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SPECIAL SECTION: AMERICAN SHAD AND RIVER HERRING

Foraging Potential of Larval Alosines in the Lower Roanoke River and Albemarle Sound, North Carolina

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Abstract

Zooplankton composition and abundances were quantified in the lower Roanoke River and Albemarle Sound, North Carolina. The spatial and temporal overlap between larval alosines, including American shad *Alosa sapidissima*, river herring (alewife *A. pseudoharengus* and blueback herring *A. aestivalis*), hickory shad *A. mediocris*, and zooplankton were examined to determine whether larval alosines in this system are food limited. Samples were collected weekly at 19 stations from March through June 2008–2009 in three habitats: River, Delta, and Sound. Spatial differences in zooplankton were observed, with the abundance in the Sound (16,546 ± 14,678 [number/m^3 ± SD]) being significantly higher than those in the River (4,934 ± 3,806) and Delta areas (4,647 ± 2,846). Zooplankton composition was dominated by Daphniidae, Bosminidae, calanoid and cyclopoid copepods, copepod nauplii, and rotifers. The spatial patterns in alosine abundance were the opposite of those for zooplankton, being highest in the River (21.0 ± 127.6) and lower in the Delta (7.5 ± 35.5) and Sound (4.6 ± 24.8). Mouth gape models for each alosine species showed that copepod nauplii and rotifers are the most suitable-sized prey for the first feeding after yolk sac absorption. There was a high degree of spatial and temporal overlap between larval alosines and size-appropriate prey items, suggesting that the larval alosines are not food limited in Albemarle Sound.

Year-class strength and recruitment of fish is strongly correlated with survival during egg and larval development. During the past century, a number of hypotheses were developed to explain fluctuations in recruitment. Temporal and spatial overlap between fish and their prey is considered one of the most influential factors affecting survival and growth during the larval phase (Cushing 1990; Leggett and DeBlois 1994; Gotceitas et al. 1996). Hjort (1914) developed the critical-period hypothesis, which directly links larval survival with feeding success. Under this hypothesis, there is a critical period, defined as the period after yolk sac absorption when a larva is transitioning from endogenous to exogenous feeding. Cushing's match/mismatch hypothesis (1972) builds on Hjort's critical-period hypothesis. The match/mismatch hypothesis extends the importance of prey

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availability and feeding success to include the entire larval period, not just that of the first feeding. Laboratory experiments and field studies that test critical-period hypotheses have received mixed reviews (De Lafontaine and Leggett 1987; Paradis et al. 1996). These studies are often confounded by attempts to balance the proportions of predators and prey. Despite this critique, substantial evidence suggests that larval nutrition and starvation are leading causes for the variability in early life history (Leggett and DeBlois 1994; Fortier et al. 1995; Houde 2008). Smaller larvae, such as alosines, are believed to highly susceptible food limitation and starvation, resulting in high mortality rates (Miller et al. 1988; Houde 1994).

In addition to having spatial and temporal overlap with potential zooplankton prey, the available prey items need to be a size capable of being consumed. In larval fish, mouth gape is a limiting factor at the onset of exogenous feeding, restricting the prey size that can be consumed (DeVries et al. 1998; Yufera and Darias 2007). Mouth gape becomes less limiting as fish grow. There is a positive relationship between fish length and mouth gape (DeVries et al. 1998; Puvanendran et al. 2004). Studies have suggested that the maximum functional mouth gape is attained when the mouth is open at a 90° angle. Optimal prey sizes are generally within 30–50% of the mouth gape (Bremigan and Stein 1994; Turingan et al. 2005; Riley et al. 2009).

The early life history of most species is intertwined with variability in biotic and abiotic factors that influence feeding and behavior in larval fish. The distribution and abundance of suitable prey is a key factor in feeding success. Prey density thresholds have been established for many species of larval fish. Baseline densities ranging from 9,000 to 100,000 zooplankton/m^3 are critically important for the growth and survival of most estuarine and marine fishes (Hunter 1981). In laboratory studies, Leach and Houde (1999) observed that zooplankton densities of 500,000 individuals/m^3 or more were necessary for the production of larval American shad *Alosa sapidissima*. Similarly, Riley (2012) showed that zooplankton densities of 100,000 individuals/m^3 or more were necessary to support larval growth after first feeding. Food deprivation for as little as 2 d can significantly affect survival and predator avoidance (Johnson and Dropkin 1995, 1996). These studies highlight the importance of food availability at varying spatial and temporal scales and underscore a multitude of factors that contribute to recruitment and year-class strength.

In most aquatic systems, zooplankton abundance is highly variable and fluctuates seasonally with primary production, water temperature, and hydrographic conditions. Low densities and patchy distributions of zooplankton are often observed in coastal rivers and estuaries that serve as primary nursery grounds for many economically important species of fish and shellfish (Hynes 1970; Chick and Van Den Avyle 1999). The coastal ecosystems of North Carolina support a high level of productivity and form the second largest estuarine complex in the United States, with over 7,500 km^2 of open water. More than 90% of North Carolina's commercial fisheries landings and over 60% of the recreational harvest are comprised of estuarine-dependent species (Street et al. 2005). These species depend on an abundance of food within coastal rivers and sounds to complete their life cycle.

Roanoke River supports numerous populations of anadromous fishes, many threatened or endangered. Anadromous alosines such as American shad, river herring (blueback herring *A. aestivalis* and alewife *A. pseudoharengus*), and hickory shad *A. mediocris* are in sharp decline and some stocks are bordering on collapse (ASMFC 2007; Greene et al. 2009; NCDMF 2010). Additionally, North Carolina and Virginia once accounted for 90% of the total commercial river herring landings in the United States. (Crecco and Gibson 1990). Shads and river herring spawn in the Roanoke River. Alewives, blueback herring, and American shad return to their natal rivers to spawn, but there is no evidence to support this with hickory shad (Green et al. 2009). Blueback herring spawn in both lotic and lentic waters over hard substrates, avoiding areas with standing water (Walsh et al. 2005; Greene et al. 2009). Alewives begin spawning in lentic waters over a variety of substrates, including gravel, sand, detritus, and submerged vegetation (O'Connell and Angermeier 1997; Able and Fahay 1998; Walsh et al. 2005). In areas where alewives and blueback herring have overlapping distributions, alewives begin spawning in late February, 3–4 weeks earlier than blueback herring, which begin spawning in late March (O'Connell and Angermeier 1997; Able and Fahay 1998). In the sympatric range, blueback herring and alewives utilize different spawning habitats. Blueback herring do not migrate as far upstream as alewives. Blueback herring spawn predominately in the main-stream flow, while alewives select shorebank eddies and deep pools for spawning (Able and Fahay 1998; Greene et al. 2009). American shad spawn when water temperatures are between 12°C and 20°C, typically between March and early June (Able and Fahay 1998; Bilkovic et al. 2002). In the Roanoke River, hickory shad were observed spawning in water less than 1 m deep with moderate to high velocity, over substrates containing cobble, gravel, and sand (Greene et al. 2009; Harris and Hightower 2010).

Alosine larvae use nursery habitats within the lower reaches of the Roanoke River and Albemarle Sound (Greene et al. 2009; Harris and Hightower 2010). One possible explanation for the failure of these stocks is high levels of larval mortality caused by food limitation. The abundance and distribution of zooplankton in the lower Roanoke River is the lowest among coastal rivers in North Carolina (Table 1). A long-term study conducted from 1984 to 1991 by Rulifson et al. (1993) and a similar study by Coggins (2005) in 2003 documented zooplankton abundances between 1 and 2 orders of magnitude lower than in neighboring systems, although the large mesh size (250 μm) used by Rulifson et al. (1993) may have in part accounted for the low numbers reported. There are no known published studies of zooplankton composition and abundances in this system prior to Rulifson et al. (1993), so it is unclear whether these low numbers are

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TABLE 1. Average zooplankton abundance in several North Carolina coastal river systems as determined by various studies.

Study	System	Mesh size (μm)	Abundance (number/m^3)
Mallin (1991)	Neuse River	76	32,877
Fulton (1984)	Newport River	76	21,900
Thayer et al. (1974)	Newport River	156	6,200
Birkhead et al. (1979)	Cape Fear River	156	7,450
Winslow (1985)	Chowan River	70	3,423
Rulifson et al. (1993)	Roanoke River	250	327
	Roanoke Delta	250	696
	Albemarle Sound	250	532
Coggins (2005)	Roanoke River	90	892

indicative of the long-term history or capture periods of low abundance.

Numerous studies suggest that stock recovery begins with habitat restoration (i.e., dam removal) and the need to improve the availability of habitat for spawning adults (Beasley and Hightower 2000; Moser et al. 2000). While we agree, we propose an alternative hypothesis. We hypothesize that the precipitous decline in anadromous alosines during the past 30 years reflects changes in the quality and availability of suitable nursery habitat for early life stages. Variability in abiotic conditions and fluctuations in food abundance could structure nursery habitat and severely restrict recruitment, thereby limiting the recovery of these important fisheries.

The goal of this study was to investigate the ecological processes influencing the recruitment of larval alosines to nursery habitats within the lower Roanoke River and Albemarle Sound. The results were compared with those of previous studies to identify long-term fluctuations in recruitment dynamics, food availability, and water quality. Larval feeding ability was assessed through development of mouth gape models for each alosine species. Spatial and temporal overlap between larval alosines and size-appropriate zooplankton prey were analyzed to determine whether match/mismatch regulation could exist and result in food limitation or starvation.

METHODS

Roanoke River and Albemarle Sound.—The Roanoke River basin is the largest basin of any North Carolina estuary, encompassing 25,035 km^2 (Konrad 1998; NCDENR 2000). The Roanoke River originates in the Blue Ridge Mountains of Virginia and flows southeast approximately 660 km to where it empties into Albemarle Sound, North Carolina (Konrad 1998; Pearsall et al. 2005). The Roanoke and Chowan rivers are the two main tributaries emptying into Albemarle Sound. The Roanoke River accounts for over 50% of the freshwater input into Albemarle Sound (Gray and Copeland 1989). It is one of the largest alluvial rivers on the East Coast. The lower region below the fall line is surrounded by bottomland hardwood floodplain forest and is the largest and least fragmented ecosystem of this type in the mid-Atlantic region (NCDENR 2000; Pearsall et al. 2005).

Albemarle Sound is a shallow estuary with mean depths less than 5 m that is part of the Albemarle–Pamlico estuarine system. This system is made up of broad, shallow, drowned river valleys. It is the second largest estuary and the largest lagoonal estuary in the United States. Pamlico Sound and Albemarle Sound are the two main basins in this system. Albemarle Sound is the northernmost basin and is separated from Pamlico Sound by Croatan and Roanoke sounds (Gray and Copeland 1989). The Outer Banks form a barrier separating Albemarle Sound from the Atlantic Ocean. Oregon Inlet is located south of Albemarle Sound and acts as the only source of saltwater intrusion. This limited saltwater intrusion, combined with high freshwater input from several rivers, results in Albemarle Sound's having salinity values less than 5‰ (Copeland et al. 1983; Pearsall et al. 2005). The Outer Banks also protect Albemarle Sound from gravitational tides, with water circulation being primarily wind driven (Copeland et al. 1983).

