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SPECIAL SECTION: AMERICAN SHAD AND RIVER HERRING

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

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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

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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; Gerking 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 $\cdot$ s^{-1} $\cdot$ 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,

$$a^2 = b^2 + c^2 - 2bc \cos \alpha, \quad (1)$$

where a is the mouth gape, b is the upper jaw length, c is the lower jaw length, and α 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

$$G = \frac{\log_e X_2 - \log_e X_1}{t_2 - t_1}, \quad (2)$$

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,

$$\alpha_i = \frac{r_i}{n_i} \frac{1}{\Sigma(r_j/n_j)} \quad i = 1, \ldots, m \tag{3}$$

where α_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 α_i ranges from 0 to 1, and selectivity is indicated when α_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 ANOVA 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

TABLE 1. Linear relationships between growth (in terms of total length [G_{TL}] and notochord length [G_{NL}]) and age for American shad larvae reared at 24°C under various dietary treatments (see text).

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

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	$G_w = 34.6$ Age + 168.2	0.32	40.6
High prey	41	229–592	$G_w = 18.8$ Age + 103.9	0.26	25.6
Medium prey	37	157–277	$G_w = 3.8$ Age + 145.8	0.51	26.0
Low prey	34	129–143	$G_w = -4.0$ Age + 147.3	0.20	23.7
No food	41	5–88	$G_w = -15.7$ Age + 165.7	0.37	16.3

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 = 5, 163; $P < 0.0001$).

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 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; $P < 0.0001$).

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 size based on larval mouth gape estimates of 30% (minimum) and 50% (maximum) ranged from 0.229 to 0.585 mm at 12 DAH, from 0.248 to 0.587 mm at 16 DAH, and from 0.271 to 0.606 mm at 20 DAH. With the exception of small copepod nauplii (<0.100 mm) and large cladocerans (>0.600 mm), these values correspond closely to the size of the zooplankton and *Artemia* nauplii used as a food in our experiments.

