Abstract

RECRUITMENT OF ESTUARINE-DEPENDENT ALOSINES TO ROANOKE RIVER AND ALBEMARLE SOUND, NORTH CAROLINA

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The deleterious effects of dams on alosine populations are widely documented in many rivers along the Atlantic coast. Alterations to the natural hydrologic regime can disrupt spawning, egg dispersal, and recruitment of larvae to nursery habitats. The goal of this study was to investigate the ecological processes that influence recruitment of river herring (blueback herring *Alosa aestivalis* and alewife *A. pseudoharengus*) to nursery habitats within lower Roanoke River and Albemarle Sound, North Carolina. It was hypothesized that variability in abiotic conditions and fluctuations in food abundance could structure nursery habitat and severely restrict recruitment. Ichthyoplankton and zooplankton samples were collected concurrently March through June 2008-09 at 19 stations, within three areas: River, Delta, and Sound. Significant spatial and temporal differences were observed in the distribution of river herring. Abundances (number/100m^3 ± SD) were significantly higher in 2009 (30.8 ± 149.8) than in 2008 (4.1 ± 20.9). Across both years, abundances within the River (21.0 ± 127.6) were significantly higher than those in Delta (7.4 ± 35.4) and Sound (4.6 ± 24.8). Yolk-sac larvae were prevalent throughout samples (32%); however, larvae collected were predominantly preflexion stage (66%). Fish ages ranged from 4 to 19 days after hatch. Growth rates were similar for blueback herring (0.29 ±

0.16 mm/d) and alewife (0.30 ± 0.14 mm/d). Growth estimates were indicative of habitat quality and suggested riverine habitats supported the highest growth rates. Mortality estimates for blueback herring (0.76 ± 0.23 per day) were significantly higher than mortality estimates for alewife (0.64 ± 0.17 per day). High mortality for both years was probably related to larval dispersal and advective loss. Larvae do not appear to be food limited in this system as indicated by diet analyses and the spatiotemporal overlap between river herring and zooplankton. Decreasing zooplankton abundance was correlated with larval abundance and suggests foraging by larval alosines could negatively alter the structure of the zooplankton community. Diets varied little with early ontogeny and the smallest taxa (copepod nauplii and rotifers) accounted for over 85% of the diet. Because of a high-level of dietary overlap, intraspecific and interspecific competition is substantial for anadromous alosines. The result of long-term data analysis (1984 – 2009) for larval and juvenile river herring confirms Roanoke-Albemarle stocks are in decline. Larval fish abundance was negatively affected by spring river flow ($r^2 = 0.62$). High flows (> 300 m^3/s) resulted in larval advection from Roanoke River. Spring river flow was positively correlated with juvenile abundance ($r = 0.95$) and best recruitment of juveniles occurs in years with moderate spring river flow (141 – 311 m^3/s).

RECRUITMENT OF ESTUARINE-DEPENDENT ALOSINES TO ROANOKE RIVER AND ALBEMARLE SOUND, NORTH CAROLINA

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Kenneth Lee Pickrell Riley

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DEDICATION

This dissertation is dedicated to my wife Kelly, for sharing my triumphs and disappointments and who has put up with me for reasons not always obvious. This work is a culmination of our life long dedication to learning about all things aquatic.

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CHAPTER 1: INTRODUCTION

Estuaries are uniquely productive ecosystems that are characterized by high levels of primary production that form the basis of a food web and support a high biomass of fish. Estuaries provide high-quality habitat that serves as feeding and nursery grounds for many economically important fisheries (Houde and Rutherford 1993; Able 2005). It is estimated that 75% of recreational and commercial fish species in the United States are dependent on estuaries (Chambers 1992). These species include residents (species that spend the entire life cycle in estuaries) and transients (species that spend only a portion of their lives there) whose spatial and temporal use of the estuarine environment varies with size and age.

By simple definition estuaries are highly variable because they serve as a zone of transition between rivers and coastal oceans. The resulting landscape fluctuates with seasons and periodic changes in the environment. Fishes that are estuarine-dependent must be tolerant of frequent changes in temperature, salinity, oxygen concentrations, turbidity, and variability in physical conditions (Day et al. 1989). While estuarine waters are highly productive, the diversity of fishes is relatively low as a consequence of the physiological stress of living in an environment with fluctuations in water quality (Costanza et al. 1993). Because younger fish are generally more tolerant of fluctuations in environmental conditions, it has long been hypothesized that estuaries primarily function as nurseries (Holliday 1991; Able and Fahay 1998; Beck et al. 2001).

Despite recent advances in fishery science (*e.g.,* ecological approaches to management), an understanding of recruitment dynamics remains a critical, unresolved problem (Houde and Hoyt 1987; Houde 2008). Efforts to quantify and determine the causes for annual variation in recruitment have been difficult (Shepherd et al. 1990). The early life history of fishes is a critical

stage that can significantly affect year-class strength. It is estimated that relatively small variations in mortality rates, growth rates, or stage duration in the early life of fishes can have fluctuations that vary by one or two orders of magnitude in recruitment (Houde 1994). Because recruitment level is primarily determined during early life stages, evaluating the influence of physical and biological conditions on survival and growth of fish larvae has become a fundamental paradigm in fishery science (Sissenwine 1984; Rose 2000).

Early Life History of Estuarine Fishes

Life history traits that influence estuarine use include residence time, habitat use, and size of arrival in the estuary (Table 1.1). With a few notable exceptions, the majority of estuarine-dependent fish produce large numbers of eggs that hatch into small pelagic larvae. Because of their buoyant nature, larvae are easily transported with river flow, water currents, and tidal action (Norcross and Shaw 1984; Hettler and Hare 1998). The maternal contribution to eggs and larvae largely determines the availability of yolk reserves for endogenous nutrition and the size of larvae at first feeding (Blaxter and Hempel 1963; Hunter 1981). Starvation is a threat to most fish larvae during the transition to exogenous nutrition. It is generally accepted that a large size "*bigger-is-better hypothesis"* at onset of feeding is an advantage, because larger larvae are able to swim faster and search a greater volume of water for food (Litvak and Leggett 1992).

Survival of eggs and larvae varies among species and conditions, but often is in the range of 30-90% per day (Houde 1989). There are several "*critical periods*" that have been described as bottlenecks in larval production (Hjort 1914; Hjort 1926; Cushing 1972). These periods include: (1) spawning and fertilization of eggs; (2) hatching; (3) first feeding; (4) yolk and oil globule exhaustion; (5) swim bladder inflation; (6) change in diet; (7) transition to gill gas exchange, and

(8) transformation (Tucker 1998). Houde (1987) presents an interesting conceptualization of the critical periods and bottlenecks contributing to high rates of mortality in the early life history of estuarine-dependent fishes (Figure 1.1). The survivorship curve shows that density-dependent processes (predation, competition, disease) are increasingly important for late-stage larvae and juveniles.

Food Limitations and Prey Availability in Estuaries

For fish larvae, estuaries are dynamic habitats where the availability prey varies spatially and temporally with light and primary productivity. Habitats with an abundance of appropriate-sized prey provide conditions for optimal growth and survival. Most larvae drift passively with plankton in the prevailing modes of circulation (Hare and Cowen 1997). Feeding is largely opportunistic and dependent on prey availability (Hjort 1914; Cushing 1990). Copepods, small naupliar stages of crustaceans, and insect larvae, particularly chironomids, are the typical food of most estuarine fishes. Phytoplankton are often observed in the guts of larvae, but it is thought that phytoplankton are an incidental food source and artifact of foraging (May 1970).

Zooplankton abundance is variable and fluctuates with seasonal cycles that peak during spring and summer. Low densities and patchy distributions are often observed in the estuarine environment. The *match-mismatch hypothesis* was proposed by Cushing (1972; 1990) to focus on temporal overlaps between peaks in larval abundance and seasonal peaks in food supply (Figure 1.2). The hypothesis was the first to propose a mechanism that would explain why successful first-feeding might vary annually. This hypothesis suggests that fish production is optimized when spawning and larval production is synchronous with zooplankton production. In contrast to the *critical period hypothesis* originally proposed by Hjort (1914) that states that

suitable prey must be available during the first-feeding stage of larvae, the *match-mismatch hypothesis* suggests that a continuous supply of suitable prey are required throughout the larval period to optimize growth and survival for recruitment success. Both Hjort's and Cushing's hypotheses speculate about the role environmental variability plays in primary production.

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 width is a critical dimension limiting consumption (Hunter 1981; Pepin and Penney 1997; Hufnagl and Peck 2011). Studies supporting this finding propose that optimal prey width ranges from 30% to 50% of mouth gape (Shirota 1970; Cunha and Planas 1999). Thus, as fish grow their preference for larger prey sizes increases in a steady proportion to their own growth (Munk 1992; Puvanendran et al. 2004).

Predation on Fish Eggs and Larvae

In the past thirty years, a wealth of research has been published on the hypothesized role of predation on eggs and larval stages of estuarine fishes (Bailey and Houde 1989; Leggett and Deblois 1994). Many carnivorous species within the major groups of pelagic invertebrates, including Medusae, Siphomedusae, Ctenophora, Chaetognatha, Cephalopoda, Amphipoda, Euphausiacea, and Copepoda, as well as juvenile and adult fishes, have been reported to feed on fish eggs and larvae (Hunter 1981; Bailey and Houde 1989). Most empirical evidence of predation has been gathered from descriptions of the food habits of predators (Bailey and Duffy-Anderson 2010). These studies indicate that eggs and young larvae (*i.e.*, individuals before first feeding) are particularly susceptible to predation. Because eggs and yolk-sac larvae rely on endogenous nutritional reserves, it is generally assumed that predation is the largest source of

mortality for these early life stages. Few studies have quantified larval mortality as a result of predation (Leggett and Deblois 1994; Wirtz 2012).

The *bigger-is-better hypothesis*, proposed by Anderson (1988), suggests that large, fast growing larvae and cohorts are less susceptible to predation because of their larger body size and increased swimming ability. Similarly, the *stage duration hypothesis* proposed by Chambers and Deblois (1994) postulates that mortality is low for larvae with a short early life history (less than 30 d) and fast specific growth rate. Using mesocosm and microcosm experiments with capelin larvae *Mallotus villosus*, Litvak and Leggett (1992) tested both hypotheses with discriminant (fish) and nondiscriminant (jellyfish) predators. There was no difference in the probability of capture of small versus large larvae of the same age. However, contrary to the *bigger-is-better hypothesis*, when the predators were presented a disparate mixture of small and large larvae, the probability of death was higher for large larvae.

Larval Growth and Environmental Variability

The theory that year-to-year changes in environmental conditions may be one of the underlying causes of recruitment variability among estuarine-dependent species (Sissenwine 1984; Rose 2000). Larval distributions are largely structured by abiotic gradients that include salinity, temperature, dissolved oxygen, and turbidity (Martino and Able 2003; North and Houde 2003b; Martino and Houde 2010).

In many estuaries, salinity is the major environmental gradient that spans the estuarine landscape. Most estuarine species are tolerant of a wide range of salinities; however, extreme fluctuations (*e.g.*, floods, tropical storms) can have lethal effects for larvae sensitive to metabolic costs of osmotic and ionic regulation. For most larvae, salinity is a directive factor signaling

migration between freshwater and the marine environment (Wooten 1999). Movement along a salinity gradient will affect the metabolic costs of osmoregulation, but movement may lead to abundant food resources so that higher rates of feeding can compensate for metabolic costs (Greenwood 2007).

Temperature can play a central role in influencing movements and distribution of larvae. If food is not a limiting factor, then temperature is the most important factor controlling growth and metabolism (Gibson and Johnston 1995). The high specific heat of water means that changes in temperature are relatively slow allowing time for fish to migrate and seek refuge from temperature extremes. Despite the higher temperatures that can occur in shallow habitats and lagoons, mortality caused by temperature extremes has rarely been observed (Gibson 1994). In contrast species overwintering in estuaries face certain constraints and possible sources of mortality either as a result of low temperatures or a loss of energy reserves (Hare and Cowen 1997).

Oxygen is probably the most important abiotic lethal factor for fish (Wooten 1999). Many estuaries worldwide experience episodic events of hypoxia or anoxia. For larvae, these conditions can lead to high rates of mortality because fish cannot escape hypoxic conditions. The Chesapeake Bay, Virginia, is a classical drowned-river-valley estuarine system that experiences episodic periods of hypoxia. The early life history of the naked goby *Gobiosoma bosc* is well studied in the Chesapeake, and goby larvae frequently succumb to hypoxic conditions significantly affecting recruitment (Breitburg 2002). The effects of hypoxia are well studied with juvenile and adult fishes (Eby and Crowder 2004), but there exists a paucity of information on how hypoxic conditions affect larvae. Additional research is also needed to address larval mortality or metabolic costs associated with sublethal oxygen concentrations.

Turbid waters are considered beneficial for larvae and offer significant contributions to recruitment. Turbid waters aggregate prey so larvae can feed optimally and avoid predation. Turbidity reduces predation pressure by limiting prey detection (Chesney 1989), suspends particles and nutrients supporting primary production (Simenstad et al. 1994), concentrates zooplankton production (Boynton et al. 1997), and retains fish and invertebrate larvae (North and Houde 2001; North and Houde 2003a). While a range of abiotic factors affect the growth and survival of fish larvae, it is probably the complex interaction of salinity, temperature, dissolved oxygen, and turbidity that contributes the most to fish growth and survival.

Research Objectives

The goal of my dissertation was to investigate the ecological processes that influence recruitment of anadromous alosines (American shad *Alosa sapidissima*, blueback herring *A. aestivalis*, and alewife *A. pseudoharengus*) to nursery habitats in lower Roanoke River and Albemarle Sound. Data were collected from short-term laboratory experiments and long-term field observations. A major finding of this project is that populations of American shad are severely depressed in Roanoke River despite fisheries management and stock enhancement. During this study, the collection of American shad larvae was rare (N = 68; ≤ 0.5% of *Alosa* spp.). Most analyses described herein focus on recruitment of blueback herring and alewife, which are also referenced as river herring.

This dissertation is presented in six chapters. In Chapter 2, the seasonal distribution, abundance, growth, and mortality of larval blueback herring and alewife were examined within three areas of lower Roanoke River and Albemarle Sound. Analysis is based on sampling ichthyoplankton and water quality at 19-stations from March through June of 2008 and 2009.