Field collection.—Larval fish and zooplankton samples were collected concurrently, beginning at sunset, from March through June in 2008 and 2009. Samples were collected from 19 stations located in three areas within the lower Roanoke River and Albemarle Sound classified as River, Delta, and Sound (Figure 1). River is the area furthest upstream with seven stations scattered throughout the main stem of the river and its tributaries and distributaries between river kilometers (rkm) 9.5 and 22 as measured from the mouth of the Roanoke River (rkm 0). Delta is the transitional region between River and Sound, where the Roanoke, Middle, and Cashie rivers converge at the Highway

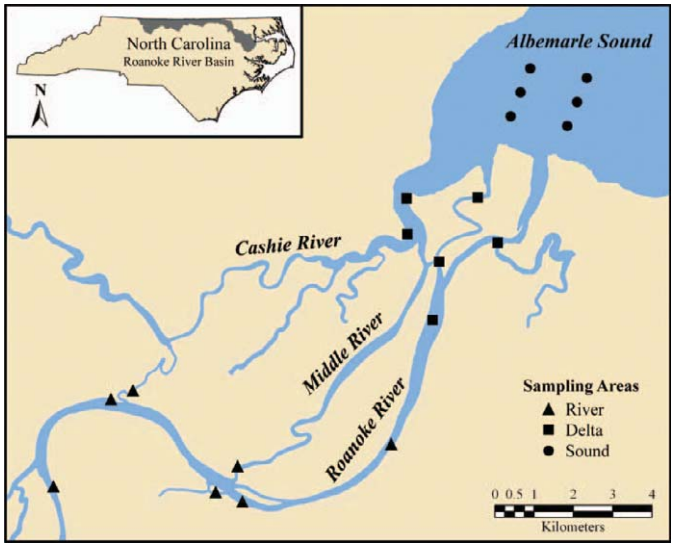


FIGURE 1. Locations of the sampling stations and delineation of the three sampling areas in the lower Roanoke River and Albemarle Sound, North Carolina.

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45 bridge before diverging and flowing into Albemarle Sound. There are two stations each in the Roanoke, Middle, and Cashie rivers, for a total of six stations. The Delta station furthest upstream is located at rkm 5 in the Roanoke River. Sound has six stations in Batchelor Bay, the western portion of Albemarle Sound. The stations extend 2–4 km from the mouths of the Roanoke and Middle rivers.

Zooplankton samples were collected using a 3:1 conical net with a 0.5-m opening and 90-μm nitex mesh. The plankton net was deployed using a vertical net haul technique whereby the net was lowered to the bottom and then pulled vertically through the water column. A preliminary study comparing the catch efficiency of vertical hauls, surface tows, and the use of a bilge pump to filter water through the net showed no significant differences in species abundance or composition when using vertical hauls or the pumping method, while abundances were significantly lower ($F_{2,45} = 21.49$, $n = 48$, $P < 0.001$) using surface tows (authors' unpublished data). The contents of the net were washed down and condensed into a sample jar and preserved with 5% buffered formalin.

Ichthyoplankton were collected using paired surface push nets mounted on the bow of the boat. Each net was housed in an aluminum frame with a 0.5-m-square opening. Each larval fish net had a 5:1 ratio and was constructed from 505-μm nitex mesh. A Sea-Gear Model MF315 flowmeter was mounted in the center of each net to estimate the amount of water filtered during each tow. The nets were pushed into the current for 2 min at a speed of 1.03 ± 0.11 m/s (Overton and Rulifson 2007). The contents of each net were condensed into a 1-L plastic collection jar. The contents of the left net were preserved with 95% ethanol, while the contents of the right net were preserved with 5% buffered formalin. The amount of ethanol used for preservation changed between the two sampling years. In 2008, the ratio of sample water to ethanol was approximately 70% sample water to 30% ethanol and there was a high amount of deterioration. In 2009, the amount of ethanol used for preservation was increased to account for 95% of the sample volume. To determine larval abundance, the catches between the two nets were averaged together. In 2009, samples were not collected during calendar week 20 in the Delta and during weeks 12, 16, and 20 in the Sound because of mechanical issues with the boat and severe weather.

Environmental parameters were recorded at each station during each sampling event. Air temperature (°C), wind speed (m/s), and direction were measured using a Skymate Model Sm-18. Surface and bottom water temperatures (°C), salinity, conductivity (μS), and dissolved oxygen concentration (mg/L) were measured using a YSI Model 85 Multiparameter Water Quality Meter. A Hanna Model HI 98128 pH meter was used to measure surface pH. Current velocity (m/s) and direction were measured 1 m below the surface using a Marsh-McBirney FLO-MATE Portable Velocity Flow Meter, Model 2000.

Data processing.—For each sampling date, three zooplankton samples from each area were randomly selected for processing. Subsamples were taken using a Hensen-Stempel pipette. Individuals were counted and identified using an Olympus Model SZX-ILLD100 stereomicroscope. Zooplankton were identified using taxonomic keys found in Thorp and Covich (2001) and Balcer et al. (1984). Zooplankton were lumped together into the following groups to allow for direct comparison with previous work by Rulifson et al. (1993) and Coggins (2005): calanoid copepods, cyclopoid copepods, copepod nauplii, rotifers, and cladocerans. Body length and widths were measured to the nearest 0.1 mm using Image-Pro Discovery 4.5.

Larval alosines were identified to species and enumerated, and their notochord lengths were measured to the nearest 0.1 mm. For the mouth gape analysis, only individuals preserved in formalin were used. Few American shad larvae were collected, so mouth gape analysis was conducted on larvae obtained from U.S. Fish and Wildlife Service's Edenton National Fish Hatchery in Edenton, North Carolina. Larvae were separated into 1-mm size bins based on notochord length, and up to 20 individuals were analyzed per size bin. All measurements were made using Image-Pro Discovery 4.5. For each fish, the upper and lower jaws were measured to the nearest 0.1 mm. The upper jaw was measured across the premaxilla and maxilla to the point of articulation with the dorsal process of the dentary. The lower jaw was measured along the length of the dentary to the point of articulation with the angular and maxillae. Mouth gape was calculated using the law of cosines for a mouth open at a 90° angle (Riley et al. 2009). This angle is considered the maximum functional degree of opening for feeding in most larval species (Turingan et al. 2005; Riley et al. 2009).

Statistical analyses.—An independent-samples *t*-test was used to evaluate whether zooplankton abundances and environmental parameters differed between sampling years. Differences in abundance between this study and previous studies (Rulifson et al. 1993; Coggins 2005) were also assessed using this test. Spatial and monthly differences between abundances and abiotic factors were evaluated using a one-way analysis of variance (ANOVA). If the ANOVA was significant, the differences were further examined using the Ryan–Einot–Gabriel–Welch post hoc test, which holds the familywise alpha at 0.05.

Primer-E version 6 (Primer-E Ltd., Plymouth, UK) was used to evaluate the spatial differences in community structure. Prior to analysis, zooplankton data were fourth-root transformed, with rare species being down-weighted (Clarke and Warwick 2001). Nonmetric multidimensional scaling was used as a visual representation, showing similarities within areas based on differences in Bray–Curtis dissimilarity values. The closer two points are located on the ordination plot, the more similar those two points are. One-way analysis of similarity (ANOSIM) was used to test whether there were significant differences in community structure among the three areas. The test statistic for ANOSIM, *R*, usually ranges from 0 to 1, with 0 indicating similarity among groups. Similarity percentages (SIMPER) were used to analyze which taxa were driving the dissimilarity among areas. The SIMPER procedure decomposes Bray–Curtis dissimilarity values and transforms them into percentage contributions from each taxon. SIMPER also allows for the identification of

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TABLE 2. Prey and American shad stocking densities from Johnson and Dropkin (1995) and Riley et al. (2012). The stocking densities given on a per-liter basis represent the values used in the experiments. Those converted to a per-cubic-meter basis allow comparison with the abundances in this study. To determine the ratio of prey to larvae, the prey density was divided by that of American shad.

Study	Prey density classification	Stocking density (/L)		Stocking density (/m^3)		Ratio
		Prey	American shad	Prey	American shad	
Johnson and Dropkin (1995)	Medium	500	8	500,000	8,000	63:1
	High	1,000	8	1,000,000	8,000	125:1
Riley et al. (2012)	Low	1	4	1,000	4,000	0.3:1
	Medium	50	4	50,000	4,000	13:1
	High	500	4	500,000	4,000	125:1

discriminating taxa, those that consistently contribute to the dissimilarity between two areas (Clarke and Warwick 2001; Clarke and Gorley 2006).

For comparisons of zooplankton abundance and composition between this study and Rulifson et al. (1993), rotifers and copepod nauplii were excluded from the analysis. Rulifson et al. (1993) collected zooplankton using a 250-μm-mesh net. Rotifers and copepod nauplii are typically less than 200 μm in size and are not efficiently collected in a 250-μm-mesh net (Thorp and Covich 2001).

The alosine abundance data did not meet normality assumptions (even with data transformation), so nonparametric tests were used for comparisons. Yearly differences in alosine abundance were evaluated using a Wilcoxon rank–sum test. A Kruskal–Wallis ANOVA was used to evaluate the differences in abundance among species and sampling areas. If the ANOVA was significant, post hoc comparisons were conducted using Wilcoxon rank–sum tests with the familywise alpha being controlled by a Dunn–Sidak adjustment.

Mouth gape models for each species were created using linear regression analysis. A one-way analysis of covariance (ANCOVA) was used to test whether mouth gapes differed significantly among species. Prey size estimates were based on the length when the yolk sac is absorbed and larvae begin to feed exogenously. Yolk sac absorption occurs at 6 mm in alewives and blueback herring, at 7 mm in hickory shad, and between 9 and 12 mm in American shad larvae (Lippson and Moran 1974). Unless otherwise noted, all statistical analyses were conducted using SAS 9.2 (SAS Institute, Cary, North Carolina).

To evaluate the spatial and temporal overlap between larval alosines and zooplankton, weekly abundances for each group were plotted against each other for each sampling area. Only zooplankton that were estimated to be size-appropriate prey at first feeding for all taxa were included, and the four alosine species were grouped together. Zooplankton abundances from American shad feeding studies were used to establish a baseline for high zooplankton–alosine overlap that supports optimal growth and survival (Johnson and Dropkin 1995; Riley et al. 2012, this special section). The stocking densities of larval fish and zooplankton in laboratory feeding trials are often inflated and do not correspond to the values observed in field studies (De Lafontaine and Leggett 1987; Paradis et al. 1996). In Johnson and Dropkin (1995) and Riley et al. (2012) both American shad and zooplankton were stocked at concentrations higher than those observed in this study. To make the concentrations of American shad and zooplankton comparable to those observed in the Roanoke River and Albemarle Sound, the concentration of zooplankton was divided by that of American shad. The baseline for high overlap, which supported optimal growth and survival in the two studies, was 125 zooplankton/L of American shad larvae (Table 2).

