fish. Oecologia 131:521–525.

Binion, S. M. 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.

Birkhead, W. A., B. J. Copeland, and R. G. Hodson. 1979. Ecological monitoring in the lower Cape Fear River estuary. Carolina Power and Light Company, Report 79-1, Raleigh, North Carolina.

Blaxter, J. H. S. 1986. Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. Transactions of the American Fisheries Society 115:98–114.

Blaxter, J. H. S., and J. R. Hunter. 1982. The biology of the clupeoid fishes. Advances in Marine Biology 20:1–223.

Boren, J., and K. D. Friedland. 2003. Sensitivity of American shad to changes in fishing mortality. Pages 267–273 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.

Bremigan, M. T., and R. A. Stein. 1994. Gape-dependent larval foraging and zooplankton size: Implications for fish recruitment across systems. Canadian Journal of Fisheries and Aquatic Sciences 51:913–922.

Carpena, R. E., and M. F. Lane. 1998. Zooplankton status and trends in the virginia tributaries and Chesapeake Bay: 1985–1996. Applied Marine Research Laboratory, Technical Report Number 3064, Final Report to the Virginia Department of Environmental Quality, Richmond, Virginia.

Chesney, E. J. 1989. Estimating the food requirements of striped bass larvae Morone saxatilis: effects of light, turbidity and turbulence. Marine Ecology Progress Series 53:191–200.

Chesson, J. 1978. Measuring preference in selective predation. Ecology 59: 211–215.

Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64:1297–1304.

Chick, J. H., and M. J. Van Den Ayre. 1999. Zooplankton variability and larval striped bass foraging: evaluating potential match/mismatch regulation. Ecological Applications 9:320–334.

Chipp, S. R., and J. E. Garvey. 2007. Assessment of diets and feeding patterns. Pages 473–474 in C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Coggin, T. C. 2005. Habitat use and seasonal abundance patterns of juvenile Alosa in the lower Roanoke River, North Carolina. Master’s thesis. East Carolina University, Greenville, North Carolina.

Crecco, V. A., and M. M. Blake. 1983. Feeding ecology of coexisting larvae of American shad and blueback herring in the Connecticut River. Transactions of the American Fisheries Society 112:498–507.

Cunha, L., and M. Planas. 1999. Optimal prey size for early turbot larvae (Scopthalmus maximus L.) based on mouth and ingested prey size. Aquaculture 175:103–110.

Cushing, D. H. 1972. The production cycle and the numbers of marine fish. Symposia of the Zoological Society of London 29:213–232.

Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Advances in Marine Biology 26:250–293.

DeVries, D. R., M. T. Bremigan, and R. A. Stein. 1998. Prey selection by larval fishes as influenced by available zooplankton and gape limitation. Transactions of the American Fisheries Society 127:1040–1050.

Durant, J. M., D. O. Hjermann, G. Ottersen, and N. C. Stenseth. 2007. Climate and the match or mismatch between predator requirements and resource availability. Climate Research 33:271–283.

Eldridge, M. B., J. A. Whipple, D. England, M. J. Bowers, and B. M. Jarvis. 1981. Effects of food and feeding factors on laboratory-reared striped bass larvae. Transactions of the American Fisheries Society 110:111–120.

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

Fuiman, L. A. 2002. Special considerations of fish eggs and larvae. Pages 31–32 in L. A. Fuiman and R. G. Werner, editors. Fishery science: the unique contributions of early life stages. Blackwell Scientific Publications, Oxford, UK.

Fulton, R. S. III. 1984. Predation, production and the organization of an estuarine copepod community. Journal of Plankton Research 6:399–415.

Gerring, S. D. 1994. Feeding ecology of fish. Academic Press, San Diego, California.

Gotte, V. P., 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.

Greene, K. E., J. L. Zimmerman, R. W. Laney, and J. C. Thomas-Blate. 2009. Atlantic coast diadromous fish habitat: a review of utilization, threats, recommendations for conservation, and research needs. Atlantic States Marine Fisheries Commission, Habitat Management Series 9, Washington, D.C.