All sampling was conducted at night. Spatial differences in water quality were evaluated using analysis of variance (ANOVA). Nonparametric statistics were used to compare distributions of blueback herring and alewife. Growth and mortality were studied by means of daily increments in sagittal otoliths. Growth based on marginal increment analysis was evaluated at different temporal scales. The distribution of back-calculated hatch dates was used to temporal variability in spawning. Larval distributions and habitat use patterns were examined using a one-way multiple analysis of variance (MANOVA) and principal components analysis (PCA).

In Chapter 3, the feeding ecology and condition of larval blueback herring and alewife were examined within three areas of lower Roanoke River and Albemarle Sound. Ichthyoplankton, zooplankton, and water quality samples were collected at weekly intervals from March through May 2009. Sampling was conducted during the day and at night to test for diel effects related to feeding, larval abundance, and zooplankton abundance. Larvae were measured and weighed for use in determination of condition indices. A number of metrics were used to assess recent feeding activity. Data from gut contents and zooplankton sampling were used to evaluate prey selectivity and ontogenetic shifts in feeding. Spatial differences in larval fish and zooplankton abundance were evaluated using ANOVA. Primer-E was used to conduct analysis of similarity (ANOSIM) and similarity percentages (SIMPER) analysis. These routines were used to assess patterns in zooplankton community structure and study dietary overlap between blueback herring and alewife. Results from ANOSIM and SIMPER were corroborated and visualized using a non-metric, multidimensional scaling (NMDS) ordination plot.

In Chapter 4, laboratory experiments were conducted to evaluate the effect of prey density on growth and survival of American shad. Larvae were reared from 11 to 20 days after hatching in five treatments: (1) no food; (2) low (1 prey/L), which simulated prey densities in Roanoke

River; (3) medium (50 prey/L), which simulated prey densities typical of coastal watersheds; (4) high (500 prey/L), and (5) Artemia spp. (500 prey/L). Survival, length-specific growth rates, and weight-specific growth rates were determined for larvae grown under different feeding regimes. Data from gut contents were used to evaluate prey selectivity and feeding peculiarities. A model for mouth gape and feeding ability was developed for American shad.

In Chapter 5, long-term datasets were used to quantify the relationship between larval recruitment in Roanoke River and juvenile recruitment in Albemarle Sound. Larval and juvenile fish were collected and summarized with environmental covariates for three periods (1984 – 1991; 2001 – 2003; 2008 – 2009). Annual growth and mortality rates for river herring larvae and juveniles were estimated using a length-based ageing method and catch-curve analysis. ANOVA was used to statistically detect differences between growth and mortality between years. Temporal patterns of larval and juvenile abundance were examined relative to variation in water temperature, precipitation, wind speed and direction, and river discharge. Stepwise multiple regression analysis was used to describe the relationship among river herring abundance, river flow, and wind.

Chapter 6 summarizes and highlights the main findings of this research. This work has extended our knowledge of recruitment dynamics for anadromous alosines. It is my intention that the results of this dissertation will have broad utility in fisheries management and can be used for restoration of American shad and river herring in the coastal rivers of North Carolina.

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Table 1.1. Pattern and variety in development and early life history of estuarine-dependent species. Adapted from Tucker (1998) and Blaxter (1988).

Common name	Species	Egg diameter (mm)	Time to hatch (d)	Length at hatch (mm)	Age at first feeding (d)	Age at transformation (d)	Length at transformation (mm)
Atlantic herring	*Clupea harengus*	1.20	15.0	7.0	4	168	40
Atlantic menhaden	*Brevoortia tyrannus*	1.61	1.7	3.2	3	65	27
Atlantic silverside	*Menidia menidia*	1.10	10.0	5.2	4	32	25
Bay anchovy	*Anchoa mitchilli*	0.80	1.2	2.0	2	33	20
Blueback herring	*Alosa aestivalis*	1.00	2.1	3.5	5	25	30
Bluefish	*Pomatomus saltarix*	1.00	2.0	2.1	4	28	21
Coho salmon	*Oncorhychus kisutch*	5.25	60.0	21.0	40	71	45
Gulf flounder	*Paralichthys albigutta*	1.02	3.1	2.6	4	56	25
Mullet	*Mugil cephalus*	0.94	1.4	2.8	3	28	45
Mummichog	*Fundulus heteroclitus*	1.88	21.0	8.0	0	20	25
Red drum	*Sciaenops ocellatus*	0.95	1.0	1.7	3	35	25
Spotted seatrout	*Cynscion nebulosus*	0.77	1.0	1.0	2	37	38
Striped bass	*Morone saxatilis*	3.60	2.0	3.0	5	37	30

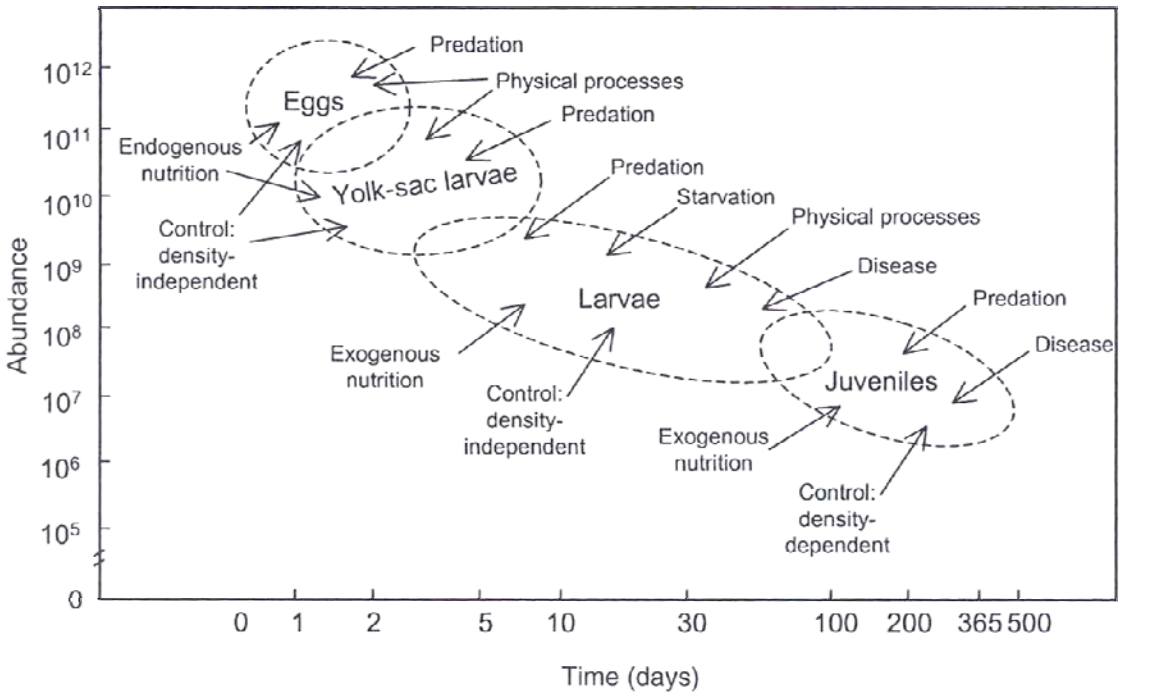

Figure 1.1. A conceptualization of the recruitment process in fishes including factors that affect mortality and growth. Log_{10} scales are used on both axes. Reproduced from Houde (1987).

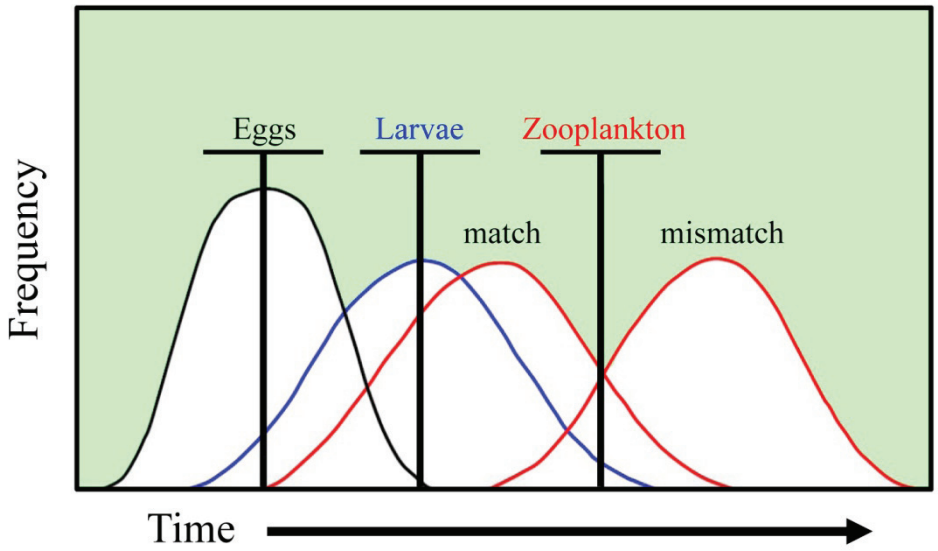

Figure 1.2. A conceptualization of the match-mismatch hypothesis as proposed by Cushing (1990). The production of zooplankton reflects seasonal processes mediated by physical conditions. Temporal variability in spawning or low stock abundance can result in fish production that does not coincide with an abundance of zooplankton.

CHAPTER 2. SPATIOTEMPORAL VARIABILITY IN RECRUITMENT OF BLUEBACK HERRING AND ALEWIFE LARVAE IN ROANOKE RIVER AND ALBEMARLE SOUND, NORTH CAROLINA

Abstract

The deleterious effects of dams on anadromous alosine populations are widely documented in many rivers along the Atlantic coast. Alterations to the natural hydrologic regime can disrupt spawning, egg dispersal, and recruitment of larvae to nursery habitats. The goal of this study was to investigate the ecological processes that influence recruitment of blueback herring *Alosa aestivalis* and alewife *A. pseudoharengus* to nursery habitats within lower Roanoke River and Albemarle Sound, North Carolina. Ichthyoplankton sampling was conducted in 2008 and 2009 at 19 stations, within three areas: River, Delta, and Sound. Larval blueback herring and alewife were collected from March through June and backcalculated hatchdates based on age of fish indicated spawning occured throughout the same period. Differences in larval abundance (number/100 m^3 ± SD) were observed between sampling years. In 2008, blueback herring (5.1 ± 12.8) and alewife (5.1 ± 16.1) abundances were not significantly different. In 2009, blueback herring abundances (39.2 ± 140.7) were significantly higher from alewife abundances (9.4 ± 32.4). Blueback herring recruitment was highest when water temperatures were 16.2 ± 2.5 °C. Alewife recruitment was highest when water temperatures were 17.2 ± 2.3 °C. The distribution of fish showed progressive downstream dispersal of larvae. Larval abundances varied significantly among the three sampling areas. Blueback herring abundances were highest in the River (35.6 ± 147.4) and Delta (14.6 ± 46.5) as compared to the Sound (7.9 ± 28.2). Similarly, alewife abundances were highest in the River (12.9 ± 37.7) and Delta (5.1 ± 11.8) as compared

to the Sound (1.5 ± 5.6). Yolk-sac larvae were prevalent throughout samples (32%) and were collected within all areas. Larvae collected were predominantly preflexion stage (66%) ranging from 5.0 to 10.0 mm standard length. Growth rates were similar for blueback herring and alewife, but revealed slightly different growth patterns for each area. Growth estimates were indicative of habitat quality and suggested riverine habitats supported the highest growth rates. High mortality for both years was probably related to larval dispersal and advective loss. Evidence from this study provides some support for review of reservoir operation and dam discharge guidelines. Adjustment of river flow may be an important consideration for restoring alosine habitat.

Introduction

Populations of anadromous alosines along the Atlantic Coast have generally declined in recent years as indicated by decreased commercial and recreational harvests and widespread fishing regulations and closures. Blueback herring *Alosa aestivalis* and alewife *A. pseudoharengus*, collectively managed and marketed as river herring, once supported large fisheries in Albemarle Sound, North Carolina (Chestnut and Davis 1975; Taylor 1992). These fishes were among the first commercially exploited species in the region and historical records indicate river herring were a major export of colonial settlements (Hightower et al. 1996). Fishing in coastal rivers and estuaries has always been seasonal and coincides with late-winter and spring spawning migrations through estuaries and coastal rivers. For over a century, Albemarle Sound contributed the majority (≥ 98%) of commercial landings in North Carolina and fishing for river herring seemed as if it was an industry with boundless frontiers (NCDMF 2007). Despite a high level of exploitation, river herring stocks remained relatively stable until

the 1970s. Populations supporting annual landings in excess of 5 million kg have since declined to less than 1% of their historical abundance (Figure 2.1).

By the end of the 20th century, the cumulative impacts of damming and altering flow regimes in rivers, habitat loss, pollution, overfishing, invasive species, and climate change caused a marked decline of anadromous fishes along the Atlantic coast (Limburg and Waldman 2009). Blueback herring and alewife populations in Albemarle Sound collapsed in the 1970s and 1980s because of successive recruitment failures, largely attributable to high mortality during the early life stages and a chronic decline in egg production (Rulifson 1994; Carmichael 1999; Greene et al. 2009). Mechanisms regulating recruitment and year-class strength are complex. They often operate on different spatiotemporal scales and are mediated by seasonal selective processes.

Alternating between strong and weak year-classes, river herring exhibit distinct patterns in abundance reflected in the fishery age structure (Messieh 1977; Jessop 1990; Carmichael 1999). Historically, periods of abundance are ascribable to the frequency and distribution of large year-classes. Adult stock abundance plays a role in controlling and regulating recruitment, but the relative size and contribution of parental stocks does not guarantee the emergence of a strong year-class (Walton 1987; Wood and Austin 2009). For most anadromous clupeids, year-class strength is established during the larval and juvenile stages and is correlated with variability in growth and mortality within nursery habitats (Crecco et al. 1983; Crecco and Blake 1983). Because growth and mortality are linked processes, variability in either process during the early life history can have fluctuations that vary by one or two orders of magnitude in recruitment (Houde 1994; Houde 2008).

Blueback herring and alewife are notorious for exhibiting wide fluctuations in larval abundance (Meador et al. 1984; Cooke and Leach 2003; O'Gorman et al. 2004). Many factors,

including physics, ontogeny, food abundance, and predation affect the distribution and dispersal of larvae (North and Houde 2004). While it is unclear how physical and biological factors interact, much of the variation in abundance results from changing hydrographic and climatic conditions (Rose 2000). River flow, river discharge, and wind-driven circulation within the estuary are responsible for transport of eggs and larvae. Convergence and mixing of currents is important for retention of larvae in nursery habitats. Proximate factors such as water temperature, salinity, pH, dissolved oxygen, and turbidity influence growth and survival of larvae (Bigelow and Schroeder 1953; Edsall 1970; Loesch and Lund 1977; Kellogg 1982). Within nursery habitats, these factors form abiotic gradients that structure larval distributions, concentrate prey resources, and often aggregate predators (Martino and Able 2003; North and Houde 2003).