RESULTS

Environmental Data

The environmental data ($n = 97$) are summarized in Table 3. Monthly patterns were observed for dissolved oxygen and air and water temperature. Dissolved oxygen followed the expected seasonal pattern of being highest in March and decreasing throughout the sampling season. Hypoxic conditions (<2.0 mg/L) occurred infrequently in late May and June, accounting for 1% of bottom dissolved oxygen readings. Dissolved oxygen also varied between years and was significantly higher in 2009 (7.9 ± 2.0 mg/L [mean ± SD]) than in 2008 (6.5 ± 1.5 mg/L). Air and water temperatures followed the opposite pattern, being lowest in March and increasing through June. Significant yearly differences were observed for pH and wind speed (Table 4). In 2008 (7.5 ± 0.2), pH was significantly higher than in 2009 (6.7 ± 0.4). Wind speed was also higher in 2008 (5.2 ± 5.1 m/s) than in 2009 (1.7 ± 1.1 m/s).

Salinity, current velocity, and wind speed were significantly higher in the Sound (Table 5). Mean salinity was 0.1 ± 0.0‰ in both the River and Delta, significantly lower ($F_{2, 94} = 35.69$, $n = 97$, $P < 0.001$) than in the Sound, where it ranged from 0.1 to 2.8‰ with a mean ± SD value of 0.5 ± 0.6‰. The majority of salinity values did not exceed 1.0‰. Current velocity was similar in the River and Delta, ranging from 0.0 to 0.83 m/s, with a mean ± SD velocity in both areas of 0.1 ± 0.1. Current velocity was significantly higher ($F_{2, 94} = 3.98$, $n = 97$, $P = 0.022$) in the Sound (0.2 ± 0.1 m/s), ranging from 0.0 to

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TABLE 3. Average monthly values (means ± SDs) for environmental variables collected in March–June 2008 and 2009 in the lower Roanoke River and Albemarle Sound.

Area	Month	Air temp. (°C)	Conductivity (μS)	Dissolved oxygen (mg/L)	pH	Salinity (‰)	Water temp. (°C)	Wind speed (m/s)
River	Mar 2008	13.1 ± 3.0	134.2 ± 99.1	8.2 ± 1.1	7.4 ± 0.1	0.1 ± 0.0	13.2 ± 1.8	4.6 ± 5.7
	Apr 2008	16.4 ± 2.8	112.6 ± 11.2	7.0 ± 1.9	7.4 ± 0.1	0.1 ± 0.0	15.7 ± 1.5	2.0 ± 2.8
	May 2008	18.8 ± 2.5	119.6 ± 8.4	5.7 ± 0.9	7.5 ± 0.1	0.1 ± 0.0	20.2 ± 1.0	2.7 ± 3.9
	Jun 2008	25.3 ± 2.8	136.6 ± 17.0	5.1 ± 1.0	7.3 ± 0.2	0.1 ± 0.0	27.2 ± 2.2	0.8 ± 1.4
	Mar 2009	11.6 ± 4.1	77.4 ± 16.2	10.3 ± 1.2	6.6 ± 0.6	0.1 ± 0.0	9.6 ± 2.3	1.1 ± 1.1
	Apr 2009	14.8 ± 3.6	91.5 ± 7.4	8.3 ± 0.6	6.5 ± 0.3	0.1 ± 0.0	16.2 ± 2.3	1.0 ± 1.3
	May 2009	20.5 ± 2.9	107.1 ± 6.8	7.0 ± 0.9	6.5 ± 0.2	0.1 ± 0.0	21.8 ± 1.5	1.0 ± 1.0
	Jun 2009	24.2 ± 0.8	110.8 ± 7.73	5.0 ± 1.4	6.5 ± 0.1	0.1 ± 0.0	24.4 ± 1.3	0.7 ± 1.0
Delta	Mar 2008	12.3 ± 4.1	203.7 ± 231.3	7.8 ± 1.4	7.4 ± 0.1	0.1 ± 0.2	13.4 ± 1.8	6.0 ± 5.4
	Apr 2008	15.7 ± 2.1	139.9 ± 59.8	6.4 ± 1.6	7.5 ± 0.1	0.1 ± 0.0	16.0 ± 1.6	2.9 ± 5.7
	May 2008	18.9 ± 2.5	133.1 ± 18.6	5.7 ± 0.9	7.5 ± 0.2	0.1 ± 0.0	21.4 ± 4.7	4.3 ± 5.0
	Jun 2008	25.1 ± 2.3	155.5 ± 19.4	5.0 ± 0.8	7.3 ± 0.2	0.1 ± 0.0	28.8 ± 5.7	1.3 ± 1.3
	Mar 2009	12.5 ± 6.2	89.1 ± 13.5	10.1 ± 1.3	6.9 ± 0.3	0.1 ± 0.0	9.9 ± 2.1	1.9 ± 1.5
	Apr 2009	14.2 ± 4.0	96.1 ± 11.7	7.8 ± 0.4	6.5 ± 0.3	0.1 ± 0.0	16.3 ± 2.4	1.7 ± 1.6
	May 2009	21.0 ± 4.1	116.7 ± 7.8	6.9 ± 0.5	6.6 ± 0.2	0.1 ± 0.0	22.2 ± 1.6	1.6 ± 1.2
	Jun 2009	24.8 ± 1.3	114.8 ± 29.5	4.9 ± 1.3	6.5 ± 0.2	0.1 ± 0.0	25.6 ± 0.9	1.3 ± 1.3
Sound	Mar 2008	12.1 ± 3.3	1,779.8 ± 1,140.4	8.8 ± 1.7	7.8 ± 0.3	1.3 ± 0.7	12.6 ± 1.6	12.0 ± 2.2
	Apr 2008	15.8 ± 1.7	642.2 ± 966.4	7.9 ± 2.1	7.6 ± 0.1	0.4 ± 0.6	15.9 ± 2.2	9.7 ± 4.3
	May 2008	19.7 ± 1.5	408.0 ± 490.0	6.4 ± 0.8	7.6 ± 0.1	0.3 ± 0.3	20.5 ± 1.0	10.7 ± 8.8
	Jun 2008	25.5 ± 1.9	835.6 ± 643.7	5.4 ± 0.8	7.4 ± 0.2	0.4 ± 0.3	26.9 ± 1.7	4.3 ± 2.1
	Mar 2009	12.1 ± 6.5	1,464.7 ± 842.3	10.9 ± 0.8	7.0 ± 0.4	1.2 ± 0.7	8.9 ± 2.5	2.3 ± 1.7
	Apr 2009	16.3 ± 2.1	174.0 ± 270.6	8.7 ± 0.7	6.6 ± 0.2	0.1 ± 0.1	16.7 ± 2.2	3.1 ± 1.9
	May 2009	20.9 ± 4.6	791.0 ± 984.5	8.6 ± 1.0	6.9 ± 0.3	0.4 ± 0.5	22.0 ± 2.4	3.0 ± 0.7
	Jun 2009	26.0 ± 1.1	646.5 ± 713.8	6.4 ± 1.3	6.8 ± 0.3	0.3 ± 0.3	26.2 ± 0.3	1.7 ± 1.1

1.2 m/s, and currents were most frequently from the west. Generally, wind speeds were less than 10.0 m/s and were typically from the south or southwest. The wind speed in the Sound (6.4 ± 5.5 m/s) was significantly higher ($F_{2, 94} = 13.69$, $n = 97$, $P < 0.001$) than in the River (1.7 ± 2.2 m/s) and Delta (2.8 ± 2.8 m/s) areas. The depth at the River (4.8 ± 0.7 m) stations was significantly higher ($F_{2, 94} = 85.44$, $n = 97$, $P < 0.001$) than at the Delta (3.2 ± 0.6 m) and Sound (3.3 ± 0.3 m) stations (Table 5).

Zooplankton Abundance and Taxonomic Composition

Zooplankton abundances were highly variable. Mean ± SD zooplankton abundances (number/m^3) were not significantly different ($t = –1.47$, df = 95, $n = 97$, $P = 0.144$) between 2008 (7,214 ± 8,048) and 2009 (9,774 ± 11,967). Area had a significant ($F_{2, 94} = 12.98$, $n = 97$, $P < 0.001$) effect on zooplankton abundance, the Sound area having a significantly higher abundance (16,547 ± 14,678) than the River (4,934 ± 3,806) and Delta (4,647 ± 2,846) areas. There were no clear

TABLE 4. Comparison between the values (means ± SDs) of environmental parameters in 2008 and 2009 in the lower Roanoke River and Albemarle Sound.

Variable	2008	2009	*t*	*P*
Air temperature (°C)	18.3 ± 5.3	18.0 ± 6.0	0.30	0.765
Conductivity (μS)	389.9 ± 593.3	270.0 ± 479.9	1.09	0.280
Dissolved oxygen (mg/L)	6.5 ± 1.5	7.9 ± 2.0	–3.74	<0.001
Flow (m/s)	0.1 ± 0.1	0.2 ± 0.1	–1.54	0.128
pH	7.5 ± 0.2	6.7 ±0.4	16.11	<0.001
Precipitation (mm)	2.5 ± 2.9	3.0 ± 2.0	–0.91	0.367
Salinity (‰)	0.2 ± 0.4	0.1 ± 0.3	0.84	0.401
Water temperature (°C)	19.4 ± 5.8	18.1 ± 6.1	0.95	0.344
Wind (m/s)	5.2 ± 5.1	1.7 ± 1.3	4.49	<0.001

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TABLE 5. Mean values of environmental variables in the three sampling areas in the lower Roanoke River and Albemarle Sound. Means with common letters are not significantly different at the 0.5 level according to the Ryan–Einot–Gabriel–Welch procedure.

	Area		
Environmental variable	River	Delta	Sound
Current velocity (m/s)	0.1 y	0.1 y	0.2 z
Depth (m)	4.8 z	3.2 y	3.3 y
Dissolved oxygen (mg/L)	7.4 z	6.8 z	7.7 z
pH	7.0 y	7.0 y	7.3 z
Salinity	0.1 y	0.1 y	0.3 z
Water temp (°C)	18.5 z	19.1 z	18.8 z
Wind speed (m/s)	1.7 y	2.8 y	6.4 z

temporal patterns in any area, so the years were evaluated separately. The abundances in the Sound were the most variable, with the widest range. Even though overall abundances were significantly higher in the Sound, the lowest observed abundance in any area was in the Sound at week 20 in 2008 (935 ± 496). The highest abundance occurred in week 12 (33,384 ± 47,621). In 2009, the lowest abundances were once again in the later part of the sampling season, occurring at week 21 (2,710 ± 466). The peak abundances in the Sound occurred the following week and were the largest observed during the study (51,816 ± 52,092). Temporal patterns were more consistent in the River. The highest abundances were observed in week 13 in 2008 (13,562 ± 10,797) and 2009 (19,751 ± 25,719). In both years, the lowest values were observed in early summer. The lowest abundances occurred in week 22 in 2008 (1,380 ± 20) and in week 23 in 2009 (1,261 ± 1,430). In the Delta, the 2 years exhibited opposite patterns. In 2008, zooplankton peaked in late June (week 26) with an abundance of 10,672 ± 7,901 and was lowest in March (week 13) with an abundance of 997 ± 598. In 2009, zooplankton abundance was highest in week 11 (12,727 ± 4,235) and lowest in week 24 (1,802 ± 940) (Figure 2).