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

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

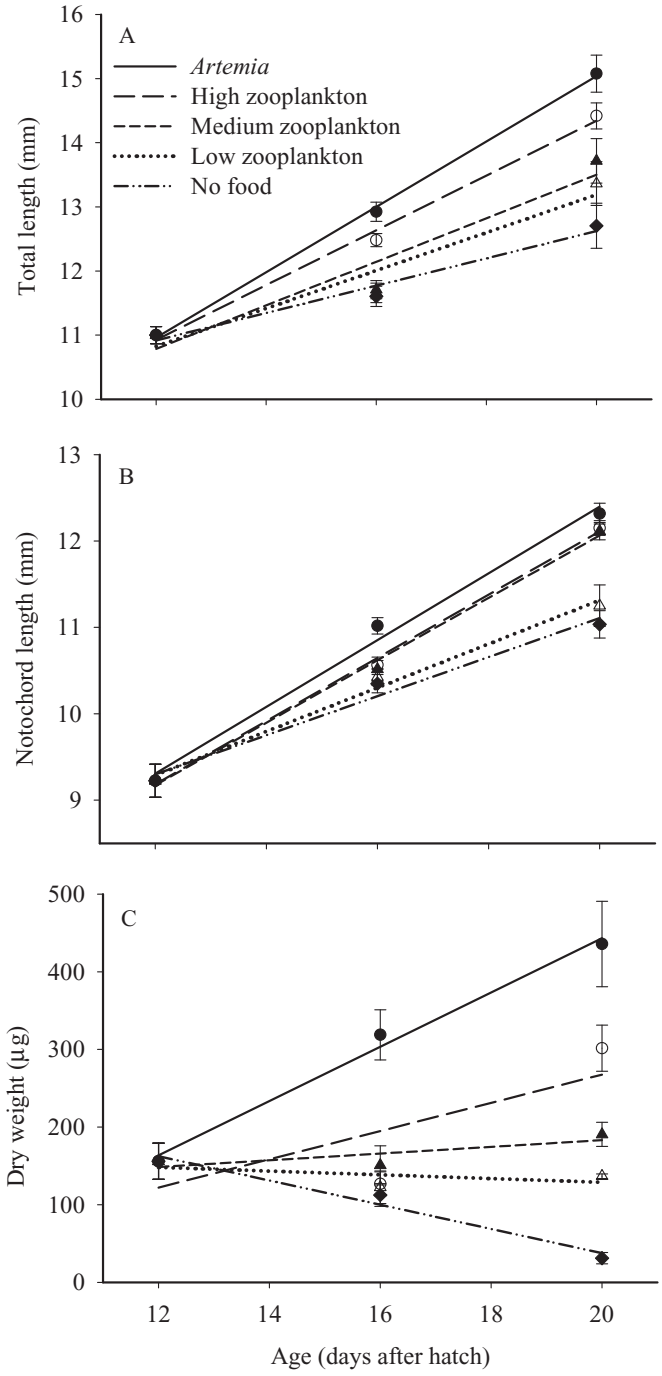

FIGURE 1. Relationships between age and **(A)** total length, **(B)** notochord length, and **(C)** dry weight of American shad larvae reared from 12 to 20 d after hatching under various conditions of food availability. The regression lines are plotted with means ± SEs.

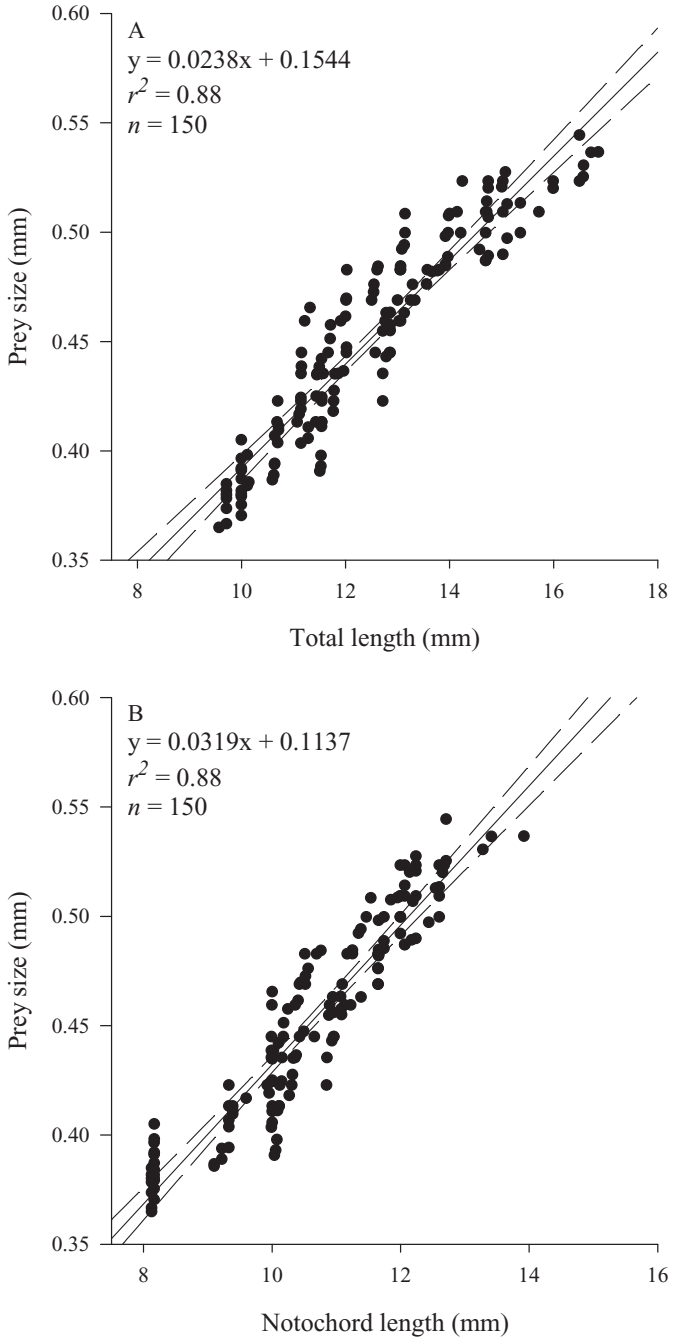

FIGURE 2. Regressions (solid lines) of theoretical prey size on **(A)** total length and **(B)** notochord length measurements for American shad larvae; the dashed lines represent the 95% confidence limits. Prey size was estimated as 50% of the mouth gape for the larvae. The data represent the combined measurements of three feeding treatments (*Artemia*, high prey density, and medium prey density), which were not significantly different (ANOVA; df = 2, 27; $P = 0.18$).