Habitat loss or deterioration has been identified as a causal factor in 73% of fish species extinctions in North America (Miller et al. 1989; Ricciardi and Rasmussen 1999). The importance of classifying and protecting nursery habitats for estuarine-dependent fishes is well established as indicated by voluminous scientific literature, intense debate, and environmental legislation (Able 2005; Kraus and Secor 2005; Kerr et al. 2010). Identification of nursery habitats that contribute a disproportionate (relative to their size) number of individuals to the adult population is especially challenging for anadromous species that traverse freshwater and marine environments during their first year of life (Beck et al. 2001). In general, the distribution of blueback herring and alewife eggs and larvae is not well defined and much of the nursery habitat has not been quantified. Most research has addressed fish at the northernmost latitudes of their range (*e.g.*, Connecticut, Massachusetts) or populations that are not anadromous (*e.g.*, Great Lakes) (Kosa and Mather 2001; Savoy and Crecco 2004; Madenjian et al. 2005).

River herring early life stages are dependent on nursery habitats adjoining the spawning grounds in most coastal river systems (Dovel 1971; Walsh et al. 2005). After spawning, eggs and larvae drift downstream through a variety of lentic (still water) and lotic (moving water) habitats. Retention in specific nursery habitats is mediated by local hydrography, precipitation and weather, and river flow. Eggs and larvae are extremely vulnerable to advection from nursery habitats by seasonal flood events and variable flows within the watershed. While the timing and magnitude of flood events is critically important to stimulate rigorous and widespread spawning of river herring, high flows also serve as a dispersal mechanism transporting larvae downstream to habitats that are often far from the spawning grounds and not well studied.

The goal of this project was to determine the spatiotemporal distribution of larval river herring in the lower Roanoke River and Albemarle Sound during peak periods of larval production (March – June), and to examine how physical properties of Roanoke River and western Albemarle Sound influence age, growth, survival, and retention of larvae. Specifically, we aim to identify nursery habitats that support fast growth and low mortality. These habitats should bolster recruitment and confer a survival advantage to individuals by decreasing the time spent in vulnerable larval stages. This study compliments previous research identifying river herring spawning and nursery habitats in Roanoke River tributaries and flooded swamps located 100 river kilometers (rkm) upstream from the river mouth. (Hayman and Holloman 1996; Peters et al. 1998; Walsh et al. 2005).

Study Area

The Roanoke River is an alluvial river system that originates in the Appalachian mountains of southwest Virginia and flows southeast for over 600 rkm through the piedmont and coastal

plain of North Carolina (Figure 2.2). The river empties into Albemarle Sound at its western end and supplies more than half the total freshwater input to the region (Giese et al. 1985). The average annual discharge is about 225 m^3 per second (cms) (USGS 2011). Since construction of a small dam in the town of Roanoke Rapids, North Carolina in 1895, Roanoke River has been extensively developed for hydroelectric power generation (Coe 1964). A modern hydroelectric dam replaced the original Roanoke Rapids Dam in 1955. With a storage capacity of 9.95×10^7 m^3 and a maximum discharge of 22,000 cms, development of best management practices for reservoir operation and dam discharge became a necessity to prevent significant alteration of the hydrologic cycle and protect the long-term health of the lower river ecosystem.

Roanoke River supports spawning runs for many anadromous species including (ranked by abundance) hickory shad *A. mediocris*, striped bass *Morone saxatilis*, alewife, blueback herring, and American shad *A. sapidissima*. None of the dams constructed along the river have provisions for anadromous fish passage. Spawning migrations are limited to the mainstem of the river and the extensive floodplain consisting of hardwood forests, backwater swamps, oxbow lakes, and small creeks (Zincone and Rulifson 1991). Flows in the lower river (below Roanoke Rapids Dam, 221 rkm) are controlled by coordinated release schedules of upstream dams. Flows are regulated from April through mid-June to provide migratory and spawning cues for striped bass and increase their access to spawning and nursery areas. During striped bass spawning season, water is discharged from Roanoke Rapids Dam to maintain river flow within the range of 167 to 240 cms (Rulifson and Manooch 1990b; Rulifson and Manooch 1990a).

The lower river is characterized by a single main stem (150 to 300 m wide) with a network of small distributaries (50 to 75 m wide) that lead to the delta. The main distributaries include Thoroughfare, Cashie River, and Middle River. The lower Roanoke River is essentially a

freshwater system because of the combination of relatively high outflow, small cross-sectional area, and low salinity in Albemarle Sound (Giese et al. 1985).

Albemarle Sound is a large estuary (1,300 km^2) that forms at the confluence of a group of rivers, including the Roanoke and Chowan. Water is well-mixed and characterized by low salinity (0-2 psu) and high turbidity. Because of its 90-km length and east-west orientation, tides and water flow in Albemarle Sound are influenced to a great extent by prevailing winds and discharge from Roanoke River.

The study area within the lower Roanoke River and western Albemarle Sound was stratified into three areas (*e.g.*, River, Delta, Sound), which were delineated using a geographic information systems database and records of historical sampling programs. Sampling was conducted at fixed stations and followed the riverine gradient from the 22-km reach within the main channel of Roanoke River to the open water of Batchelor Bay, located on the western boundary of Albemarle Sound (Table 2.1; Figure 2.2). Stations were distributed throughout each strata. Stations were selected on the basis of the following criteria: (1) physiographic and biotic characteristics, (2) accessibility for sampling at night, and (3) ability to provide broad scale information on spatiotemporal abundance of alosine larvae.

Methods

Field Sampling Procedures

Water quality and ichthyoplankton samples were collected at weekly intervals from March through June of 2008 and 2009. These months represent the bulk of alosine production in Roanoke River and permit the collection of fish at various stages between hatching, yolk-sac absorption, and juvenile transformation (Rulifson and Overton 2005). Sampling was conducted at night after sunset (1900-0400) because several studies indicate daytime sampling produces

negatively bias abundance estimates (O'Gorman 1984; Höök et al. 2007). Strata and stations were sampled in random order sequence to minimize the variance related to temporal variation inherent to ichthyoplankton communities. Sampling gear efficiencies were assumed to be equal in all areas.

Ichthyoplankton were collected using paired surface pushnets supported from an aluminum frame mount on the bow of a 5.8-m boat. Each net had a 0.5-m square opening and a mouth-to-tail ratio of 1:5. Nets were constructed of 505-µm nitex mesh with a Dacron® collar sewn at the mouth. The net mesh size was selected because it allowed comparative analysis with long-term ichthyoplankton sampling programs and the size prevents excessive clogging of nets with detritus and floating debris (Zincone and Rulifson 1991; Overton and Rulifson 2007). Each net was equipped with a calibrated flowmeter mounted inside the mouth of the net to estimate the volume of water filtered. The surface nets were pushed into the prevailing water current at a uniform speed of 1.5 m/s for 2.0 minutes. Each sample, filtered from 20 to 40 m^3 of water, was condensed and preserved at the site of collection. The contents from one net (left side) were preserved with 95% ethanol for use with age and growth studies. The contents of the second net (right side) were preserved with 5% buffered formalin for use with feeding studies and diet analysis (see Chapter 3).

Several environmental and hydrographic parameters were recorded for each area and station. These parameters were selected based on their relationship with habitat, water quality, and food resources. Air temperature (°C) and wind speed (m/s) were measured using a portable digital anemometer (Skymate Model SM-18, Campbell Scientific, Inc., Logan, UT). Water quality was measured 1 m below the surface and 1 m above the bottom substrate using a multiparameter dissolved oxygen probe (Model 85, YSI, Inc., Yellow Springs, OH). Surface water samples (100

ml) were collected for analysis of pH (Model 98128, Hanna Instruments, Woonsocket, RI) and turbidity (Model DRT15, HF Instruments, Ltd., Bolton, Ontario, Canada). Water flow was measured at each station from an anchored position. Current velocity (m/s) and direction were measured 1 m below the surface using a portable electromagnetic flow meter (FLO-MATE 2000, Marsh-McBirney, Inc., Frederick, MD). Readings were averaged over ten seconds to determine velocity.

To determine long-term trends in water temperature, data loggers were deployed within each region (IBCod Type 22L, Alpha Mach, Inc., Mont St-Hilaire, Quebec, Canada). Temperatures were recorded at 15-min intervals for the duration of the project. Precipitation and air temperature data were obtained from a 2-m weather station located at Tidewater Research Station in Plymouth, North Carolina. The State Climate Office of North Carolina operates the weather station and data are maintained by the National Climatic Data Center (SCONC 2009). Daily water discharge rates were obtained from Roanoke Rapids Dam water monitoring gage, located 4.5 km downstream of the dam and 221 km upstream from the study area (USGS 2011).

Laboratory Processing of Samples

Larval fish

Ichthyoplankton samples were transferred to fresh ethanol within 24 h of collection. Fish larvae were separated from debris, sorted, and counted using a dissecting microscope (Olympus SZX-ILLD100, Tokyo, Japan). Alosines were identified using a variety of larval taxonomic keys and criteria based on external morphological features (Lippson and Moran 1974; Auer 1982; Sismour 1994a; Walsh et al. 2005). Species identifications were confirmed using hatchery-reared reference samples. Intact alosines were identified to species, whereas degraded

fish were classified as either "*Alosa* species" (2% of total) or "river herring" (6% of total) based on length measurements and meristic characters. To determine larval abundance, the catches between the two nets were averaged together. Abundances of larval fish were then standardized to catch per unit effort (CPUE; number of fish sampled per 100 m^3 of water filtered). Abundance estimates within each strata were calculated by averaging the CPUE at each station.

All blueback herring and alewife were initially measured using a dissecting microscope equipped with an ocular micrometer (Olympus SZX-ILLD100, Tokyo, Japan). Notochord lengths (preflexion larvae) and standard lengths (postflexion larvae) were measured to the nearest 0.25-mm, and these lengths will henceforth be referred to as standard length (SL). From each sample preserved in ethanol, a subsample up to 10 alewife and 10 blueback herring were used for precise measurement of length, measurement of gut fullness, and collection of otoliths. Specimens were randomly selected to ensure that observations of age, size, body condition, and recent feeding history were well represented. Larvae were digitally photographed on a glass microslide and using a dissecting microscope at 40-x magnification. Ethanol droplets were frequently added to prevent desiccation of larvae on the microslide. 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 were measured and analyzed using image analysis software (Image-Pro Discovery software version 4.5, Media Cybernetics, Inc., Silver Spring, MD). All morphometric measurements were recorded to the nearest 0.001 mm and calibration errors were maintained at less than 1 μm (≤0.1% of 1 mm). Body lengths were recorded as total

length (TL) and standard length (Snyder 1983). For each larva, gut length and gut fullness were recorded. Gut fullness was measured as presence or absence of food in proportion to the length of the entire alimentary canal.

Otolith preparation and analysis

Accurate aging of individual fish can improve the estimation of population growth rates, age-specific growth, and individual variation in growth and survival. This study carries the explicit assumption that otolith increments are formed daily and they provide a historical record of growth. After each fish was measured, sagittal otoliths were dissected from larvae using tweezers and fine dissecting needles. Larval remains were discarded and the otoliths were washed in ethanol and cleaned of adherent tissues. Otoliths were air dried and mounted on a glass microslide using low-viscosity epoxy resin (DePeX mounting medium, Electron Microscopy Sciences, Fort Washington, PA). All otoliths were mounted prior to independent age determination and marginal increment analysis.

Otoliths were analyzed at 1000-x magnification using a compound microscope (Olympus BH-2 microscope) and oil immersion. As previously described, the microscope was equipped with a high-resolution video camera and computer with image analysis software. Polarizing light and filters were used to improve the contrast of otolith microstructure in digital photographs and allowed increments to be measured precisely. Image analysis was used to measure the radius and diameter of each otolith and its nucleus. Increment widths were measured along the longest axis from the center of the nucleus to the outer edge (Stevenson and Campana 1992). The distance between each pair of consecutive rings was used to estimate daily growth. To estimate age, increments were counted from the nucleus, beginning at the first clearly defined mark

encircling the primordium, to the outer edge of the otolith. Each growth increment showed a common bipartite structure consisting of an incremental zone that appeared light and translucent, and a discontinuous zone that appeared dark and opaque (Secor et al. 1995). Otolith increments were counted blind (no sample information available) on two separate occasions by a single reader. If the difference in increment counts was two increments or less, the average of the two counts was used to estimate age, otherwise, the sample was discarded. A correction factor of 2 days was added to all age estimates to account for the number of days between spawning and first increment formation (Essig and Cole 1986; Sismour 1994b). To compare temporal hatching distributions among areas, hatch dates were calculated by subtracting the estimated age from the date of collection. Ages were predicted for nonaged larvae through the use of species-specific age-length relationships calculated using least-squares regression.

Back-calculations of length-at-age were based on marginal increment analysis and the assumption that there is proportionality between otolith and somatic growth rates (Jones 1992; Campana 2001). The assumption of constant periodicity in otolith formation has been validated in both blueback herring and alewife (Essig and Cole 1986; Sismour 1994b). The back-calculation of length-at-age for each fish was determined using the biological intercept (BI) method (Campana 1990). This method is a modified variation of the Fraser-Lee linear back-calculation model that includes a BI in the model to reduce the influence of variable growth rates in the population (*i.e.*, the growth effect). In this study, the BI method was used because a large proportion of fish were very young or had recently hatched. The BI method was calculated using the equation:

$$L_i = L_c + (L_c - L_0) \times \frac{(O_i - O_c)}{(O_c - O_0)} \quad (1)$$

where L is fish length at age i (L_i), at the BI (L_0) and at capture (L_c), and O is otolith radius at age i (O_i), at the BI (O_0), and at capture (O_c). We assumed that the increment closest to the nucleus was formed at the day of hatching and the average length of fish at hatch (L_0) was 3.5 mm SL (Auer 1982; Sismour 1994a). The otolith radius at first increment (O_0) was calculated by averaging the nucleus radii for each species. Growth based on back-calculated methods was evaluated at different temporal scales: (1) within 2 d of capture, to evaluate habitat-specific growth, and (2) the time between hatching and capture, to evaluate overall growth.