Zooplankton communities were dominated by five taxa: calanoid copepods, cyclopoid copepods, copepod nauplii, rotifers, and cladocerans. Calanoid and cyclopoid taxa include both copepodite and adult life stages. Several families of cladocerans were identified in this study, including Daphniidae, Bosminidae, Sididae, Chydoridae, and Leptodoridae. These five taxa account for a minimum of 96% of the composition of each area across both years. Some of the less common taxa included ostracods, gammarid amphipods, and harpacticoid copepods.

Zooplankton community structure varied both temporally and spatially. Temporal differences occurred on both monthly and yearly scales. In 2008, monthly changes in composition were observed. In the River, rotifers were dominant in March, representing over 60% of zooplankton. Rotifers were less abundant in April, and cladocerans were the dominant taxa,

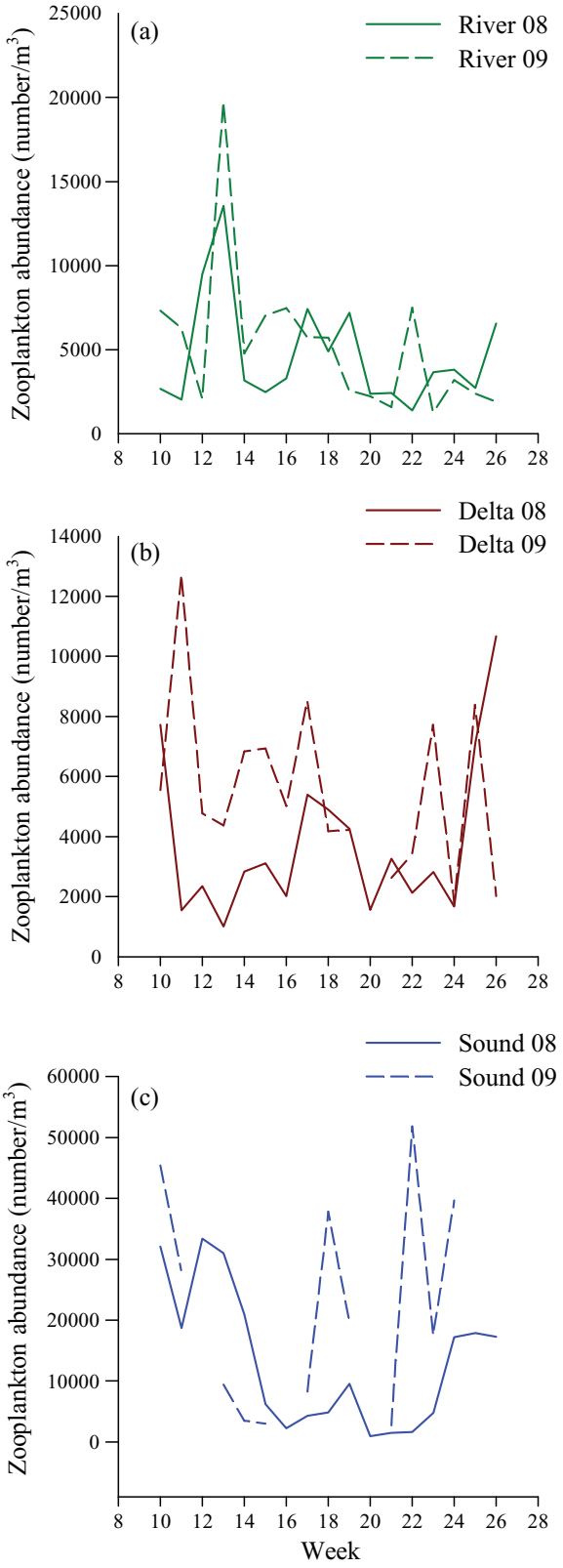


FIGURE 2. Weekly zooplankton abundance in **(a)** River, **(b)** Delta, and **(c)** Sound in 2008 and 2009. Note the differences in the scale of the *y*-axis.

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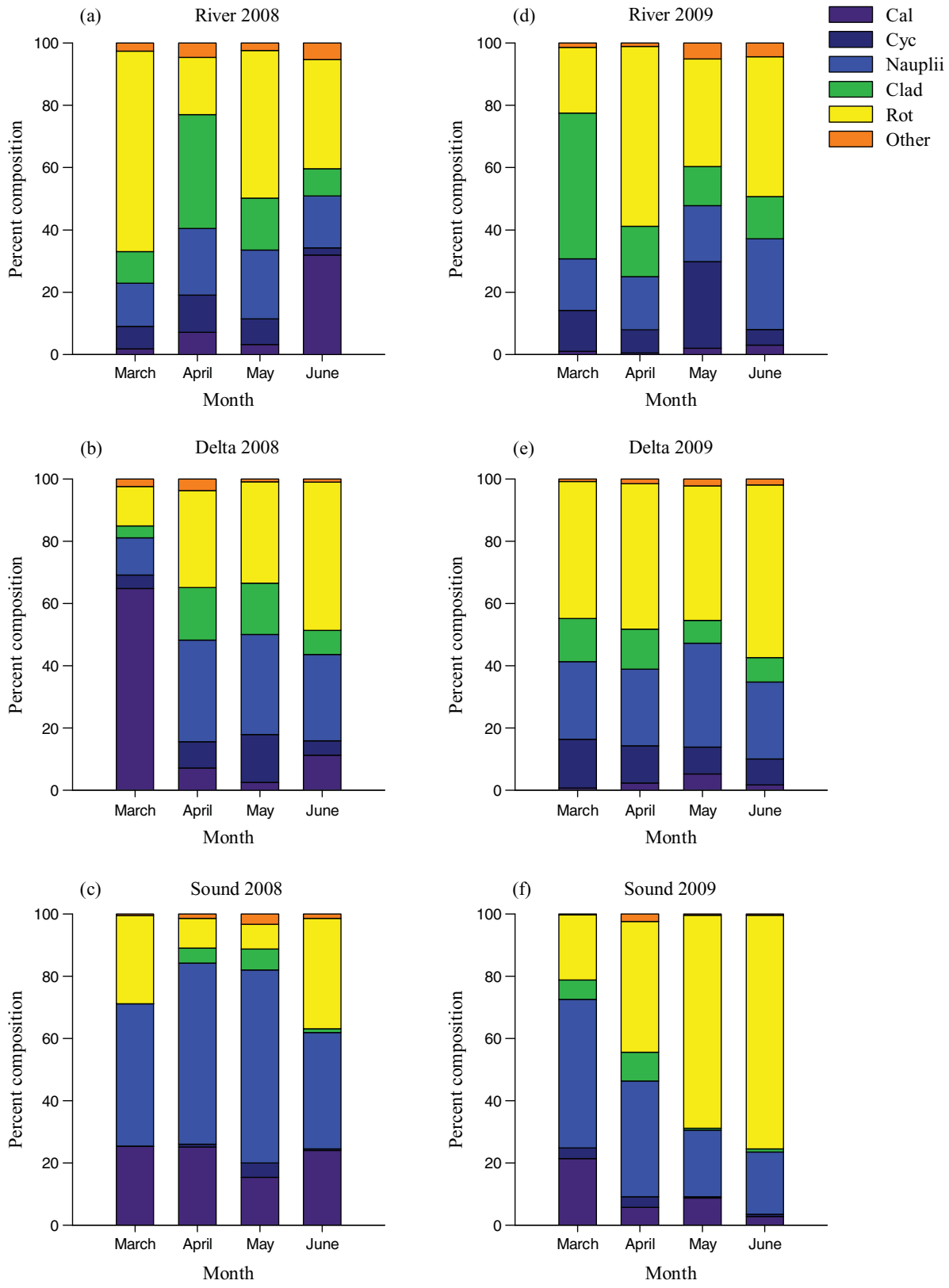


FIGURE 3. Monthly zooplankton composition in **(a)** River, **(b)** Delta, and **(c)** Sound in 2008 and **(d)** River, **(e)** Delta, and **(f)** Sound in 2009. Abbreviations are as follows: Cal = calanoid copepods, Cyc = cyclopoid copepods, Nauplii = copepod nauplii, Clad = cladocerans, and Rot = rotifers.

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representing 37% of zooplankton. In May (47%) and June (36%) rotifers were again dominant. From March through May calanoid copepods were not common in the River, but in June there was an increase in abundance (32%) and they were almost as abundant as rotifers. In the Delta, calanoid copepods (65%) were dominant in March but had low abundances April–June. In April and May, copepod nauplii and rotifers had similar abundances and were the most common taxa. Rotifers accounted for 32% of the composition in April and 33% in May. Copepod nauplii represented 33% in April and 32% in May. Rotifers were the dominant taxa in June (48%). In the Sound, copepod nauplii were the dominant taxa for all of 2008. In 2009, zooplankton communities did not follow the temporal patterns observed in 2008. One of the biggest differences was the increased dominance of rotifers. Rotifers were the dominant taxa, except during March in the River and Sound, and always accounted for at least 35% of the zooplankton (Figure 3).

The zooplankton communities in this study were similar to those in Rulifson et al. (1993) in the River and Delta but differed in the Sound. In the River and Delta, Bosminidae, Daphniidae, and cyclopoid copepods were the most abundant taxa in both studies (when copepod nauplii and rotifers are excluded). In the Sound, the zooplankton community was dominated by Bosminidae, Daphniidae, and unknown cladoceran species in Rulifson et al. (1993). Throughout the multiyear study, cladocerans always accounted for at least 40% of zooplankton in the Sound. In contrast, in this study the zooplankton composition was dominated by calanoid copepods, which made up 76% of the Sound community.

There were also major differences in the River community structure between this study and Coggins (2005). In this study, the main River taxa were rotifers (41%), copepod nauplii (18%), Daphniidae (11%), Bosminidae (11%), and cyclopoid copepods (10%). The zooplankton community in Coggins (2005) was dramatically different. The main difference is the lack of rotifers, which accounted for 0% of the composition in Coggins (2005). The main River zooplankton taxa in Coggins (2005) were cyclopoid copepods (35%), Daphniidae (19%), copepod nauplii (13%), Bosminidae (12%), and Diptera (10%). Daphniidae, Bosminidae, and copepod nauplii had similar prevalences in the zooplankton communities in the two studies. Few insects were collected in this study, composing less than 1% of the community versus 10% in Coggins (2005).