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

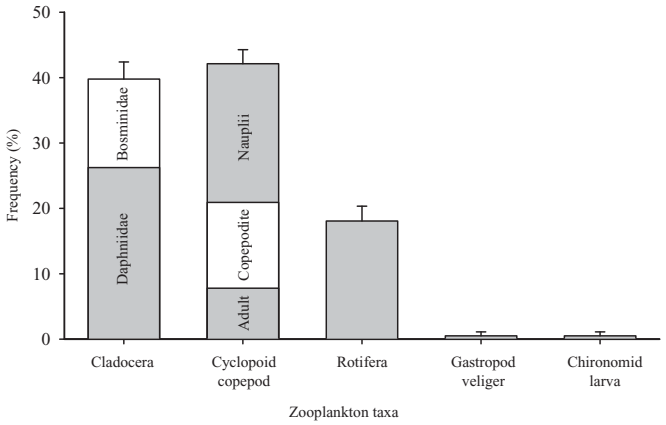

FIGURE 3. Frequency distribution of size-sorted, wild zooplankton collected and used as food in larval rearing trials with American shad. The samples were washed through an 800-μm-mesh sieve to prevent the introduction of ichthyoplankton, insects, and other predatory species. The data represent the mean distribution of invertebrate taxa among daily samples collected from the field.

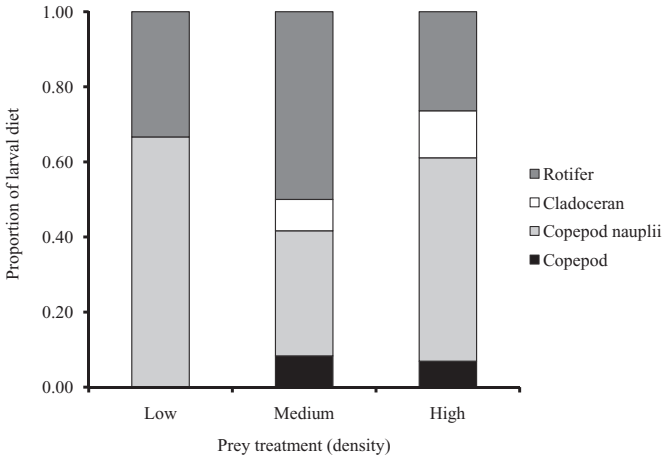

FIGURE 4. Diet composition of American shad reared 12–20 d after hatch in three treatments with varying densities of zooplankton prey: low (1 prey/L), medium (50 prey/L), and high (500 prey/L).

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 period 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

Relative Preference for Prey Species and Size

Larvae were observed feeding in all treatments with prey available. Microscopic analysis and dissection of 20-DAH larvae revealed that small prey items (80–250 μm BW), such as copepod nauplii, rotifers, and cladocerans (i.e., bosminids), were most commonly eaten (Figure 4). Chironomids and gastropods were the only prey taxa observed in plankton samples but not observed in the stomachs of larvae. American shad displayed strong selection for copepod nauplii and rotifers in all treatments with wild zooplankton (Table 5). Larvae had 5.1 ± 2.7 prey in their stomachs in the high-density treatments and 0.8 ± 0.7 prey in the medium-density treatments. Gut fullness was not significantly different among treatments with *Artemia* (90 ± 12%), high prey density (78 ± 19%), and medium prey density (63 ± 19%), but it was significantly higher in these treatments than in the treatments with low prey density (12 ± 12%; ANOVA; df = 5, 117; $P < 0.0001$).

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

TABLE 5. Mean preference index (α_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

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/m^3 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 1995; 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/m^3)
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	327
	Albemarle Sound	NC	250	532
Coggins (2005)	Roanoke River	NC	90	892

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 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 when river flow rates are controlled for striped bass production (Rulifson and Manooch 1990) and when zooplankton densities are historically low (≤1,000 prey/m^3; 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.

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