Data Analysis

Environmental factors

Environmental parameters including river discharge, depth, water flow, water temperature, dissolved oxygen, salinity, pH, and precipitation were analyzed to detect differences in sampling periods and locations. To satisfy assumptions relating to parametric tests and univariate normality, Shapiro-Wilk's W-test and residual plots were used to analyze the distribution of each data series (Shapiro and Wilk 1965; Royston 1992). When necessary, environmental data were logarithmically transformed ($\log_{10}$) before statistical analysis to normalize observations and stabilize the variance. Independent samples t-tests were used to detect differences between sampling years. Spatial and monthly differences between environmental parameters were evaluated using a one-way analysis of variance (ANOVA). If the ANOVA was significant ($P \leq 0.05$), differences were further examined using the Ryan-Einot-Gabriel-Welch (REGWQ) post-hoc test, which holds family wise alpha at 0.05. Unless otherwise noted, all statistical analyses and visualization techniques were performed using SAS statistical software (SAS 9.2; SAS Institute, Cary, NC, USA).

Distribution of larval fishes

An exploratory statistical analysis was conducted to determine whether area, station, or environmental parameters accounted for a significant amount of variability in the spatiotemporal distribution of river herring. Abundances were analyzed with respect to environmental parameters that included river discharge, depth, water flow, water temperature, dissolved oxygen, salinity, and pH. Directions of larval dispersal and dispersal rates were examined relative to river flow conditions. To determine the loss of larvae from Roanoke River mainstem through distributaries (Thoroughfare and Middle River), daily CPUE estimates were converted to total number of larvae based on the volume of water at each station. River volumes (m^3) represented by each site were calculated from data in Rulifson et al. (1992). T-tests were used to test the hypothesis that the loss of larvae from the mainstem was greater than the volume of water lost through Thoroughfare and Middle River. Hypotheses were based on data from Lebo (1998), which showed that 16% of water in the mainstem is distributed through Thoroughfare and 30% of water in the mainstem is distributed through Middle River. Regression analysis was used to evaluate larval advection through distributaries as related to river discharge.

Nonparametric statistics were used evaluate distributions of alosines, because data did not always meet the underlying conditions of normality and homogeneity of variances. CPUE means and standard deviations were significantly affected by a large number of true zero observations related to the seasonal distribution of alosines. CPUE data were transformed by using lognormal data and adding 0.001 to account for zeros. A Wilcoxon Rank-Sum Test was used to compare differences in alosine CPUE between sampling years. Spatial and monthly differences in alosine CPUE were analyzed using the non-parametric ANOVA for repeated measures (Friedman test). This repeated measures procedure is especially useful when sampling

fixed stations through time (Maceina et al. 1994). The stations within each strata were considered a repeated measure. In cases where the Friedman test was significant ($P \leq 0.05$), post-hoc comparisons were conducted using Dunn's Test on rank means.

A one-way multiple analysis of variance (MANOVA) tested whether the three sampling areas were significantly different when both river herring and environmental data were included in the analysis. In addition to testing for significant differences among groups, MANOVA also provides a value, Λ, measuring how large the differences are among groups. Λ ranges from 0 to 1, with 0 indicating strong differences (Tabachnick and Fidell 2007). To protect against multicollinearity, a Pearson correlation matrix was conducted using all environmental variables. If a pair of variables had an $r \geq 0.9$, one of the variables was deleted from MANOVA and principal component analysis.

Distribution and habitat use patterns of larval blueback herring and alewife were examined with principal component analysis (PCA). The PCA was conducted using standard routines in Primer-E v6 (Primer-E Ltd, Plymouth, UK). Combined environmental and hydrographic variables in 593 samples were normalized and used to calculate variable loadings and generate principal component scores. PCAs were run on correlation matrices of centered data. To facilitate visualization and simplify comparisons between habitats, eigenvalues and eigenvectors were extracted from the correlation matrices for each species and each area sampled (River, Delta, and Sound). Component axes retained for interpretation were those that explained > 60% of the cumulative variance and those with an eigenvalue greater than 1.0 (Jolliffe 2002). Environmental variables with eigenvectors (correlations) larger than 0.40 were considered biologically important (Hair et al. 2009). For visual comparisons of habitat use in three-dimensional principal component space, the mean eigenvalue for each component was plotted as a centroid and the variance about the centroids was estimated as the means of standard errors on

each of the principal component axes (Switzer et al. 2004). Confidence intervals (95%) about the centroids were estimated by doubling the standard errors.

Sagittal otolith comparison

To determine differences in increment number and otolith morphology, left and right sagittae were compared using paired *t*-test. The precision of independent age determinations were calculated through procedures for percent agreement (± 2 d), coefficient of variation (Campana 2001), and average percent error (Beamish and Fournier 1981).

Age and growth

The relationship between length and age was evaluated using regression analysis. Six age-length keys were developed, one for each species and area. Evidence of different growth trajectories was interpreted as a significant interaction effect with habitat. Analysis of covariance (ANCOVA) was used to compare slopes of age-length regressions for blueback herring and alewife caught in each area.

Individual mean growth rate was (MGR, mm/d) was calculated for each larvae using the equation:

$$MGR = \frac{L_c - L_0}{t} \quad (2)$$

where L_c is the standard length at capture, L_0 is the standard length at hatch, and t is the age since hatching (d). ANOVA was used to compare MGR for each species and area.

Mortality

Habitat specific mortality rates were estimated using catch curve analysis of data pooled throughout the study (Ricker 1975). All blueback herring and alewife larvae ≥ 5 mm SL were

considered equally vulnerable and fully recruited to the gear. Instantaneous mortality rates were estimated by fitting an exponential model of decline in abundance with respect to age. Mortality was calculated using the equation:

$$N_t = N_0 e^{-Zt} \quad (3)$$

where N_t is larval abundance age t, N_0 is estimated abundance at time of hatching (y-intercept of regression), Z is the instantaneous mortality coefficient, and t is the age since hatching (d). Data were fit to the log-linear form of the model after log-transformation of abundance data. Confidence intervals of 95% around the mortality estimates were calculated using standard regression techniques. ANCOVA was used to compare mortality estimates for blueback herring and alewife caught in each area and at varying temporal scales. Models detecting a significant treatment effect were further examined with Tukey's HSD multiple-comparisons to test for differences ($\alpha = 0.05$) among treatment means.

Results

Habitat and environmental factors

Seasonal air temperatures (-9.4 – 37.8 °C) and precipitation (33.9 ± 1.9 cm) exhibited climatic and weather patterns typical of southeastern United States. Air temperature and precipitation were not significantly different between years (Table 2.2). Several cold fronts that passed through the region in 2009 resulted in unusually cold, wet conditions, a characteristic of climates influenced by El Niño-Southern Oscillation. These cold fronts often produced periods of heavy rainfall leading to daily accumulations in excess of 4 cm. In 2008 and 2009 during the peak spawning periods for anadromous clupeids (late March through early May), air temperatures were 14.5 ± 5.0 ºC and precipitation accumulated to 13.5 ± 3.0 cm.

Mean daily discharge from Roanoke Rapids Dam varied from 64 to 416 cms during 2008 and from 77 to 623 cms in 2009 (Figure 2.3). The temporal pattern of flows differed between years. Discharge rates for 2008 followed an approximately normal distribution pattern with flows exceeding 200 cms for 67% of the sampling period. Low flows (70.9 ± 10.1 cms) were observed for most of March. During striped bass spawning and recruitment, flows were maintained within management guidelines for 57% of the regulatory period. Discharge rates for 2009 exhibited a bimodal distribution pattern with peak flows observed before and after striped bass spawning. In 2009, flows exceeded 200 cms for 90% of the sampling period and were maintained within striped bass management guidelines for 87% of the regulatory period. High flows in excess of 500 cms were observed on March 4 and June 9 through June 18. The magnitude of these flows was evidenced by heavy spring rains and local flooding events. Corresponding with highly variable flows, river gage height was significantly different between years (t_{121}= 6.98, $p < 0.001$, $g = 0.9$). River height was 4.8 ± 1.2 m for 2008 and 5.9 ± 1.1 m for 2009. Water depth at fixed stations in Roanoke River and Albemarle Sound ranged from 0.9 to 8.5 m. Stations located in the River were significantly deeper (4.7 ± 1.4 m; $F_{2,149} = 60.56$, $P < 0.001$) than stations in Delta (3.2 ± 1.0 m) and Sound (3.3 ± 0.4 m).

Water quality parameters were within ranges expected for river herring migration, spawning, and larval development (Greene et al. 2009). Significant yearly differences were observed for dissolved oxygen, pH, and turbidity (Table 2.2). Water temperatures were lowest in March and increased steadily through June. The difference between surface and bottom temperature was minimal (0.1 ± 0.7 °C). There was no evidence of water mass stratification during any of the sampling months. Water temperatures were 14.5 ± 0.4 °C during the peak capture periods for blueback herring in April and 21.3 ± 0.1 °C during the peak capture periods for alewives in May.

Water temperature and turbidity were not significantly different among areas (Table 2.3). Turbidity ranged from 5 to 220 ntu, and measured values were not correlated with river discharge, surface currents, wind speed, or other hydrographic phenomena. Although surface pH levels were not significantly different between the River and Delta, surprisingly low pH levels ranging from 5.3 to 6.0 were recorded in these regions following rainy days and high-flow periods in March and April 2009. High pH levels in the Sound corresponded to elevated salinities.

Dissolved oxygen followed the expected seasonal pattern of being highest in March and decreasing through the summer (Figure 2.4). Dissolved oxygen levels were generally above 70% saturation throughout the sampling period. Hypoxia (< 3.0 mg/L) occurred infrequently in late May and June accounting for 3% of bottom dissolved oxygen readings. Anoxic conditions (< 0.5 mg/L) were observed on several occasions within Warren Neck Creek, a small tributary off the mainstem of the Roanoke River. These conditions were prevalent when flow within the creek was less than 0.01 m/s and water temperatures exceeded 25 ºC.

Salinity within the Sound ranged from 0.1 to 2.5 psu and was significantly higher than other areas ($F_{2,149} = 41.38$, $P < 0.001$). The River and Delta were predominantly freshwater with salinities < 0.1 psu. Water within the River and Delta flowed downstream and surface currents were similar in both areas, ranging from 0.01 – 0.83 m/s, with a mean velocity of 0.14 ± 0.11 m/s. Net surface flow within these regions was not correlated with river discharge or rainfall. Inland stations along the River and Delta were generally protected from prevailing winds from the east (36%) or southwest (32%). These winds affected the open waters of the Sound causing wave action, wind rows, and visible signs of circulation patterns (*i.e.*, Langmuir circulation). Surface currents within the Sound were strongly correlated with wind speed (Figure 2.5; r^2 =

0.80, $F_{1,46} = 185.49$, $P < 0.001$). Surface currents were significantly higher ($F_{2,149} = 6.46$, $P = 0.002$) in the Sound (0.3 ± 0.2 m/s), ranging from 0.0 – 1.2 m/s, and currents most frequently originated from the west (61%) or northeast (28%).

Larval abundance

A total of 50,435 fishes were collected from 1,186 pushnet samples. Larvae and juveniles were caught throughout the areas sampled. The total catch between paired samples was not significantly different ($t_{1185} = 1.68$, $P = 0.09$). Overall, no significant differences were observed in the total catch of fish between sampling years. The River and Delta were not significantly different and comprised 88.9 ± 0.3 % of the fish caught. Significantly fewer fish were caught in the Sound (11.2 ± 0.3%) than the River or Delta ($\chi^2 = 21.72$, df = 2, $P < 0.001$).

Larval alosines identified to species included blueback herring (53%), hickory shad *A. mediocris* (28%), alewife (15%), and American shad *A. sapidissima* (0.5%). The frequency of occurrence for shads and river herring varied with area (Table 2.4). Anadromous alosines (N = 12,901) comprised 11% of the total catch in 2008 and 38% of the catch in 2009. Alosines were collected during all weeks of sampling in 2008, but were not present the first week of sampling in 2009. Other clupeiformes present in samples were Atlantic menhaden *Brevoortia tyrannus*, gizzard shad *Dorosoma cepedium*, and bay anchovy *Anchoa mitchilli*.

Differences in alosine abundance (number/100 m^3 ± SD) and composition were observed between sampling years. With all species combined, larval alosine abundance in 2009 (28.5 ± 67.8) was significantly higher than in 2008 (7.7 ± 11.0; $z = 2.36$, $P = 0.02$). These differences were primarily driven by the abundance of blueback herring in 2009 (98.1 ± 209.8; $z = 2.76$, $P = 0.006$), because no significant differences were observed in the abundance of other

Alosa species between sampling years. Alewives (35.1%) were the most abundant alosine in 2008 followed closely by blueback herring (32.7%) and hickory shad (29.6%). In contrast, blueback herring (59.1%) were the most abundant alosine in 2009 followed by hickory shad (29.2%) and alewife (11.6%). American shad were the least common alosine for both years (< 3%).

The initial arrival of larval river herring to the nursery grounds was different between the two years. Peaks in river herring recruitment were observed several weeks earlier in 2008 as compared to 2009 (Figure 2.4). Blueback herring were collected during all weeks of sampling in 2008 and 2009, with exception of the first week of March 2009. Peak recruitment for blueback herring occurred during the third week of March and was sustained through the first week of May in 2008. Peak recruitment of blueback herring was of shorter duration in 2009. Blueback herring abundances were highest during the first week of April and remained high for two weeks. For both years, blueback herring recruitment was highest when water temperatures were 16.2 ± 2.5 °C and ranged from 14.5 to 18.5 °C. Alewife abundances were highly variable, and peak recruitment was of shorter duration. In 2008, alewife peak recruitment coincided with high abundances of blueback herring in March and remained high for the first weeks in April. Recruitment of alewife occurred later in 2009 and abundances peaked during the latter half of April. Similar to blueback herring, peaks in alewife recruitment were highly correlated with temperature. For both years, alewife recruitment was highest when water temperatures were 17.2 ± 2.3 °C and ranged from 14.5 to 20.5 °C.

Blueback herring and alewife were collected within all areas (Table 2.5); although, distribution and abundance varied spatially. While most river herring were collected within the River (70%; $N = 6{,}334$), abundances generally declined moving downstream along the river

gradient (Figure 2.6). This trend was consistent across both years and for each species. The percentage of larvae lost from Roanoke River to the distributaries was different for Thoroughfare and Middle River. The percentage of larvae lost from the mainstem channel to Thoroughfare (27.2 ± 28.6 %) was significantly greater than the percentage of water (16%) lost to Thoroughfare (t_{19} = 2.37; P = 0.03). The percentage of larvae lost from the mainstem channel to Middle River (32.3 ± 27.6 %) was not significantly different than the percentage of water (30%) lost to Thoroughfare (t_{18} = 1.47; P = 0.72). Larval dispersal through the distributaries was highly correlated to river flow (Figure 2.7; r^2 = 0.95, $F_{1,22}$ = 185.6, P < 0.001) and was not significantly different between Thoroughfare and Middle River (ANCOVA; F = 0.01, P = 0.94).