A one-way ANOSIM indicated weak (global $R = 0.298$) but significant ($P = 0.001$) differences in zooplankton composition among the areas (Figure 4). Post hoc comparisons revealed that the River and Delta were not significantly different ($R = 0.054$, $P = 0.13$), while the Sound was significantly different from both the River ($R = 0.527$, $P = 0.001$) and Delta ($R = 0.357$, $P = 0.001$). SIMPER analysis comparing the Sound with both

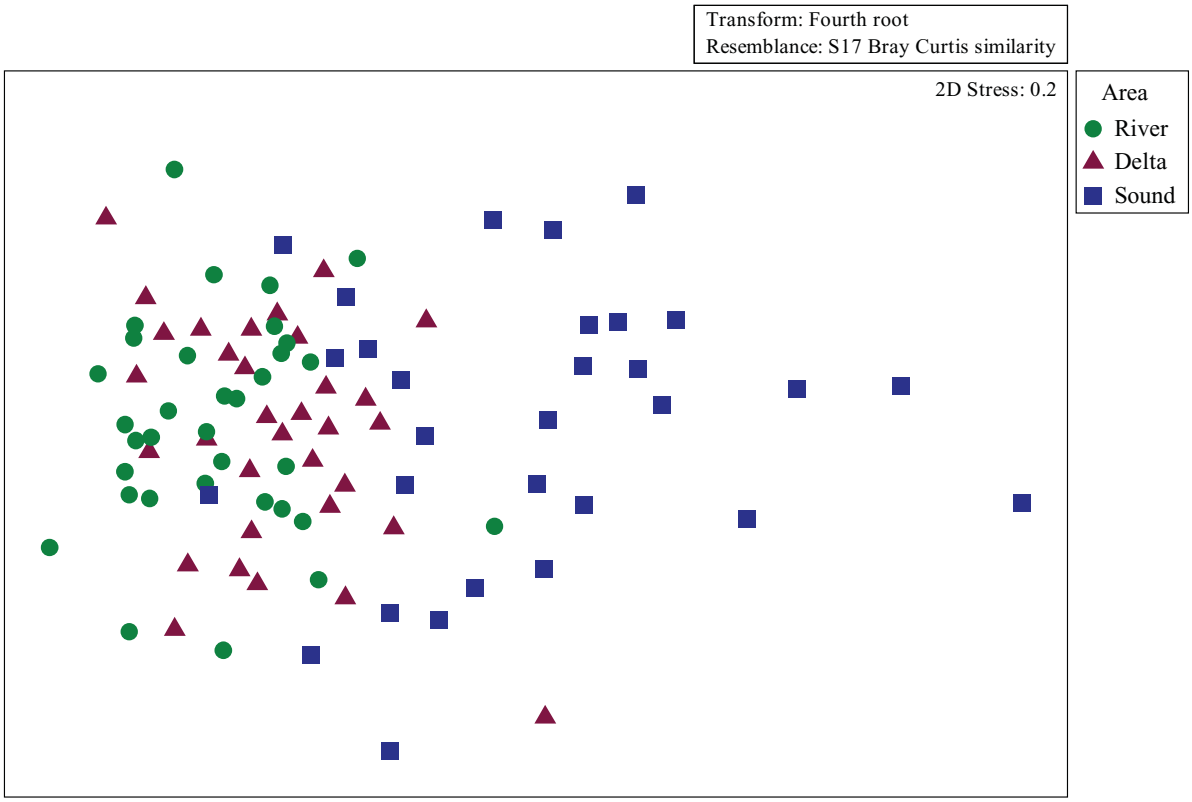


FIGURE 4. Nonmetric multidimensional scaling ordination plot illustrating the similarity among samples in respect to area for zooplankton samples collected in the Roanoke River and Albemarle Sound.

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TABLE 6. SIMPER analysis evaluating the dissimilarity between areas identified as significantly different using ANOSIM. Abundances are fourth-root transformed. The average Bray–Curtis dissimilarity scores are listed as average dissimilarity. Diss/SD identifies how consistently taxa contribute to the dissimilarity. Asterisks identify discriminating taxa. The contribution percentage is the amount of dissimilarity that can be attributed to a taxon.

		Average abundance				
Comparison	Taxa	Sound	Comparison area	Average dissimilarity	Diss/SD	Contribution (%)
Sound and River	Calanoida	5.8	2.9	4.8	1.4	12.9
	Copepod nauplii	8.1	5.2	4.1	1.4	11.1
	Rotifera	7.2	6.2	3.8	1.2	10.3
	Daphniidae	2.2	4.1	2.8	1.3	7.6
	Ostracoda	0.6	2.5	2.8	1.7*	7.6
	Chydoridae	0.7	2.4	2.7	1.7*	7.4
	Bosminidae	3.3	3.8	2.6	1.3	7.0
	Cyclopoida	3.0	4.2	2.5	1.3	6.8
	Harpacticoida	2.5	1.3	2.5	1.4	6.6
	Gammarus spp.	1.5	0.1	2.0	1.1	5.5
	Diptera	0.7	1.8	1.9	1.4	5.3
	Sididae	0.5	0.9	1.4	0.9	3.9
Sound and Delta	Calanoida	5.8	3.3	4.6	1.4	13.4
	Rotifera	7.2	6.0	3.9	1.2	11.5
	Copepod nauplii	8.1	5.6	3.9	1.4	11.4
	Harpacticoida	2.5	1.0	2.7	1.5*	7.9
	Cyclopoida	3.0	4.4	2.6	1.3	7.5
	Chydoridae	0.7	2.0	2.5	1.4	7.2
	Bosminidae	3.3	3.7	2.4	1.3	7.1
	Ostracoda	0.6	1.8	2.1	1.4	6.1
	Daphniidae	2.2	3.3	2.1	1.2	6.1
	Gammarus spp.	1.5	1.0	2.1	1.2	6.0
	Diptera	0.7	1.4	1.7	1.2	5.0
	Sididae	0.5	0.8	1.4	0.8	4.0

the River and Delta showed the level of dissimilarity among comparisons. The Bray–Curtis average dissimilarity was 36.9 in the Sound–River comparisons and 34.0 in the Sound–Delta comparisons. Calanoid copepods contributed the most to the differences between the Sound and other areas. Copepod nauplii and rotifers were also important to the dissimilarity among the areas, ranking as the second- and third-highest contributors. Their order differed between the Sound–River and Sound–Delta comparisons. In the Sound–River comparisons, Ostracoda and Chydoridae were identified as discriminating taxa. Harpacticoid copepods were the discriminating taxa in the Sound–Delta comparisons (Table 6).

ALOSINE ABUNDANCE AND DISTRIBUTION

Differences in alosine abundance (number/100 m^3) and composition were observed between sampling years. Abundances were significantly higher in 2009 (30.8 $\pm$ 149.8; $P \leq 0.001$) than in 2008 (4.1 $\pm$ 20.9). Alewives (28.5%) were the most abundant alosine in 2008, followed closely by blueback herring (26.7%) and hickory shad (24.4%). In 2009, blueback herring were dominant, accounting for 64.8% of the larval alosines collected. Hickory shad (23.8%) were the second most abundant species. American shad were the least common alosine in both years.

Weekly patterns were different between the two years. Larval alosines were collected during all weeks of sampling in 2008 but were not present the first week of sampling in 2009. Blueback herring were the first species collected in both years. Alewives were observed earlier in 2008 and were the second species collected. In 2009, hickory shad were the second species collected. American shad larvae were not common (Figure 5). Mean alosine abundances were significantly different ($P \leq 0.001$) among the three sampling areas. The highest abundances were observed in the River (21.0 $\pm$ 127.6), with successively lower ones in the Delta (7.4 $\pm$ 35.5) and Sound (4.6 $\pm$ 24.8). This trend was consistent across both years and for all species.

There are no clear patterns when species abundance is analyzed on temporal and spatial scales. Alewife abundances were highest in the River during March of both years. In 2008 alewife

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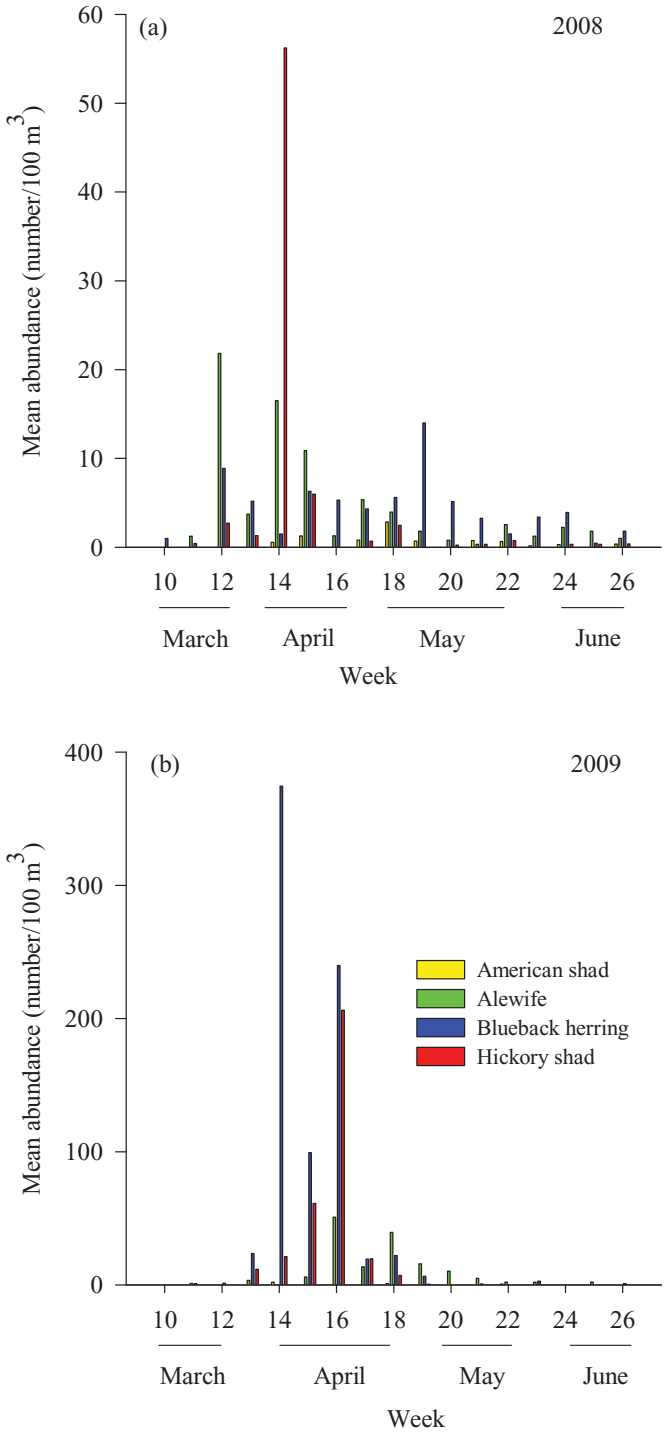


FIGURE 5. Mean weekly abundance of larval alewives, blueback herring, and hickory shad in **(a)** 2008 and **(b)** 2009 in the Roanoke River and Albemarle Sound. Note the differences in the scale of the *y*-axis.

abundances peaked in March, whereas in 2009 peak abundances were observed in April. In the Sound, alewives were present in all months in 2008 but were absent in March of 2009. Blueback herring abundances were consistent in 2008 across all months and within each area. There was an increase in blueback herring abundances in 2009 and abundances varied across the months. In all areas, abundances peaked in April and were at least twice as large as those observed in March. After peaks in April, there was a sharp decrease in abundances for the remaining months. In 2009, the abundance patterns for hickory shad were similar to those for blueback herring. Hickory shad abundance also increased in 2009 with peaks in April. In 2008, monthly hickory shad trends were similar in the River and Delta, with highest abundances in April (Figure 5).