Harris, J. E., and J. E. Hightower. 2010. Evaluation of methods for identifying spawning sites and habitat selection for alosines. North American Journal of Fisheries Management 30:386–399.

Hassler, W. W., N. L. Hill, and J. T. Brown. 1981. The status and abundance of striped bass, Morone saxatilis, in the Roanoke River and Albemarle Sound, North Carolina, 1956–1980. North Carolina Department of Natural Resources, Division of Marine Fisheries, Special Scientific Report 38, Morehead City.

Hendricks, M. L., T. R. Bender Jr., and V. A. Mudrak. 1991. Multiple marking of American shad otoliths with tetracycline antibiotics. North American Journal of Fisheries Management 11:212–219.

Hightower, J. E., and K. L. Sparks. 2003. Migration and spawning habitat of American shad in the Roanoke River, North Carolina. Pages 193–199 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.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe in the light of biological research. Rapports et Proces-Verbaux des Réunions Conseil International pour l’Exploration de la Mer 20:1–228.

Hjort, J. 1926. Fluctuations in the year classes of important food fishes. Journal du Conseil, Conseil International pour l’Exploration de la Mer 1: 5–38.

Horn, M. H., and L. A. Ferry-Graham. 2006. Feeding mechanisms and trophic interactions. Pages 387–410 in L. G. Allen, D. J. Pondella II, and M. H. Horn, editors. The ecology of marine fishes: California and adjacent waters. University of California Press, Berkeley.