Warren Neck Creek was the only tributary sampled that does not receive flows directly from Roanoke River. The creek is connected to the mainstem channel. Approximately 20% of all blueback herring (N = 1,496) and alewife (N = 195) were caught in Warren Neck Creek, and the total number of river herring caught in Warren Neck Creek in 2009 was nearly equal to the total catch of river herring in 2008 for all stations combined.

Larval abundances varied significantly among the three sampling areas for both blueback herring (Friedman's test; χ^2 = 10.24, df = 2, p = 0.006) and alewife (χ^2 = 19.65, df = 2, p < 0.001). Post-hoc comparisons revealed that blueback herring abundances were significantly higher in the River (35.6 ± 147.4) and Delta (14.6 ± 46.5) as compared to the Sound (7.9 ± 28.2). Although alewife were considerably less abundant, their distribution was similar with abundances highest in the River (12.9 ± 37.7) as compared to the Delta (5.1 ± 11.8) and Sound (1.5 ± 5.6).

Relationship between fish abundance and environmental factors

Air temperature and conductivity were both highly correlated ($r \geq 0.9$) with other parameters and were excluded from MANOVA and PCA analyses. A one-way MANOVA indicated that strong and significant differences were observed among areas sampled (Wilk's $\Lambda = 0.03$, F = 15.48, $\eta^2 = 0.97$, $P < 0.001$). Area explained 97% of the variance in the environmental and river herring abundance data. These results indicated the three sampling areas can be clearly distinguished from each other when both environmental data and larval abundances are analyzed together.

Principal components analysis was used to corroborate the results of the MANOVA and summarize the variation observed between habitats. The PCA identified three factorial axes that explained 77% of the total variability (Table 2.6). All environmental or hydrographic variables were biologically important on at least one principal component. Principal Component I accounted for most of the variation (41%) and was characterized by a positive correlation with water temperature and negative correlation with dissolved oxygen. This component was interpreted as a seasonal component. Principal Component II explained 22% of the variability and was associated with a positive correlation with depth and negative correlations with pH and salinity. This component was interpreted as a spatial component that clearly defined the three stratified areas. Principal Component III explained 14% of the variability and was associated with a positive correlation with turbidity and negative correlation with surface current. Three-dimensional spatial analysis of the PCA revealed differences in relationships among abiotic factors and their level of influence on the distribution of river herring (Figure 2.8). Plots of the

centroids were well separated in PCA space and indicated a high degree of separation between habitats. The close proximity of centroids for blueback herring and alewife showed these species coexist and occupation of each area is similar.

Larval ontogeny and size distribution

River herring yolk-sac larvae were prevalent throughout samples (32%). Most blueback herring yolk-sac larvae (48%) were collected during the first two weeks of April. Blueback herring yolk-sac larvae averaged 5.3 ± 0.7 mm SL with a few fish measuring up to 7.0 mm SL. Most alewife yolk-sac larvae (42%) were collected in the latter part of April and early May. Alewife yolk-sac larvae averaged 4.8 ± 0.8 mm SL with a few fish measuring up to 6.5 mm SL. River herring larvae collected were predominantly preflexion stage (66%) ranging from 5.0 to 10.0 mm SL. Larvae in later stages of development were rare and collections of these larvae were not correlated with a specific temporal period. Gut fullness was low (< 10%) for both species and fish collected from all areas. Gut fullness was not correlated with fish length (r^2 = 0.02, $F_{1,563}$ = 5.4, P < 0.02). A small proportion (< 10%) of yolk-sac larvae had transitioned to exogenous feeding as indicated by gastrointestinal differentiation and the presence of food in stomachs (Table 2.7).

River herring lengths ranged from 3.5 – 12.7 mm SL, with 97% of larvae ≤ 8 mm. Mean length was similar between blueback herring 5.9 ± 1.1 mm SL and alewives 5.4 ± 1.1 mm SL. Larval lengths were positively correlated with water temperature (Figure 2.9; Table 2.8). The results of an ANCOVA based on standard length as the response variable and temperature as the covariate showed a significant difference between species (F = 20.36, N = 798, P < 0.001). Size distributions varied with area and year. In 2008, no significant differences were observed in the

size distribution of blueback herring ($F_{2,300} = 0.65$, $P = 0.52$) or alewife ($F_{2,371} = 0.46$, $P = 0.63$) within any area. In 2009, significantly larger blueback herring were collected in the River and Delta compared to fish collected in the Sound ($F_{2,494} = 4.80$, $P = 0.009$). Although the largest alewives were collected in the River and Delta in 2009, length was not significantly different among areas ($F_{2,279} = 0.27$, $P = 0.76$).

Otolith analysis

Sagittal otoliths were collected from 594 (9%) blueback herring and 392 (22%) alewife. Pairs of sagittal otoliths were collected from 446 blueback herring and 380 alewife. Deposition of subdaily increments were observed in some fish. These increments were distinguished from daily growth increments based on continuity of rings around the nucleus and the relative spacing of discontinuous zones. Size distributions of larvae for age determination were similar between species and ranged from 3.5 – 12.0 mm SL. Otolith radius at capture was 13.8 ± 3.4 μm for blueback herring and 12.4 ± 2.5 μm for alewife. Otolith radius at first increment formation (hatching) was 2.9 ± 0.7 μm for blueback herring and 3.0 ± 0.9 μm for alewife. Comparisons of otolith microstructure and increment counts were not significantly different between left and right sagittae (Table 2.9). Consequently, sagittae from either side were randomly selected for age determination.

Otoliths from 5% of blueback herring ($N = 30$) and 3% of alewife ($N = 12$) were discarded because increments were not discernable or did not meet the acceptance criteria. Increment counts ranged from 2 to 17. Increment counts showed a high degree of precision between the two enumerations (Table 2.10). The percent agreement exceeded 90% for enumerations within 1 day. Average percent error was 2.9 ± 4.6 for blueback herring and 6.8 ± 5.4 for alewife, and the

coefficient of variation for increment counts for both species was extremely low (4.6 ± 7.9). Habitat-specific differences in precision and percent agreement of increment counts were a result of sample size with fewer fish collected in the Sound than the other areas.

Age, growth, and mortality

The distribution of ages for blueback herring and alewife were not significantly different between species or years. Fish ages ranged from 4 to 19 days after hatch. Age distributions varied among nursery areas; however, age distributions generally increased down the river gradient (*i.e.*, distance from the spawning grounds). As expected, significantly older blueback herring were caught in the Sound (4.2 ± 1.3 d) as compared to the River (3.9 ± 1.1 d) and Delta (3.7 ± 0.9 d; ANOVA, $F_{2,1400} = 15.00$, $P < 0.001$). Older alewife were also caught in the Sound (5.9 ± 1.6 d) as compared to the Delta (4.5 ± 1.3 d) and River (3.7 ± 1.5 d; $F_{2,814} = 71.32$, $P < 0.001$).

Larval lengths were strongly correlated with otolith size for blueback herring ($r^2 = 0.97$, $F_{1,503} = 19{,}510.5$, $P < 0.001$) and alewife ($r^2 = 0.94$, $F_{1,291} = 4485.1$, $P < 0.001$). This supports the validity of the regression and use of the BI method for backcalculating the lengths of river herring larvae. Differences in body length-otolith radius relationships were not detected between species, year, or area. Length-at-age relationships were best described ($r^2 > 0.85$) using linear regression (Figure 2.10). Length-at-age relationships were not significantly different between species (ANCOVA, $F = 0.05$, $P = 0.83$). Length-at-age comparisons of endogenous and exogenous feeding stages were not significantly different for blueback herring (ANCOVA, $F = 0.86$, $P = 0.35$) or alewife ($F = 3.11$, $P = 0.08$). Using pooled data of larvae at various stages, length-at-age relationships were significantly different between areas for blueback herring

(ANCOVA, $F = 5.57$, $P = 0.004$) and alewife ($F = 5.59$, $P = 0.004$). The results suggest blueback herring in the Delta were significantly larger at younger ages than cohorts in other areas. In contrast, alewife in the Sound were significantly larger at younger ages than cohorts in other areas.

Growth rates of larval river herring estimated by aggregate methods indicated that growth varied between species, years, and areas. Individual MGR for blueback herring was 0.29 ± 0.16 mm/d and ranged from 0.17 to 0.75 mm/d. Alewife MGR was 0.30 ± 0.14 mm/d and ranged from 0.25 to 0.64 mm/d. Overall, daily growth was significantly faster for alewife ($t_{1900} = 2.34$, $P = 0.02$). Analysis of MGR by year and species revealed alewife MGR (0.33 ± 0.15 mm/d) was significantly faster than blueback herring MGR in 2008 (0.22 ± 0.20 mm/d; $t_{475} = 7.79$, $P < 0.001$), but not in 2009. During the second year of the project, blueback herring MGR (0.31 ± 0.15 mm/d) was significantly faster than alewife (0.28 ± 0.13 mm/d; $t_{979} = 2.98$, $P = 0.003$). Analysis of individual MGR by area and species (Table 2.11) showed for both years daily growth was significantly faster for alewife in the River (ANOVA; $F_{2,814} = 23.32$, $P < 0.001$). Blueback herring MGR was not significantly different between areas in 2008, but was significantly faster in the Delta in 2009 ($F_{2,1400} = 3.94$, $P = 0.02$).

Instantaneous growth estimates based on back calculations and marginal increment analysis of otoliths from hatch (G_{max}) and within 2 d of capture (G_c) varied with species and area (Table 2.11). Blueback herring G_{max} was not significantly different from alewife (0.09 ± 0.03). In contrast, alewife G_c (0.09 ± 0.04) was significantly higher than blueback herring (0.07 ± 0.03; $t_{412} = 6.24$, $P < 0.001$). Instantaneous growth estimated from either G_{max} or G_c for blueback herring was not significantly different between areas. Alewife G_{max} was significantly higher in the River (0.10 ± 0.03) compared to the Delta (0.08 ± 0.02) and Sound (0.08 ± 0.02; $F_{2,290}$ =

10.09, $P < 0.001$). Alewife G_c followed a similar distribution and was significantly higher in the River (0.11 ± 0.05) than in the Delta (0.08 ± 0.03) or Sound (0.06 ± 0.03; $F_{2,290} = 29.78$, $P < 0.001$).

Mortality estimates for blueback herring (0.76 ± 0.23 per day) were significantly higher than mortality estimates for alewife (0.64 ± 0.17 per day; $t_{46} = 2.03$, $P = 0.048$). River herring mortality estimates were not different between years, but significant differences were observed between months sampled (Table 2.12). Blueback herring mortality was highest in March (0.98 ± 0.10 per day), while alewife mortality was highest in April (0.77 ± 0.13 per day). Both species experienced the lowest mortality in June (0.50 ± 0.17 per day). Comparisons of mortality between endogenous and exogenous feeding stages of larvae were not significant for either species. Blueback herring mortality was highest in the River and Sound (0.88 ± 0.20 per day); however, mortality was not significantly different from the Delta (0.75 ± 0.22). Significant differences in mortality with nursery habitat were observed for alewives. Alewife mortality was significantly higher in the River (0.71 ± 0.15 per day) and Delta (0.68 ± 0.15 per day) compared to the Sound (0.51 ± 0.16 per day; $F_{2,21} = 3.79$, $P = 0.04$).

Spawning season

Analysis of back-calculated hatch dates indicated that blueback herring and alewife spawned throughout the period sampled from March through June. Previously unreported for North Carolina, blueback herring and alewife yolk-sac larvae were collected from fish that spawned in late June. While temporal differences in spawning were correlated to recruitment patterns, water temperature was a critical factor in determining peaks in spawning. Blueback herring spawning was strongest when water temperatures were 14.4 ± 0.5 °C and most spawning (75%) was

completed when water temperatures were 17.5 ± 1.4 °C. Temperatures corresponding to peaks in alewife spawning were warmer than those for blueback herring. Alewife spawning was strongest when temperatures were 16.5 ± 1.3 °C and most spawning (75%) was complete when temperatures were 19.0 ± 2.7 °C.

Discussion

Evidence from this study provides some support for review of reservoir operation and dam discharge guidelines to optimize river flow regimes for production of anadromous alosines in Roanoke River. Our results emphasize the importance of river flow on distribution of larval fish in a large river system. The Roanoke is a large river, with roughly the same mean flow as the Colorado River through the Grand Canyon (Manring and Pearsall 2005). Best management practices for dam discharge have long supported the recovery of Roanoke River-Albemarle Sound stock of striped bass (Reinert et al. 2005; Greene et al. 2009). Dam discharge regulations that extend from April through mid-June dampen the natural variability in river flow and eliminate high-magnitude flood events. Established discharge rates and river flow regimes are beneficial to striped bass migration and spawning, egg and larval transport, larval retention in primary nursery habitats, and larval distributions in relation to food resources (Rulifson and Manooch 1990a). River flow has been implicated as a significant determinant of alosine recruitment success. Negative effects of high river flow (*e.g.*, > 300 cms) include reduced residence time of eggs and larvae in nursery habitats and variable water quality (Meador et al. 1984). Positive effects of high river flow include spawning and migratory cues, access to inundated backwater habitats, and transport of larvae from spawning to nursery grounds (Martin and Paller 2008).

In this study, high flows (300 – 600 cms) and water temperatures ranging from 5 to 13 °C in March 2009 probably served as a distinct migratory and spawning cue for river herring and resulted in widespread and unusually high production of larvae. Moderate to high flows (186 to 387 cms) serving as migratory and spawning cues for striped bass in April swiftly transported alosine eggs and larvae downstream. The collection of large numbers of yolk-sac (32%) and preflexion larvae (66%) in the River, Delta, and Sound suggests larvae are being transported downstream from spawning grounds and fish are possibly being advected from primary nursery habitats.