ALOSINE MOUTH GAPE ANALYSIS AND PREY SIZE ESTIMATES

Larval alosine notochord lengths ranged from 3 to 14 mm, with 97% of larvae having lengths of 7 mm or less. Over 90% of the alewives, blueback herring, and American shad were between 4 and 7 mm, with lengths exceeding 8 mm rarely being collected. American shad larvae had the narrowest length distribution and were typically larger, with all but one larva being 7 mm or more (Figure 6). The mean $\pm$ SD length was similar between alewives (4.7 $\pm$ 1.2 mm) and blueback herring (4.6 $\pm$ 1.0 mm). The mean length of hickory shad (6.5 $\pm$ 1.0 mm) was larger than those of alewives and blueback herring. American shad larvae had the largest mean length (8.7 $\pm$ 2.1 mm)

For all species, there was a strong linear relationship between mouth gape and notochord length (Figure 7). A one-way ANCOVA indicated that there were significant differences ($F_{4,459} = 2{,}115.0$, $P < 0.001$) in mouth gape size among species. American shad larvae had the largest mean mouth gape (mean, 0.67 mm), followed by alewives (0.57 mm), blueback herring (0.56 mm), and hickory shad (0.53 mm). The alewife and blueback herring mouth gapes did not significantly differ from each other, while all other comparisons were significantly different.

For mouth gapes calculated at a 90° opening, the estimated prey size at yolk sac absorption was similar among alewives, blueback herring, and hickory shad larvae but larger for American shad larvae. At 6 mm, alewives and blueback herring have a 400-μm mouth gape with an estimated maximum prey size of 200 μm. Hickory shad at 7 mm have a 430-μm mouth gape and an estimated prey size of 215 μm. At 9 mm, American shad have a mouth gape that is twice as wide at first feeding, 820 μm with a maximum prey size of 410 μm (Figure 7).

The zooplankton size distribution was estimated for the most abundant taxa. These taxa included calanoid and cyclopoid copepods, copepod nauplii, rotifers, Daphniidae, and Bosminidae, which accounted for 98% of total abundance. Mean zooplankton body lengths and widths are plotted in Figure 8. Based on these measurements, zooplankton taxa were separated into two size-classes. The smaller taxa included rotifers and copepod nauplii, with remaining taxa comprising the larger size-class. Along the length axis the two groups begin to separate at 200 μm, and across the width axis they begin to separate at approximately 120 μm. Based on mouth gape estimates, copepod

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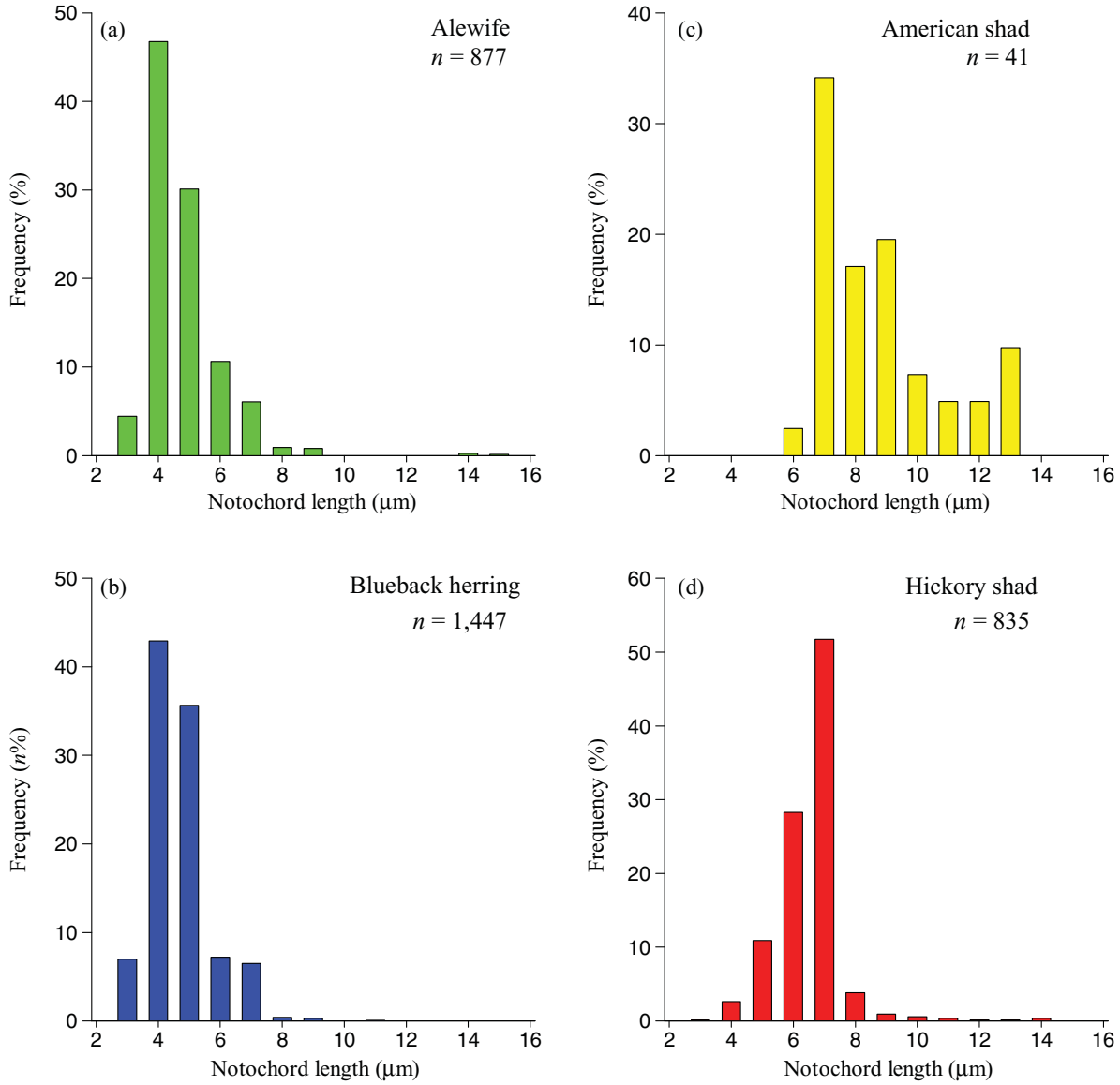


FIGURE 6. Frequency distributions of four alosine species based on notochord length. Note the differences in the scale of the *y*-axis.

nauplii and rotifers are size appropriate for alewives, blueback herring, and hickory shad larvae at first feeding. Bosminidae and cyclopoid copepods at the low end of their size distributions could also serve as prey for these species. American shad larvae have a wider potential prey choice, including rotifers, copepod nauplii, cyclopoid copepods, and Bosminidae. Smaller Daphniidae and calanoid copepods are also within the estimated prey size range of American shad.

LARVAL ALOSINE AND ZOOPLANKTON SPATIAL AND TEMPORAL OVERLAP

There was a high degree of spatial and temporal overlap between larval alosine and zooplankton abundances in all three sampling areas. Weekly mean alosine abundances were generally less than 1/m^3. Mean weekly zooplankton abundances, including all taxa, ranged from 934 to 51,815/m^3. When the most suitable prey (copepod nauplii and rotifers) were evaluated separately, weekly abundances ranged from 283 to 51,034/m^3. There was always overlap between larval alosines and size-appropriate prey. Spatially, the highest overlap occurred in the Sound, where zooplankton abundances were the highest and larval alosine abundances were the lowest. Higher weekly peaks occurred in the River than in the Delta, but there was still overlap in zooplankton and larval alosines in all areas (Figure 9).

DISCUSSION

Zooplankton Trends

The zooplankton abundances in all three areas were significantly higher than those reported in previous work and more

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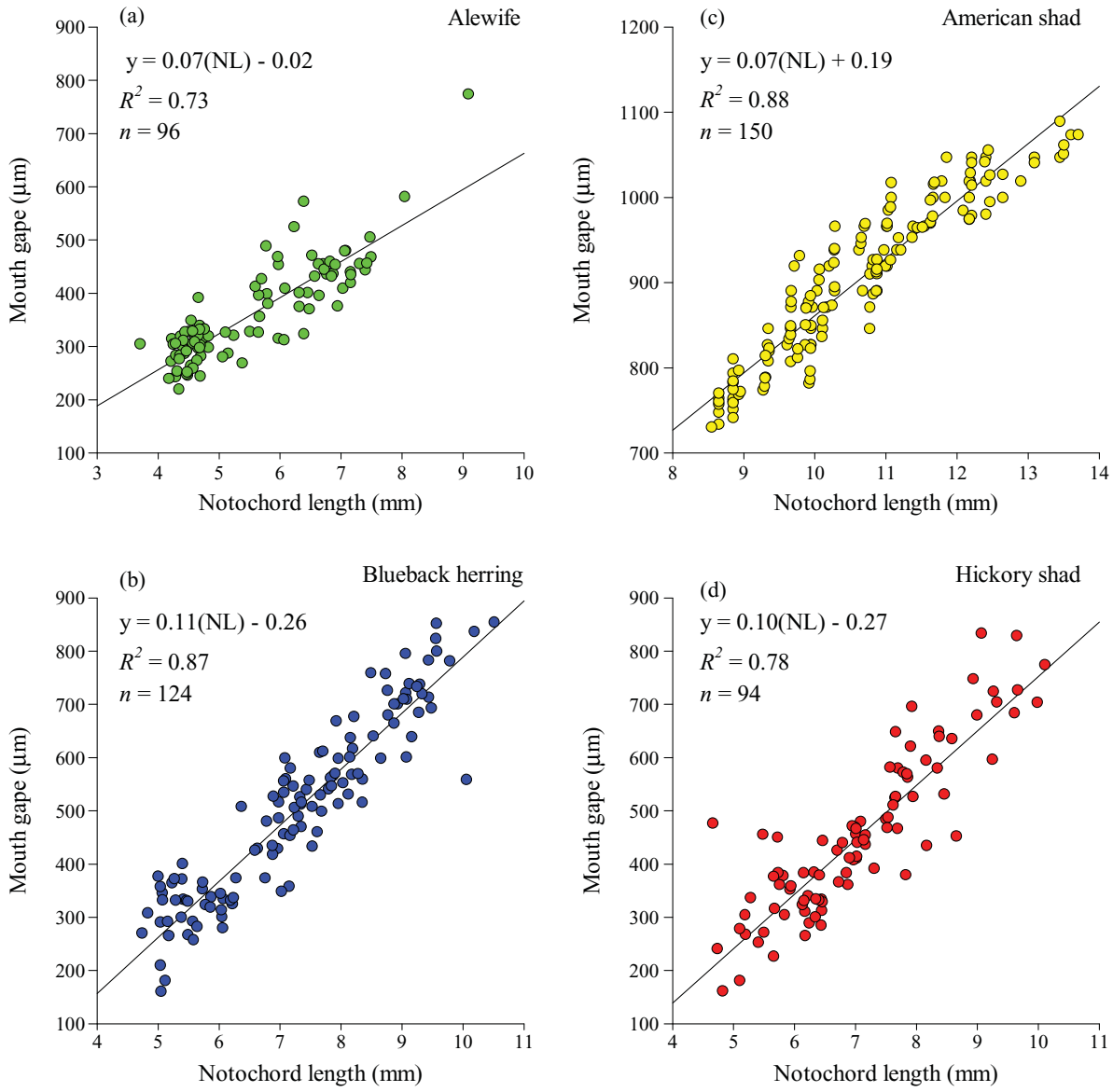