Houde, E. D. 1994. Differences between marine and freshwater fish larvae: implications for recruitment. ICES (International Council for the Exploration of the Sea) Journal of Marine Science 51:91–97.
Johnson, J. H., and D. S. Dropkin. 1992. Predation on recently released larval
Hunter, J. R. 1981. Feeding ecology and predation of marine fish larvae. Pages
Kamler, W. 1992. Early life history of fish: an energetics approach. Chapman
Hunter, J. R. 1972. Swimming and feeding behavior of larval anchovy, \textit{En-
graulis mordax}, larvae. U.S. National Marine Fisheries Service Fishery Bul-
letin 70:821–838.
Hunter, J. R. 1981. Feeding ecology and predation of marine fish larvae. Pages
Howey, R. G. 1985. Intensive culture of juvenile American shad. Progressive
Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marshall. 1988. Larval size and
Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P .
Mallin, M. A. 1991. Zooplankton abundance and community structure in a
Leach, S. D., and E. D. Houdé. 1999. Effects of environmental factors on
Ross, R. M., T. W. H. Backman, and R. M. Bennett. 1993. Evaluation of the
Riley et al., editors. 1993. Roanoke River water flow committee report for 1991–
Rulifson, R. A., J. E. Cooper, D. W. Stanley, M. E. Shepherd, S. F. Wood, and
Schael, D. M., L. G. Rudstam, and J. R. Post. 1991. Gape limitation and prey se-
Salgado, S. D., and R. D. Hoyt. 1996. Early behaviour formation in fathead min-
Snyder, D. E. 1983. Fish eggs and larvae. Pages 165–167 in R. L. Nielsen and
Shirota, A. 1970. Studies on the mouth size of fish larvae. Bulletin of the
Sterner, R. W. 1979. Early feeding in striped bass larvae. Marine Biology 54:
Sternberg, J. 1975. Early feeding and development in striped bass larvae. American
Swain, K. C., and K. M. Duellman. 1984. Larval size and feeding behavior of the
Teh, C. M. K. 1995. A model for certain types of selection experiments. 
Thayer, G. W., D. E. Hoss, M. A. Kjelson, W. F. Hettler Jr., and M. W. Lacroix. 
U.S. Environmental Protection Agency, Project APES 90–16, Washington, D.C. 
U.S. Environmental Protection Agency, Project APES 93–18, Washington, D.C. 
U.S. National Marine Fisheries Service Fishery Bulletin 107:318–328.
Waser, J. 1977. Sexual dimorphism in fish larvae, p. 149–168 in J. H. S. Blaxter, editor. 
The early life history of fish. J. H. S. Blaxter, editor. The early life history of fish. 
Springer-Verlag, New York.
Thayer, G. W., D. E. Hoss, M. A. Kjelson, W. F. Hettler Jr., and M. W. Lacroix. 
1974. Biomass of zooplankton in the Newport River estuary and the influence of postlarval fishes. 
Chesapeake Science 15:9–16.
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.
Werner, R. G., and J. H. S. Blaxter. 1980. Growth and survival of larval herring 
\textit{Clupea harengus} in relation to prey density. Canadian Journal of Fisheries 
and Aquatic Sciences 37:1063–1069.
Winslow, S. E. 1985. North Carolina anadromous fisheries management pro-
gram. Anadromous Fish Conservation Act, Project AFCS-22, Morehead City, 
North Carolina.
Yasuda, F. 1960. The feeding mechanisms in some carnivorous fish. Records of 
Oceanographic Works in Japan 5:153–160.
Riley et al., editors. 1993. Roanoke River water flow committee report for 1991–
Rulifson, R. A., and C. S. Manooch III, editors. 1990. Roanoke River water flow 
committee report for 1982 and 1988. Albemarle-Pamlico estuarine study, U.S.
Environmental Protection Agency, Project APES 90–16, Washington, D.C.
Rulifson, R. A., and C. S. Manooch III, editors. 1993. Roanoke river water flow 
committee report for 1991–1993. Albemarle-Pamlico estuarine study. U.S.
Environmental Protection Agency, Project APES 93–18, Washington, D.C.
Rulifson, R. A., J. E. Cooper, D. W. Stanley, M. E. Shepherd, S. F. Wood, and
D. A. Daniel. 1993. Food and feeding of young striped bass in Roanoke 
River and western Albemarle Sound, North Carolina, 1984–1991. North Car-
olina Wildlife Resources Commission, Completion Report for Project F-27, 
Greenville.
Salgado, S. D. and R. D. Hoyt. 1996. Early behaviour formation in fathead min-
now larvae, \textit{Pimephales promelas}: implications for sensory function. Marine 
and Freshwater Behaviour and Physiology 28:91–106.
Schael, D. M., L. G. Rudstam, and J. R. Post. 1991. Gape limitation and prey se-
lection in larval yellow perch (\textit{Perca flavescens}), freshwater drum (\textit{Aplodino-
tus grunniens}), and black crappie (\textit{Pomoxis nigromaculatus}). Canadian Jour-
nal of Fisheries and Aquatic Sciences 48:1919–1925.
Shirota, A. 1970. Studies on the mouth size of fish larvae. Bulletin of the 
Japanese Society of Scientific Fisheries 36:353–368.
Snyder, D. E. 1983. Fish eggs and larvae. Pages 165–167 in L. Nielsen and
D. L. Johnson, editors. Fisheries techniques. American Fisheries Society, 
Bethesda, Maryland.
Thayer, G. W., D. E. Hoss, M. A. Kjelson, W. F. Hettler Jr., and M. W. Lacroix. 
1974. Biomass of zooplankton in the Newport River estuary and the influence of postlarval fishes. 
Chesapeake Science 15:9–16.
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.
Werner, R. G., and J. H. S. Blaxter. 1980. Growth and survival of larval herring 
\textit{Clupea harengus} in relation to prey density. Canadian Journal of Fisheries 
and Aquatic Sciences 37:1063–1069.
Winslow, S. E. 1985. North Carolina anadromous fisheries management pro-
gram. Anadromous Fish Conservation Act, Project AFCS-22, Morehead City, 
North Carolina.
Yasuda, F. 1960. The feeding mechanisms in some carnivorous fish. Records of 
Oceanographic Works in Japan 5:153–160.