Despite spatial coverage (108 km^2) and extensive sampling within the lower reaches of this coastal river system, spawning was not directly observed for any *Alosa* species. We also did not detect spawning through collection of fertilized eggs using either pushnets or vertical plankton hauls (Coggins 2005). Previous studies suggest river herring are spawning far upstream from our study area (75 to 200 rkm). In recent years, river herring fertilized eggs have been collected in habitats adjacent to Roanoke Rapids Dam tailrace (218 rkm) and downstream (209 rkm) near Weldon, North Carolina (Harris and Hightower 2010). Other alosines such as hickory shad and American shad also spawn in this region (Harris and Hightower 2011). Further downstream from the dam (100 rkm), river herring have been observed spawning in backwater tributary systems (Walsh et al. 2005). Yolk-sac larvae collected from flooded swamps and small creeks allowed these authors to infer river herring were spawning in the immediate vicinity. Drainage of backwater tributary systems dispersed eggs and larvae downstream through the main river channel.

To understand the natural characteristics and the effects of hydrologic alteration on fish communities, studies relating river discharge with time of travel were conducted in the 1950s

(Fish 1959) and 1980s (Herrmann 1993). Using fluorescent dye additions and gaged discharge from Roanoke Rapids dam under varying hydrologic regimes (74 to 277 cms), time of travel for eggs and larvae to reach our study location was estimated at 4 to 9 d and water mass movement ranged from 1.5 to 2.3 km/h (Herrmann 1993). Estimated transport times correspond closely with river herring ages and stages of development observed in this study. Although the geomorphology of Roanoke River has changed over time with increased sediment and siltation from anthropogenic sources (Hupp et al. 2009), discharge and flows tested 30 years ago were within current management guidelines. Unless mechanisms exist for retention of larvae in upstream habitats, our findings coupled with Walsh et al. (2005) suggest a large proportion of larvae drift downstream in narrow, channelized river reaches until they are entrained in low-velocity habitats at the mouth of the river or dispersed into Albemarle Sound.

The abundance of young fish (3 d) collected provides evidence river herring are spawning in close proximity to the study area. High numbers of yolk-sac larvae (59% of blueback herring; 73% of alewife) collected from Warren Neck Creek (Station 4) further suggests river herring are spawning within the upper reaches of this tributary. Warren Neck Creek extends 3 km southwest from Roanoke River and is characteristic of spawning habitat for river herring. The shallow creek has low flows (0.08 ± 0.04 m/s) and is bounded by forested wetlands, wooded swamps, and dense vegetation. Our observations contradict numerous studies that report blueback herring and alewives spawn near headwaters or 150 to 200 km upstream in rivers of the southeastern U.S. (Davis and Cheek 1966; Street 1970; Street et al. 1975; Meador et al. 1984; O'Connell and Angermeier 1997; Cooke and Leach 2003; Harris and Hightower 2010). Our findings are similar to populations of landlocked or non-anadromous alewives, where adult fish migrate from

offshore open-water habitats to spawn in inshore areas that include rivers, tributaries, drowned river mouths, and bays (Goodyear et al. 1982).

While it was not within the scope of this study to identify spawning habitats for river herring, there are a variety of habitats within the lower Roanoke River that would support spawning populations of blueback herring and alewife under certain environmental conditions (Loesch 1987). The floodplain within our study area supports the largest and least fragmented bottomland hardwood forest ecosystem on the Atlantic coast (Hupp 2000). Spawning habitats characteristic of river herring and those located within the Roanoke floodplain include slow-flowing tributaries, flooded bottomlands, deep creeks draining hardwood swamps, sloughs, oxbows, and mill ponds. River herring spawning in these habitats would benefit from benthic substrates that provide cover for eggs, stream flow to supply oxygen and transport larvae, and an abundance of zooplankton and microinvertebrates for food. Additional research is needed to confirm blueback herring and alewife spawn at different habitats within lower Roanoke River ecosystem (*i.e.*, $\leq$ 50 rkm).

Temperature has a profound effect on spawning and was a critical factor in determining peaks in spawning and larval recruitment. We found no evidence of divergent spawning activity between species. Alewife did not spawn in February or weeks before blueback herring as previously reported (Tyus 1974; Jones 1978; O'Connell and Angermeier 1997). Similar to other studies in Roanoke River, spawning for blueback herring and alewife was continuously sustained from March through May (Walsh et al. 2005; Harris and Hightower 2010). Unique to this study and our region was the observation that larval blueback herring and alewife were produced from spawns in late June. This broad distribution of spawning events may help dampen annual fluctuations in larval recruitment. While proportionately low, larvae collected from fish

spawning in June accounted for 10% of river herring in 2008 and 3% of fish in 2009. Late spawning fish in 2008 and 2009 experienced temperatures within the range of 24 to 30 °C. These warm temperatures approach the upper threshold for spawning blueback herring and alewife; however, environmental conditions may convey survivorship advantages to larvae.

While blueback herring spawn at temperatures ranging from 13 to 27 °C, water temperature for optimal spawning has a narrower range, 20 to 25 °C, and closely corresponds with temperatures for hatching and larval development (Klauda et al. 1991). Temperatures for alewife spawning are generally cooler than temperatures for spawning blueback herring; however, there is much overlap. For alewives, water temperature at the time of spawning does not always correspond to thermal regimes that support high growth rates for larvae. Water temperatures for optimal spawning and larval development can differ by as much as 10 °C (Kellogg 1982). Water temperature for alewife spawning varies with location and latitude, but ranges from 10 to 22 °C. Peak spawning typically occurs from 14 to 16 °C, and fish cease spawning when temperatures exceed 28 °C (Edsall 1970). Water temperatures for normal embryonic development and hatching range from 17 to 22 °C with maximum hatching success occurring at 21 °C (Edsall 1970; Kellogg 1982). Highest survival and growth of larval alewife occurs at 26 °C (Kellogg 1982).

Larvae produced during warm months may have experienced survivorship advantages related to differential growth and mortality. Although substantially fewer fish were collected in June, river herring growth was significantly higher and mortality was significantly lower than the other months sampled (Table 2.12). Under these conditions, fish would have grown faster and spent less time in early larval stages. Mortality estimates in June reflect fast growing larvae were less vulnerable to starvation and predation than slower-growing cohorts in earlier months. These

findings support 'growth-mortality' hypotheses, which contend fast growing larvae benefit from a large length-at-age, fast swimming, and advanced sensory and locomotor systems to escape predation (Anderson 1988; Dower et al. 2009). Fast growing larvae are also resistant to starvation or food deprivation by possessing abilities to search greater volumes of water for food, feed on prey of variable sizes, and efficiently capture prey (Hunter 1981; Litvak and Leggett 1992; Leggett and Deblois 1994).

The abundance of blueback herring and alewife decreased along the river gradient. We found no evidence suggesting larval blueback herring and alewife selectively use a specific nursery habitat. Distributions reflected transient larval stages and strong advective forces of riverine transport. Abundances were consistently higher and more evenly distributed in the River and Delta. River herring abundances from the Sound were patchy in distribution and signified widespread dispersal into a large body of water from multiple sources. The distribution of sampling locations in Albemarle Sound did not offer sufficient resolution to detect larval distributions associated with a river plume, frontal boundary, or other known hydrographic feature. The physical and biological attributes of such features are often hypothesized as important nursery areas for larval fishes, because they concentrate fish larvae and zooplankton and provide turbidity-mediated refuge from predation (Reichert et al. 2010). The rivers investigated in this study did not produce a distinctive frontal boundary identified by measurable gradients in salinity or turbidity.

Advective transport of larvae from Roanoke River mainstem to distributaries was predictable and was not significantly different between Thoroughfare and Middle River (Figure 2.7). During periods of low river flow, larval advection from the mainstem channel was high and was not correlated with proportional rates of water loss from the river. In contrast, during periods of high

river flow the advective transport of larvae through distributaries was low. These results suggest that during high flow periods larvae are carried downstream and fish are relatively confined within the mainstem channel. Larvae preferentially drift through the smaller distributaries during low flow periods. Advective losses to Thoroughfare were higher than expected. This distributary is narrow and receives considerably less water than Middle River. The high percentages of larvae transported through Thoroughfare, Middle River, and other distributaries indicate these waterways are an important conduit to backwater nursery habitats. Key attributes that distinguish backwater nursery habitats from main-channel habitats are reduced water flow and exchange, shallow depth, refuge from predation, and concentration of food resources (Niles and Hartman 2011). Retention of river herring larvae in these nursery habitats could bolster growth and survival.

Comparable growth rates and a high degree of overlap in spawning and larval recruitment support management of river herring as a single stock. Daily growth rates for blueback herring and alewife were not significantly different. Growth rates observed in this study were similar to previous reports for wild-caught blueback herring and alewife in the southeastern U.S. (Street 1970; Burbidge 1974; Walsh et al. 2005; Overton et al. In press). Interestingly, growth rates for alewife were noticeably slower (~50%) than populations distributed at northern latitudes or for fish produced in the laboratory (Heinrich 1981; Essig and Cole 1986; Höök et al. 2007). Suppressed growth among alewives could be attributed to warm temperatures at the southern limit of their native range. Within the context of climate change, species such as alewives that are tightly coupled with specific spawning and nursery habitats will potentially experience the largest effects of long-term changes in temperature. Recruitment of alewives in the region could be negatively affected by warming temperatures.

Interannual variability in abundance, growth, and mortality of anadromous fishes has been linked to synoptic-scale climatology and hydrological variability (Wood and Austin 2009). Weather conditions, especially temperature, precipitation, wind, and storms, exert major influences on fish migration, spawning, and larval recruitment. During years characterized by a cold and wet spring, larval alosines benefit from climate patterns that produce favorable water temperatures, high river flows, and a large forage base (Kimmel and Roman 2004; Martino and Houde 2010). In this study, interannual differences in growth and mortality were observed for blueback herring and alewife (Figure 2.12). The cold, wet conditions that occurred in 2009 resulted in the production of a strong year class that also overlapped with record abundances of zooplankton (see Chapter 3). Growth rates of yolk-sac larvae transitioning to feeding as well as growth rates among older individuals would have increased with a large forage base. High mortality for both years was probably related to larval dispersal, advective loss, and failed retention in nursery habitats.

Year-class strength for many fishes is established during early life stages and size-specific growth is an important determinant of survivorship (Heath 1992). Variability in growth leads to fluctuations in recruitment and year-class success. Houde (1987) suggested that growth rates are so important that it might be possible to predict recruitment potential of larvae from their growth rates alone. In this study, the aim of using different methods to estimate growth was to evaluate larval production in specific habitats. Variability in larval growth was reflected differently through measures of somatic growth and instantaneous growth. Simple linear regression of length on age provided a good estimate of growth, because larvae were relatively uniform in age and stage of development. The advantage of using marginal increment analysis of otoliths is it provided an immediate reflection of growth during a specific temporal period and when larvae

were occupying a specific area. This technique proved to be a useful tool for determining recent growth of fish under the influence of riverine transport. Estimates of G_{max} and G_c were similar for blueback herring and alewife, but revealed slightly different growth patterns for each area (Table 2.11). Growth estimates were indicative of habitat quality and suggested riverine habitats supported the highest growth rates. Variability in growth of blueback herring and alewives was mediated by seasonal selective processes and reflected intraspecific and interspecific competition for food and resources.

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Table 2.1. Comparison of areas and physiographic characteristics for stations sampled in the lower Roanoke River and Albemarle Sound, North Carolina. Station numbers correspond to sites in Figure 1. Unless indicated otherwise, values represent means (SD).

Station	Area	Channel width (m)	Depth (m)	Surface flow (m/s)	Total fishes (*N*)	River herring abundance (larvae / 100 m^3)	River herring maximum abundance (larvae / 100 m^3)
1	River	119 (10)	5.7 (0.2)	0.18 (0.13)	1,224	17 (39)	224
2	River	225 (9)	5.4 (0.2)	0.21 (0.12)	5,540	51 (145)	989
3	River	46 (6)	5.2 (0.2)	0.16 (0.16)	3,838	37 (106)	598
4	River	34 (2)	3 (0.1)	0.07 (0.06)	3,553	87 (348)	2,111
5	River	66 (11)	5.2 (0.2)	0.14 (0.10)	2,543	39 (175)	1,245
6	River	166 (30)	4.1 (0.1)	0.19 (0.09)	2,419	35 (113)	672
7	River	156 (13)	4.8 (0.2)	0.12 (0.08)	3,757	44 (159)	888
8	Delta	289 (16)	3.5 (0.2)	0.18 (0.14)	4,455	16 (31)	170
9	Delta	132 (7)	3 (0.2)	0.1 (0.06)	5,177	11 (20)	84
10	Delta	77 (6)	2.8 (0.1)	0.13 (0.06)	3,695	10 (14)	60
11	Delta	86 (6)	3.5 (0.1)	0.12 (0.10)	1,489	10 (23)	110
12	Delta	224 (34)	3.3 (0.2)	0.17 (0.17)	3,636	34 (105)	665
13	Delta	327 (3)	3.4 (0.1)	0.14 (0.09)	3,476	16 (31)	179
14	Sound	-	2.9 (0.1)	0.21 (0.19)	914	9 (26)	148
15	Sound	-	3.2 (0.1)	0.19 (0.17)	601	12 (44)	283
16	Sound	-	3.2 (0.1)	0.19 (0.19)	365	8 (29)	185
17	Sound	-	3.3 (0.1)	0.14 (0.12)	2,149	9 (25)	136
18	Sound	-	3.5 (0.1)	0.18 (0.15)	1,090	6 (23)	161
19	Sound	-	3.8 (0.1)	0.25 (0.27)	514	4 (21)	155

Table 2.2. Comparison between average values (±SD) for environmental parameters in 2008 and 2009 in lower Roanoke River and Albemarle Sound, North Carolina.

Environmental parameter	2008	2009	*t*	*p*
Air temperature (^{o}C)	18.3 (5.3)	17.8 (6.1)	0.07	0.947
Current velocity (m/s)	0.1 (0.1)	0.2 (0.1)	-1.42	0.132
Dissolved oxygen (mg/L)	6.8 (1.8)	8.0 (2.0)	-4.28	<0.001
pH	7.5 (0.2)	6.6 (0.4)	27.75	<0.001
Precipitation (mm/d)	2.5 (2.9)	3.0 (2.0)	-0.91	0.367
Salinity (psu)	0.2 (0.4)	0.2 (0.3)	0.35	0.726
Turbidity (ntu)	88.5 (39.4)	80.3 (38.1)	3.31	0.001
Water temperature (^{o}C)	19.3 (5.5)	18.0 (6.2)	0.89	0.372
Wind speed (m/s)	5.1 (5.8)	1.6 (1.5)	7.30	<0.001

Table 2.3. Mean values (±SD) for environmental parameters from each sampling area in lower Roanoke River and Albemarle Sound, North Carolina. Means sharing a letter in their superscript are not significantly different at the 0.5 level according to a Ryan-Einot-Gabriel-Welch (REGWQ) procedure.