FIGURE 7. Mouth gape regression models for **(a)** alewives, **(b)** blueback herring, **(c)** American shad, and **(d)** hickory shad. The models were calculated with the mouth open at 90°. Note the differences in the scales of the both axes.

similar to those observed in other North Carolina coastal river systems (Table 1). Many factors could be attributing to this increase in zooplankton abundance. Rulifson et al. (1993) measured phytoplankton concentrations in the Roanoke River and Albemarle Sound and found that they were large enough to support much higher zooplankton abundances than were observed. The authors hypothesized that various environmental factors were responsible for these abundances. The values for dissolved oxygen, salinity, temperature, turbidity, and pH were similar between this study and Rulifson et al. (1993). The main difference between the two studies was the mesh size used to collect zooplankton. Rulifson et al. (1993) used a 250-µm-mesh net and we used a 90-µm-mesh net. We attempted to correct for the differences in the sizes of plankton by removing rotifers and copepod nauplii from our analysis. These two groups are typically less than 200 µm and are not efficiently collected in a 250-µm-mesh net (Thorp and Covich 2001). Even after removing the smaller plankton from the analysis the zooplankton concentrations and composition were still different between the two studies (Binion 2011). These differences are most likely simply due to the difference in mesh size.

Significant differences in zooplankton composition and abundance were observed between the Sound and the other areas sampled. SIMPER analysis showed that calanoid copepods were the taxa most responsible for these differences. Calanoid copepods were more abundant in the Sound and comprised a higher

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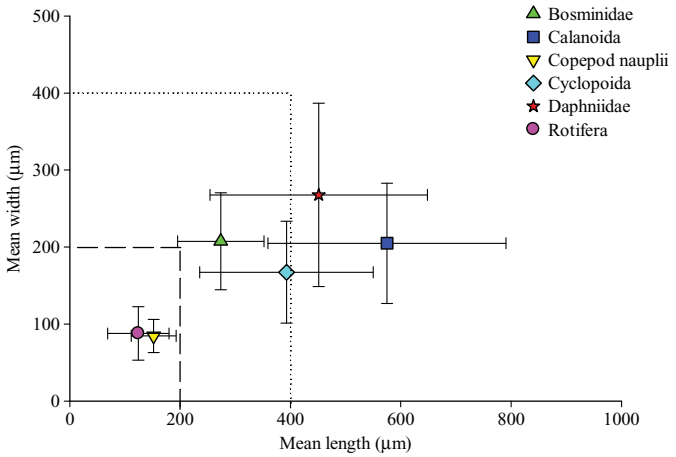


FIGURE 8. Body lengths and widths for the most common zooplankton taxa. Values are means ± SDs. The dashed lines represent the maximum prey size for larval alewives, blueback herring, and hickory shad at first feeding. The dotted lines represents the maximum prey size for larval American shad at first feeding.

percentage of the zooplankton. Higher abundances of copepod nauplii and rotifers also contributed to the Sound's being significantly different. In the River and Delta, higher abundances of cyclopoid copepods, cladocerans, and ostracods also contributed to the significant differences from the Sound (Table 6). Salinity was significantly higher in the Sound and these differences in composition may be explained by the salinity preferences of the different taxa.

The results of the one-way MANOVA suggest that the majority of the variance ($\eta^2 = 89\%$) in zooplankton trends and the environment can be explained by the effect of area. Significant differences in zooplankton abundance and composition were not observed between the River and Delta, despite the strongly significant MANOVA. Differences between the two areas were more pronounced in 2008, but in 2009 rotifers were consistently dominant and the composition was similar between the areas (Figure 3). It is possible that the surge of rotifers is masking the differences between the River and Delta. In the Rulifson et al. (1993) study, Delta zooplankton abundances were significantly higher in the River.

Larval Prey Size and Mouth Gape

Differences in mouth gape in coexisting larvae allow for a reduction in interspecific competition (Crecco and Blake 1983; Bremigan and Stein 1994; Makrakis et al. 2008). In this study, alewife and blueback herring mouth gapes were not significantly different from each other but all comparisons with American shad and hickory shad showed significant differences. Our mouth gape calculations for blueback herring and hickory shad are comparable to those calculated by Crecco and Blake (1983). When mouth gape size at yolk sac absorption was calculated, alewife, blueback herring, and hickory shad had similar mouth gapes and American shad larger ones. Within this system, there appears to be interspecific prey competition among those first three alosine species.

Zooplankton abundances were higher in this study than in those previously conducted and there was a high ratio of zooplankton to larval alosines. This high overlap was observed even when only taxa that could be consumed by all alosine species, copepod nauplii and rotifers, were included in the analysis. Competition between larval alewives, blueback herring, and hickory shad may be reduced by the large volume of available prey. Studies evaluating diet niche overlap found dissimilarities among larval fish with similar mouth gapes (Gaughan and Potter 1997; DeVries et al. 1998; Makrakis et al. 2008). It has been hypothesized that when zooplankton abundances are high, competition is reduced and larval fish with similar mouth gapes exhibit different feeding behaviors and selectivity that is afforded by high prey availability (Gaughan and Potter 1997).

The maximum larval fish mouth gape is typically estimated for 90°, but some larval fish are capable of opening their mouths to 120° (Riley et al. 2009). The mouth morphology of hickory shad is different from that of the other alosine species. The lower jaw of hickory shad slopes at an angle more than 40°, while the lower jaws of the other species slope at angles less than 40° (Walsh et al. 2005). This difference in morphology may allow hickory shad to open their mouths at larger angles, enabling them to consume larger prey at smaller sizes. This could be one of the reasons that hickory shad populations have remained more stable than those of the other alosines. In the Roanoke River and Albemarle Sound, previous zooplankton abundances have been significantly lower (Rulifson et al. 1993; Coggins 2005). During this time, American shad and river herring stocks were below historical levels despite increased regulations and management. Hickory shad stocks have declined slightly but are not considered depleted (ASMFC 2007; Greene et al. 2009; NCDMF 2010). If hickory shad are capable of feeding at a larger mouth gape opening, this may reduce competition between them and river herring. At first feeding, hickory shad may be capable of consuming larger prey items than predicted in this study, allowing them to feed on prey resources not available to river herring. Feeding studies need to be conducted with hickory shad to determine whether they are capable of opening their mouths at larger angles.

The hypothesized mouth gape and maximum prey size estimates for alewives and blueback herring are supported by diet analyses of larvae collected in the Roanoke River and Albemarle Sound (Figure 7). For larvae of all sizes, copepod nauplii and rotifers accounted for 85% of stomach contents. First-feeding larvae feed primarily on copepod nauplii, rotifers, small Bosminidae, and small cyclopoid copepods, as predicted by the mouth gape models. Throughout ontogeny, there was little change in the diet composition of larval alewives and blueback herring, but as larval size increased prey size increased as well. American and hickory shad larvae were not included in the stomach content analysis (Riley 2012).

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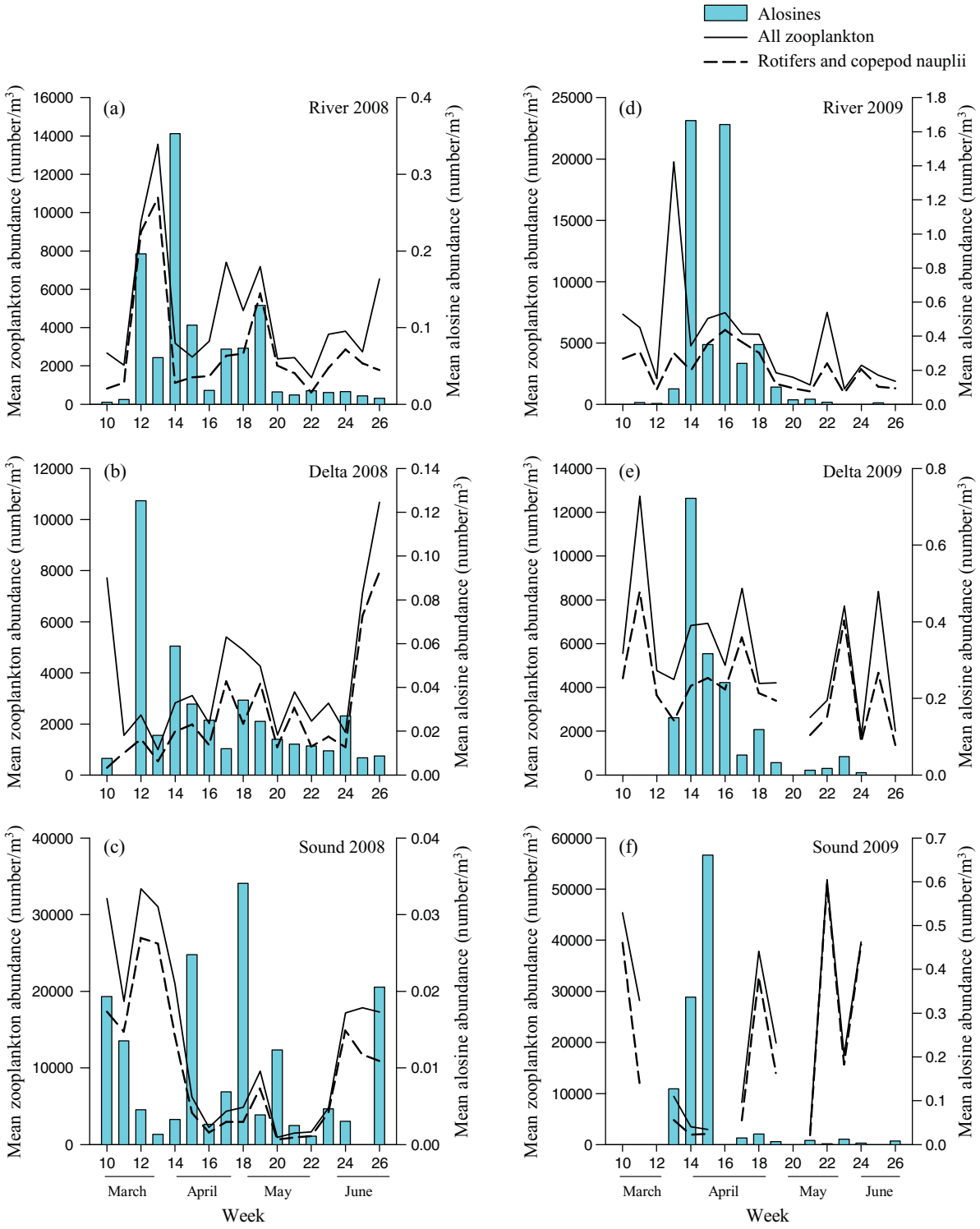


FIGURE 9. Zooplankton and larval alosine spatiotemporal overlap in **(a)** River in 2008, **(b)** Delta in 2008, **(c)** Sound in 2008, **(d)** River in 2009, **(e)** Delta in 2009, and **(f)** Sound in 2009. Note the differences in the scale of the *y*-axes (left and right).

LARVAL ALOSINE AND ZOOPLANKTON SPATIAL AND TEMPORAL OVERLAP

Across both years in all areas, there was a high amount of overlap between zooplankton and larval alosines. Laboratory studies examining growth and survival are typically conducted with larval alosine and zooplankton abundances higher than those observed in this study. In Riley et al. (2012), larval American shad growth and survival were evaluated at three

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different prey abundances equivalent to 1,000, 50,000, and 500,000/m^3. These abundances reflect all zooplankton and not just size-appropriate prey. Larval American shad were stocked at abundances equivalent to 4,000 individuals/m^3. Growth was significantly higher in treatments with the two highest abundances, but survival rates were similar in all three. Except for one observation in the Sound, zooplankton abundances never exceeded 50,000, but alosine abundances were typically less than 1/m^3. In Johnson and Dropkin (1995), larval American shad were stocked at the equivalent of 8,000/m^3 and *Artemia* nauplii were stocked at 500,000 and 1,000,000/m^3. Growth was not different between the two treatments, but survival was higher in the treatment with larger nauplii abundances. If zooplankton abundance is divided by larval shad abundance, the ratio of zooplankton to fish is 125:1 for both studies (Table 2). Ratios this low were never observed during this study, even when zooplankton abundances were calculated with rotifers and copepod nauplii only (Figure 9). This suggests that the larval alosines in this system are not food limited and that all three areas are suitable as larval alosine nursery habitat based on prey availability.

The reasons for the declining recruitment of river herring in Albemarle Sound remain unclear. The variability in the annual recruitment of alewives in the Great Lakes has been linked to spawning stock size, salmonid predation, and winter severity (Henderson and Brown 1985; Madenjian et al. 2005). River herring are included in the diet of large estuarine predators, including striped bass *Morone saxatilis*. However, predation by striped bass is not the cause of poor recruitment in Albemarle Sound (Tuomikoski et al. 2008). The failure of alosine stocks to recover in this system is not the result of food limitation during early life history. Recruitment failure may be related to the demographics of the spawning population or other factors operating on multiple scales.

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REFERENCES

Able, K. W., and M. P. Fahay. 1998. The first year in the life of estuarine fishes in the middle Atlantic Bight. Rutgers University Press, New Brunswick, New Jersey.

ASMFC (Atlantic States Marine Fisheries Commission). 2007. American shad stock assessment report for peer review volume III. ASMFC, Washington, D.C.

Balcer, M. D., N. L. Korda, and S. I. Dodson. 1984. Zooplankton of the Great Lakes: a guide to the identification and ecology of the common crustacean species. University of Wisconsin Press, Madison.

Beasley, C. A., and J. E. Hightower. 2000. Effects of a low-head dam on the distribution and characteristics of spawning habitat used by striped bass and American shad. Transactions of the American Fisheries Society 129:1316–1330.

Bilkovic, D. M., J. E. Olney, and C. H. Hersner. 2002. Spawning of American shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis)* in the Mattaponi and Pumunkey rivers, Virginia. U.S. National Marine Fisheries Service Fishery Bulletin 100:632–640.

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, North Carolina.

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

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 31:913–922.

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

Clarke, K. R., and R. N. Gorley. 2006. PRIMER version 6: user manual/tutorial. PRIMER-E, Plymouth, UK.

Clarke, K. R., and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition. PRIMER-E, Plymouth, UK.

Coggins, 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.

Copeland, B. J., R. G. Hodson, S. R. Riggs, and J. E. Easley Jr. 1983. The ecology of Albemarle Sound, North Carolina: an estuarine profile. U.S. Fish and Wildlife Service FWS-OBS-83/01.

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.

Crecco, V. A., and M. Gibson. 1990. Stock assessment of river herring from selected Atlantic coast rivers. Atlantic States Marine Fisheries Commission, Special Report 19, Washington, D.C.

Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Advances in Marine Biology 26:249–293.

De Lafontaine, Y., and W. C. Leggett. 1987. Effect of container size on estimates of mortality and predation rates in experiments with macrozooplankton and larval fish. Canadian Journal of Fisheries and Aquatic Sciences 44: 1534–1543.

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

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

Fulton, R. S. 1984. Distribution and community structure of estuarine copepods. Estuaries 7:38–50.

Gaughan, D. J., and I. C. Potter. 1997. Analysis of diet and feeding strategies within an assemblage of estuarine larval fish and an objective assessment of dietary niche overlap. U.S. National Marine Fisheries Service Fishery Bulletin 95:722–731.

Gotceitas, V., V. Puvandendran, 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.

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Gray, J., and B. J. Copeland. 1989. The Albemarle-Pamlico estuarine system, preliminary technical analysis of status and trends. North Carolina Department of Environment, Health, and Natural Resources, Albemarle-Pamlico Study Report 89-13A, Raleigh.

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 Number 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.

Henderson, B. A., and E. H. Brown Jr. 1985. Effects of abundance and water temperature on recruitment and growth of alewife (*Alosa pseudoharengus*) near South Bay, Lake Huron, 1954–82. Canadian Journal of Fisheries and Aquatic Sciences 42:1608–1613.

Hjort, J. 1914. Fluctuation in the great fisheries of northern Europe reviewed in the light of biological research. Rapports et Procès-Verbaux des Réunions du Conseil Permanent International pour l'Exploration de la Mer 1:5–38.

Houde, E. D. 1994. Differences between marine and freshwater larvae: implications for recruitment. ICES Journal of Marine Science 41:91–97.

Houde, E. D. 2008. Emerging from Hjort's shadow. Journal of Northwest Fishery Science 41:53–70.

Hunter, J. R. 1981. Feeding ecology and predation of marine fish larvae. Washington Sea Grant Program, Seattle.

Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto.

Johnson, J. H., and D. S. Dropkin. 1995. Effects of prey density and short term food deprivation on the growth and survival of American shad larvae. Journal of Fish Biology 46:872–879.

Johnson, J. H., and D. S. Dropkin. 1996. Feeding ecology of larval and juvenile American shad (*Alosa sapidissima*) in a small pond. Journal of Applied Ichthyology 12:9–13.

Konrad, C. E., II. 1998. A flood climatology of the lower Roanoke River basin in North Carolina. Physical Geography 19:15–34.

Leach, S. D., and E. D. Houde. 1999. Effects of environmental factors on survival, growth, and production of American shad larvae. Journal of Fish Biology 54:767–786.

Leggett, W. C., and E. DeBlois. 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages. Netherlands Journal of Sea Research 32:119–134.

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

Makrakis, M. C., K. Nakatani, A. Bialetzki, L. C. Gomes, P. V. Sanchess, and G. Baumgartner. 2008. Relationship between gape size and feeding selectivity of fish larvae from a neotropical reservoir. Journal of Fish Biology 72: 1690–1707.

Mallin, M. A. 1991. Zooplankton abundance and community structure in a mesohaline North Carolina estuary. Estuaries 14:491–488.

Madenjian, C. P., T. O. Höök, E. S. Rutherford, D. M. Mason, T. E. Croley II, E. B. Szalai, and J. R. Bence. 2005. Recruitment variability of alewives in Lake Michigan. Transactions of the American Fisheries Society 134:218–230.

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

Moser, M. L., A. M. Darazsdi, and J. R. Hall. 2000. Improving passage efficiency of adult American shad at low-elevation dams with navigation locks. North American Journal of Fisheries Management 20:376–385.

NCDENR (North Carolina Department of Environment and Natural Resources). 2000. Basinwide assessment report Roanoke River basin. NCDENR, Raleigh.

NCDMF (North Carolina Division of Marine Fisheries). 2010. Stock status of important coastal fisheries in North Carolina 2010. NCDMF, Morehead City.

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

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

Paradis, A., P. Pepin, and J. Brown. 1996. Vulnerability of fish eggs and larvae to predation: review of the influence of the relative size of prey and predator. Canadian Journal of Fisheries and Aquatic Sciences 53:1226–1235.

Pearsall, S. H., B. J. McCrodden, and P. A. Townsend. 2005. Adaptive management of flows in the lower Roanoke River, North Carolina, USA. Environmental Management 35:353–367.

Puvanendran, V., K. Salies, B. Laurel, and J. A. Brown. 2004. Size-dependent foraging of larval Atlantic cod (*Gadus morhua*). Canadian Journal of Zoology 82:1380–1389.

Riley, K. L. 2012. Recruitment of estuarine-dependent alosines to the lower Roanoke River and Albemarle Sound, North Carolina. Doctoral dissertation. East Carolina University, Greenville, North Carolina.

Riley, K. L., S. M. Binion, and A. S. Overton. 2012. Estimating the food requirements and prey size spectra of larval American shad. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 4:228–238.

Riley, K. L., C. R. Weirich, and D. Cerino. 2009. Development and growth of hatchery-reared larval Florida pompano (*Trachinotus carolinus*). U.S. National Marine Fisheries Service Fishery Bulletin 107:318–328.

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 Carolina Wildlife Resources Commission, Completion Report for Project F-27, Greenville.

Street, M. W., A. S. Deaton, W. S. Chappell, and P. D. Mooreside. 2005. North Carolina coastal habitat protection plan. North Carolina Department of Environment and Natural Resources, Division of Marine Fisheries, Morehead City.

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.

Thorp, J. H., and A. P. Covich. 2001. Ecology and classification of North American freshwater invertebrates, 2nd edition. Academic Press, New York.

Tuomikoski, J. E. P., J. Ruderhausen, J. A. Buckle, and J. E. Hightower. 2008. Effects of age-1 striped bass predation on juvenile fish in western Albemarle Sound. Transactions of the American Fisheries Society 137:324–339.

Turingan, R. G., J. L. Beck, J. M. Krebs, and J. D. Licamele. 2005. Development of feeding mechanics in marine fish larvae and the swimming behavior of zooplankton prey: implications for rearing marine fishes. Pages 119–132 *in* C. S. Lee, P. J. O'Bryen, and N. H. Marcus, editors. Copepods in aquaculture. Blackwell Scientific Publications, Ames, Iowa.

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.

Winslow, S. E. 1985. North Carolina anadromous fisheries management program. Anadromous Fish Conservation Act, Project AFCS-22, Morehead City, North Carolina.

Yufera, M., and M. J. Darias. 2007. The onset of exogenous feeding in marine fish larvae. Aquaculture 268:53–63.

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