Environmental parameter	River		Delta		Sound	
Current velocity (m/s)	0.15	$(0.1)^{A}$	0.13	$(0.1)^{A}$	0.20	$(0.1)^{B}$
Depth (m)	4.78	$(1.2)^{A}$	3.23	$(0.6)^{B}$	3.32	$(0.4)^{B}$
Dissolved oxygen (mg/L)	7.07	$(1.8)^{A}$	6.75	$(1.7)^{A}$	7.89	$(1.8)^{B}$
pH	6.97	$(0.4)^{A}$	7.02	$(0.4)^{A}$	7.21	$(0.4)^{B}$
Salinity (psu)	0.1	$(0.0)^{A}$	0.1	$(0.0)^{A}$	0.50	$(0.4)^{B}$
Turbidity (ntu)	81.8	$(20.9)^{A}$	86.5	$(22.2)^{A}$	84.16	$(26.0)^{A}$
Water temperature (^{o}C)	18.7	$(5.7)^{A}$	19	$(5.8)^{A}$	18.79	$(6.0)^{A}$
Wind speed (m/s)	1.77	$(1.7)^{A}$	2.62	$(2.1)^{A}$	5.85	$(4.1)^{B}$

Table 2.4. Number and percent frequency of occurrence in samples of larval alosines identified from ichthyoplankton samples collected in lower Roanoke River and western Albemarle Sound, North Carolina during spring 2008 and 2009.

	River		Delta		Sound	
Species	*N*	%	*N*	%	*N*	%
Blueback herring	4,724	38.0	1,390	11.2	712	5.7
Alewife	1,380	11.1	423	3.4	102	0.8
Hickory shad	3,135	25.2	355	2.9	153	1.2
American shad	57	0.5	9	0.1	2	0.0

Table 2.5. Number of ichthyoplankton samples collected, mean abundance (larvae / 100 m^3), minimum (min), maximum (max), and mean (SE) standard length of blueback herring and alewives collected in lower Roanoke River and western Albemarle Sound, North Carolina, during 2008 and 2009. Mean abundances sharing a letter in their superscript are not significantly different at the 0.5 level according to Dunn's Test on rank means.

		Abundance		Standard length					
				Blueback herring			Alewife		
Area	*N*	Blueback herring	Alewife	Min	Max	Mean	Min	Max	Mean
River	460	35.6^{A}	12.9^{A}	3.9	11.8	6.1 (0.1)	3.5	9.1	5.7 (0.2)
Delta	380	14.6^{A}	5.1^{A}	3.7	10.3	5.9 (0.1)	3.5	8.5	5.4 (0.1)
Sound	346	7.9^{B}	1.5^{B}	4.2	7.5	5.7 (0.1)	3.8	8.5	5.2 (0.1)

Table 2.6. Principal component scores for environmental and hydrographic parameters measured in lower Roanoke River and Albemarle Sound, North Carolina. Magnitude and signs of individual component loadings indicated strength and direction of each variable's influence on a principal component. The variance explained by the eigenvalue associated with each principal component is expressed as absolute, proportional, and cumulative values.

	Principal Component		
Environmental variable	PC1	PC2	PC3
Current velocity (m/s)	- 0.009	0.049	- **0.721**
Depth (m)	- 0.190	**0.454**	0.349
Dissolved oxygen (mg/L)	- **0.668**	0.055	- 0.140
pH	0.161	- **0.610**	0.192
Salinity (psu)	- 0.247	- **0.610**	- 0.178
Turbidity (ntu)	- 0.137	- 0.199	**0.516**
Water temperature (^{o}C)	**0.642**	0.069	- 0.059
Eigenvalue	2.89	1.51	1.01
Variance explained (%)	41.3	21.6	14.4
Cumulative variance explained (%)	41.3	62.9	77.3

Table 2.7. Endogenous and exogenous feeding history of blueback herring and alewives collected in lower Roanoke River and western Albemarle Sound, North Carolina, during 2008 and 2009. Values for yolk-sac, yolk-sac and food present, and food present represent mean (SE) percentage of occurrence. Values for gut fullness represent means (SE).

	Blueback herring					Alewife				
Area	*N*	Yolk-sac	Yolk-sac and food present	Food present	Gut fullness	*N*	Yolk-sac	Yolk-sac and food present	Food present	Gut fullness
River	228	57.0 (3.3)	6.1 (1.6)	28.1 (2.9)	3.2 (0.4)	204	37.3 (3.3)	7.8 (1.9)	28.4 (3.2)	2.8 (0.3)
Delta	174	25.3 (3.3)	5.7 (1.8)	51.7 (3.8)	6.0 (0.5)	104	34.6 (4.7)	11.5 (3.1)	53.8 (4.9)	7.1 (0.8)
Sound	162	34.6 (4.7)	8.6 (2.2)	42.0 (4.9)	8.6 (0.9)	72	13.9 (4.1)	8.3 (3.3)	55.6 (5.9)	8.5 (1.1)
Combined	564	40.8 (2.1)	6.7 (1.1)	39.4 (2.1)	5.6 (0.3)	380	32.1 (2.4)	8.9 (1.5)	40.5 (2.5)	5.1 (0.4)

Table 2.8. Descriptive statistics and estimated parameters for river herring standard length (SL) and water temperature (°C). Samples primarily consisted of larvae within yolk-sac or preflexion stages collected in lower Roanoke River and Albemarle Sound, North Carolina. Slope (B_1) and intercept (B_0) estimates were generated using linear regression techniques.

Species	B_0	B_1	r^2	P	95% Confidence Interval
Blueback herring	0.789	0.337	0.47	< 0.001	0.31 - 0.37
Alewife	0.670	0.252	0.70	< 0.001	0.23 - 0.27

Table 2.9. Comparison of otolith diameter, nucleus diameter, and number of daily growth increments between paired left and right sagittae.

					Left sagitta			Right sagitta		
Species	Comparison	df	$t_{0.05}$	*P*	Mean	SD	SE	Mean	SD	SE
Blueback herring	Otolith diameter	444	0.71	0.48	27.3	6.9	0.5	27.3	7.0	0.5
	Nucleus diameter	444	1.64	0.10	5.6	2.1	0.1	5.5	1.5	0.1
	Increment count	444	0.41	0.68	5.8	1.6	0.1	5.8	1.6	0.1
Alewife	Otolith diameter	378	1.61	0.11	24.9	4.3	0.3	24.5	4.0	0.3
	Nucleus diameter	378	1.84	0.07	5.5	1.2	0.1	5.4	1.3	0.1
	Increment count	378	0.54	0.59	5.6	2.0	0.1	5.6	2.1	0.2

Table 2.10. Results of two independent age determinations using sagittae from larval blueback herring and alewife collected from lower Roanoke River and Albemarle Sound, North Carolina. CV is coefficient of variation, APE is average percent error.

Species	Area	Sample size	Percent agreement (± 0 d)	Percent agreement (± 1 d)	CV	APE
Blueback herring	River	228	78.1	94.7	3.6	2.2
	Delta	174	71.3	95.4	4.4	2.8
	Sound	162	56.8	92.6	6.5	4.1
	Total	564	69.9	94.3	4.7	2.9
Alewife	River	204	63.7	98.0	6.1	7.3
	Delta	104	84.6	100.0	1.9	6.7
	Sound	72	94.4	100.0	0.7	5.8
	Total	380	75.3	98.9	3.9	6.9

Table 2.11. Growth and mortality of blueback herring and alewives collected in lower Roanoke River and western Albemarle Sound, North Carolina. Instantaneous growth was evaluated using back-calculations and marginal increment analysis of otoliths. Growth was estimated for fish over their entire early life history (G_{max}) and within 2 days of capture (G_c). Values represent means (SD). Means sharing a letter in their superscript are not significantly different ($P > 0.05$).

	Blueback herring				Alewife			
Area	Mortality	Growth rate (mm/d)	Instantaneous growth (G_{max})	Instantaneous growth (G_c)	Mortality	Growth rate (mm/d)	Instantaneous growth (G_{max})	Instantaneous growth (G_c)
River	0.88 (0.20)^{A}	0.28 (0.18)^{B}	0.09 (0.03)^{A}	0.07 (0.03)^{A}	0.71 (0.15)^{A}	0.33 (0.14)^{A}	0.10 (0.03)^{A}	0.11 (0.05)^{A}
Delta	0.75 (0.22)^{A}	0.31 (0.14)^{A}	0.09 (0.02)^{A}	0.08 (0.03)^{A}	0.68 (0.15)^{A}	0.26 (0.12)^{B}	0.09 (0.02)^{B}	0.08 (0.03)^{B}
Sound	0.88 (0.20)^{A}	0.28 (0.12)^{B}	0.08 (0.02)^{A}	0.08 (0.02)^{A}	0.51 (0.16)^{B}	0.25 (0.11)^{B}	0.08 (0.03)^{B}	0.06 (0.02)^{C}

Table 2.12. Instantaneous mortality (Z) and daily growth (mm/d) for blueback herring and alewife collected in lower Roanoke River, North Carolina. Values represent means (SD) for 2008 and 2009. Means sharing a letter in their superscript are not significantly different ($P > 0.05$).

	Blueback herring		Alewife	
Month	Instantaneous mortality (Z)	Mean daily growth (mm/d)	Instantaneous mortality (Z)	Mean daily growth (mm/d)
March	0.98 (0.10)^{A}	0.15 (0.17)^{A}	0.68 (0.12)^{A}	0.31 (0.10)^{B}
April	0.82 (0.19)^{A,B}	0.31 (0.15)^{B}	0.77 (0.13)^{A}	0.31 (0.10)^{B}
May	0.66 (0.19)^{B,C}	0.29 (0.11)^{B}	0.64 (0.13)^{A}	0.27 (0.13)^{B}
June	0.55 (0.19)^{C}	0.54 (0.15)^{C}	0.43 (0.13)^{B}	0.47 (0.12)^{A}

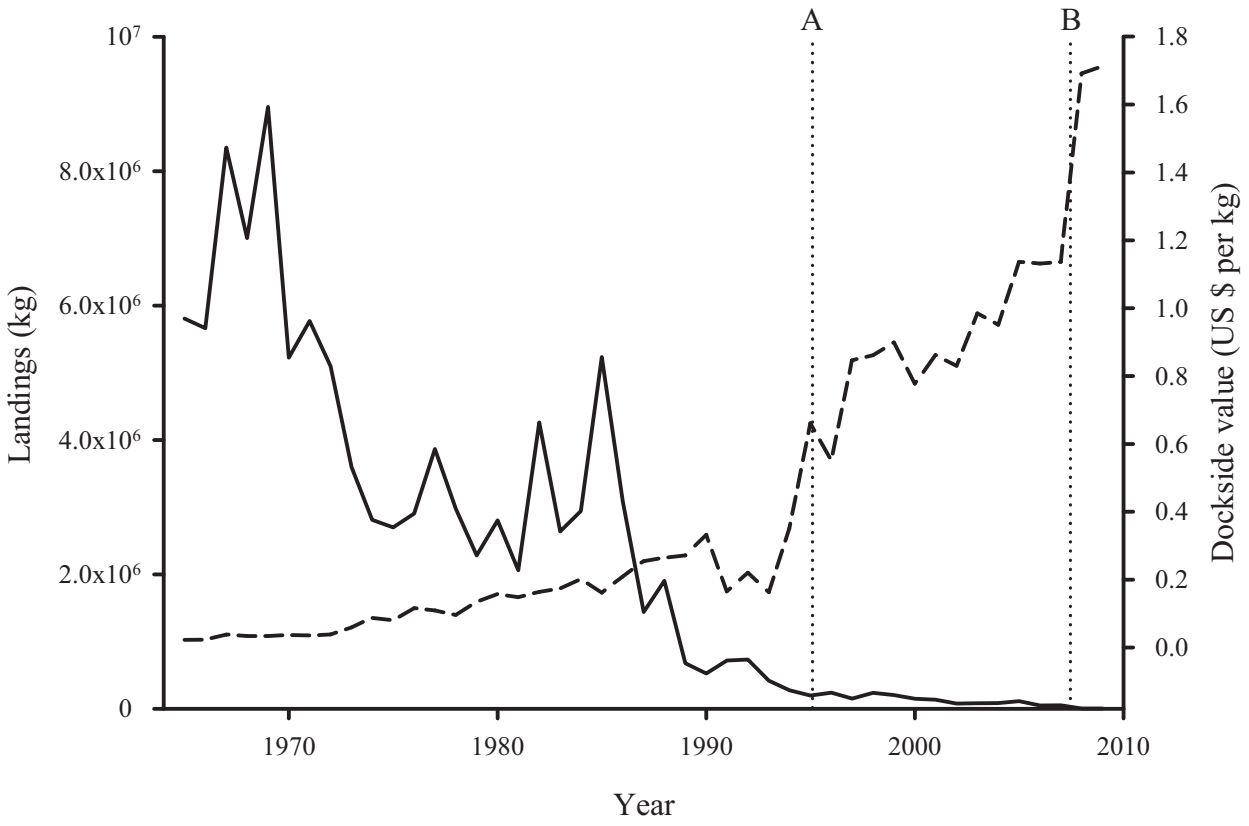

Figure 2.1. Total reported landings (solid line) of river herring for Albemarle Sound from 1965 – 2009. With a declining catch and increased demand, river herring have steadily increased in value (dashed line) over the last 40 years. Data reflect harvest restrictions imposed since 1995 (A) and a moratorium on commercial harvests beginning in 2007 (B).

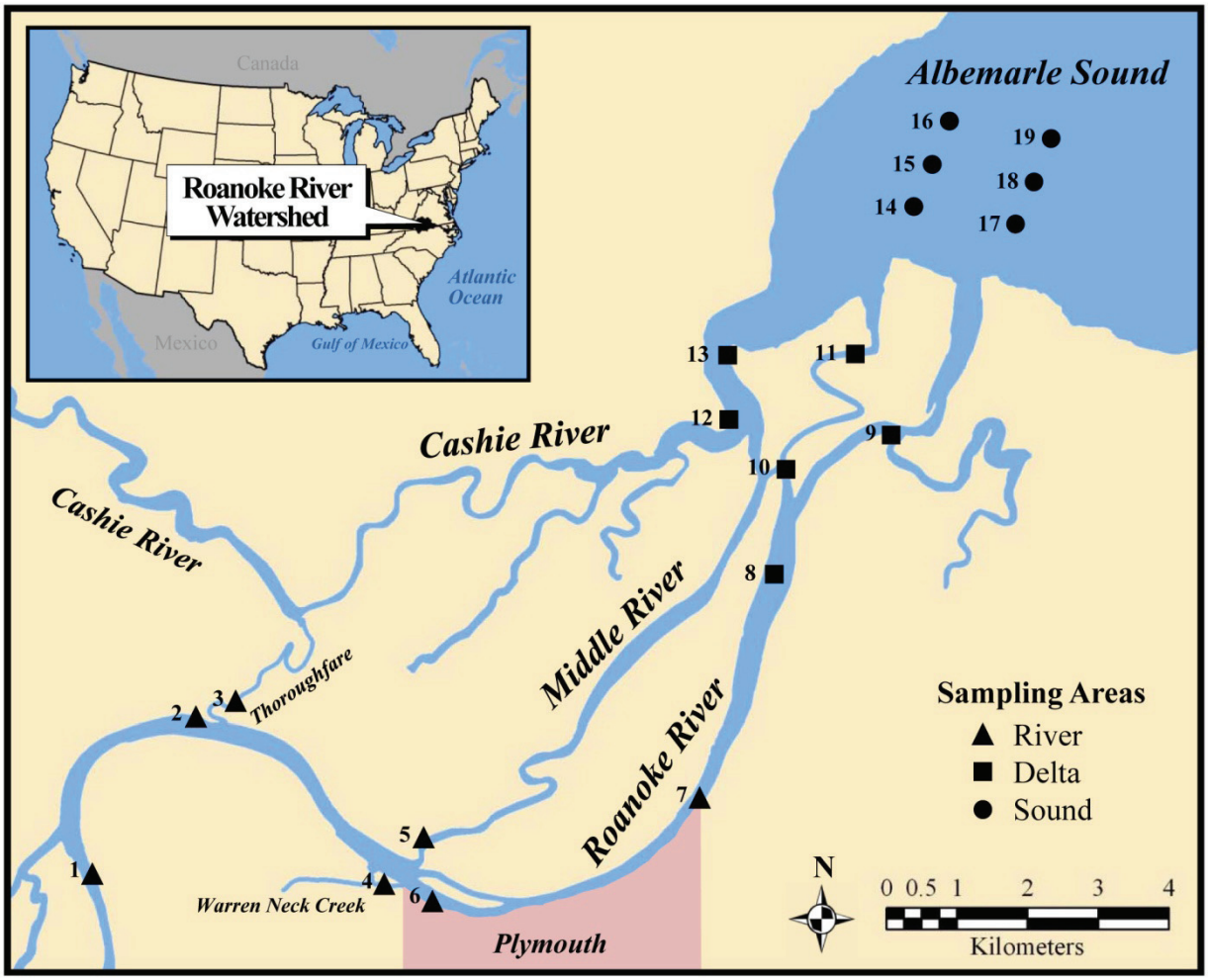

Figure 2.2. Map of fixed stations within three stratified areas (River, Delta, Sound) sampled by pushnet to determine the abundance and distribution of blueback herring and alewife. Stations followed the riverine gradient from the 22-km reach within the main channel of Roanoke River to the open water of Albemarle Sound, North Carolina.

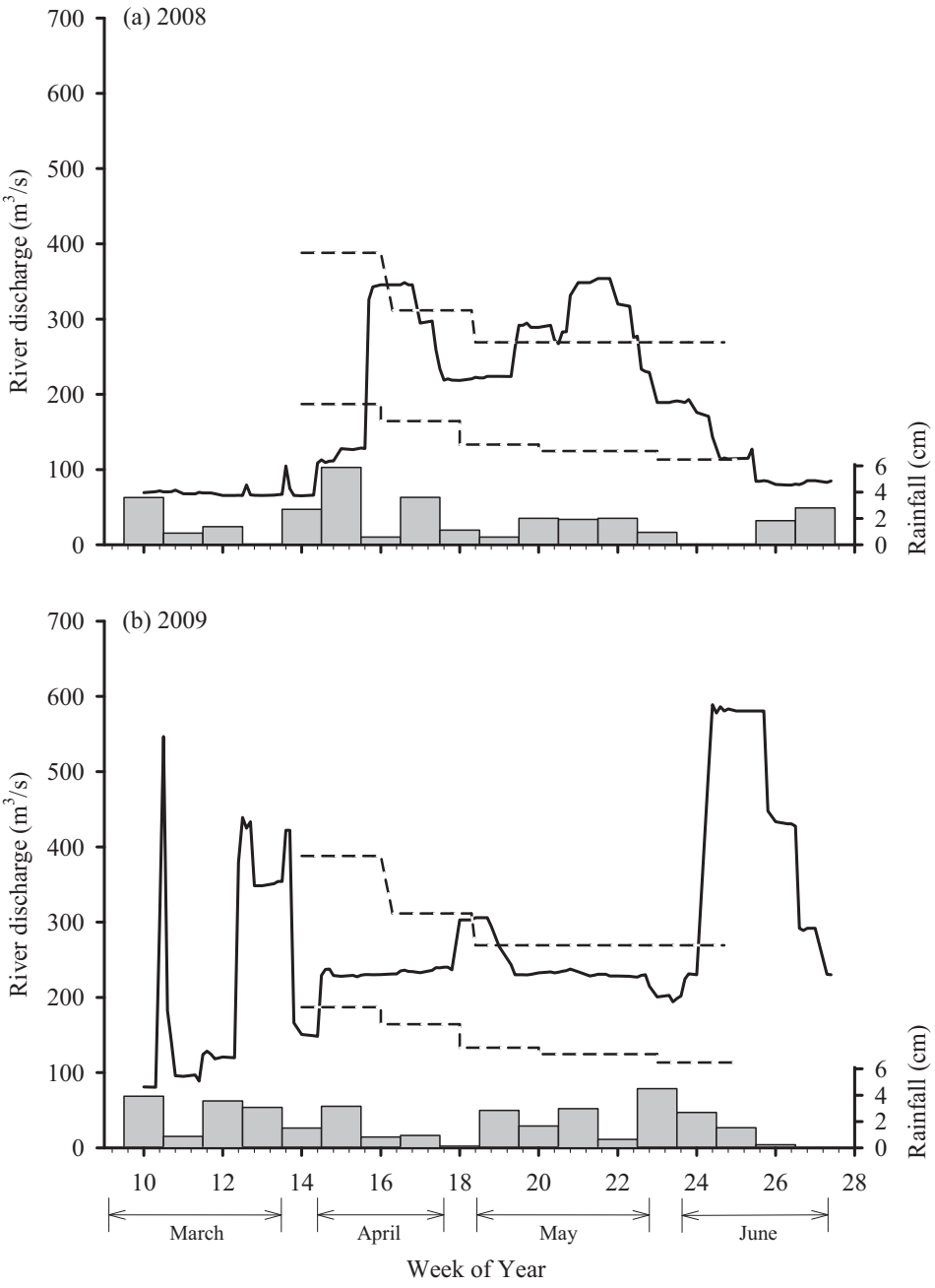

Figure 2.3. River flow (solid line) for 2008 (a) and 2009 (b) recorded by gage located 4.5 km downstream of Roanoke Rapids Dam and 221 km upstream from the study area. Dashed lines indicate the lower and upper regulated flow rates for management of striped bass, *Morone saxatilis*. In addition, outflow from the dam is limited to 42 m^3/s flow differential per hour. Rainfall data were obtained from a weather station located within the study area in Plymouth, North Carolina.

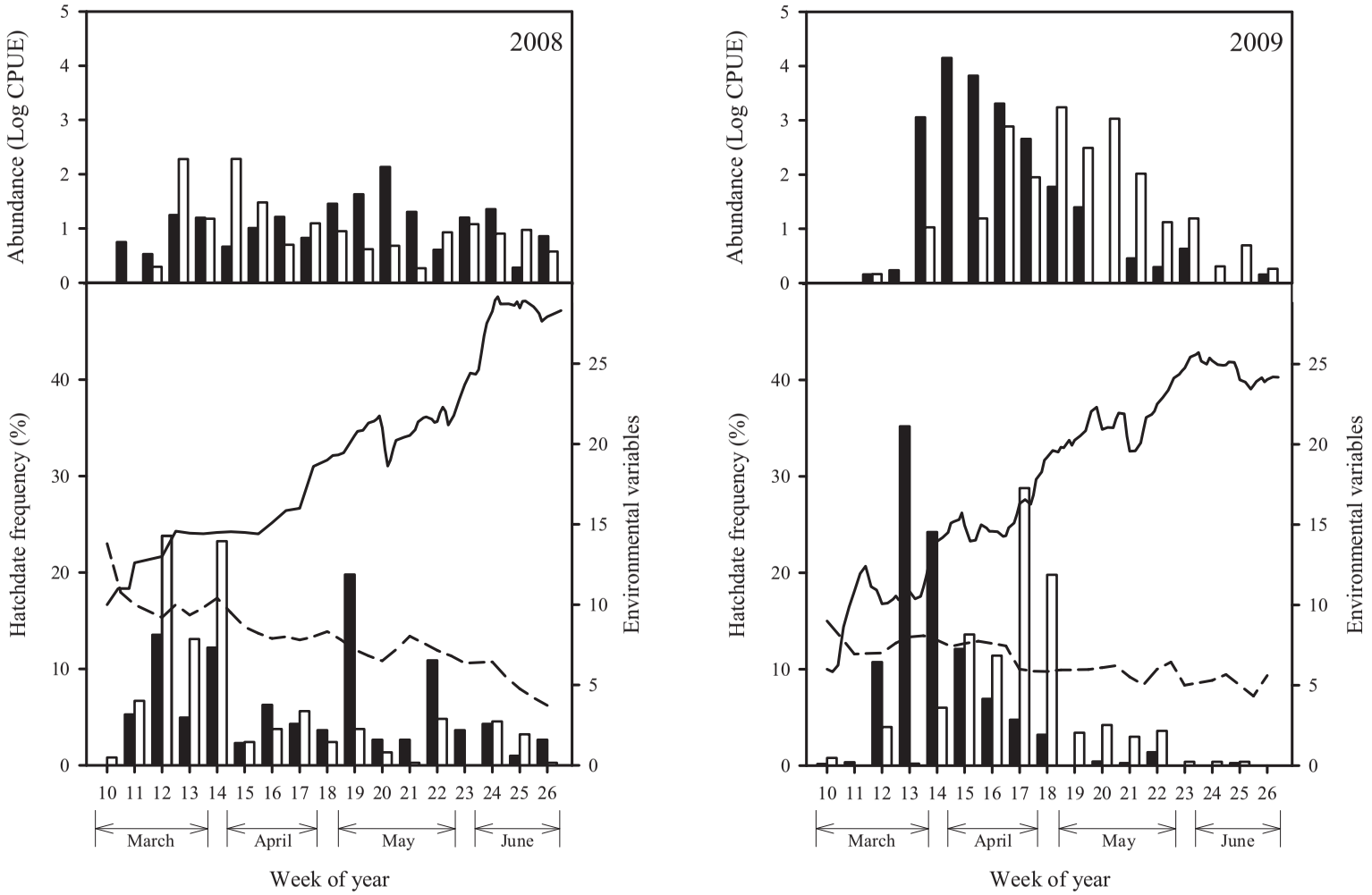

Figure 2.4. Abundance and hatch date distribution of blueback herring (solid bars) and alewife (empty bars) from lower Roanoke River and western Albemarle Sound in 2008 and 2009. During the study period from March through May, water temperatures (solid line) generally increased while dissolved oxygen concentrations (dashed line) decreased. Values for abundance (fish /100 m3), water temperature (°C), and dissolved oxygen (mg/L) represent means.

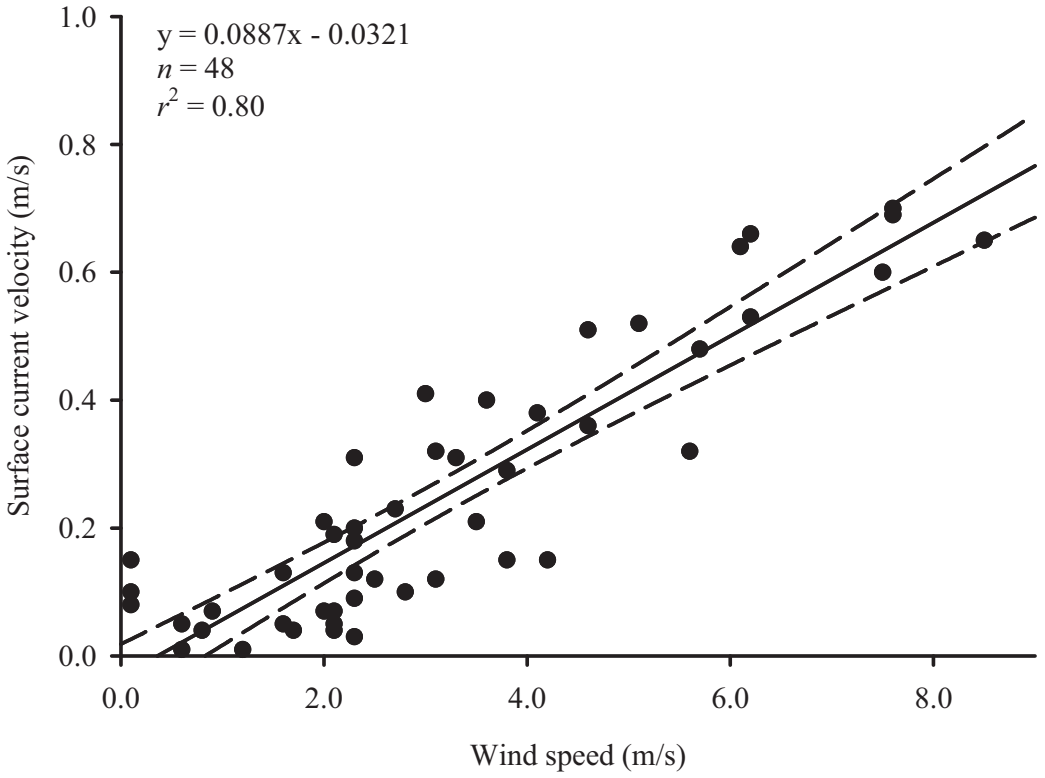

Figure 2.5. Linear regression analysis of wind speed and surface water currents in Albemarle Sound during spring 2008 and 2009. Because of the east-west orientation of the Sound that spans 1,300 km^2, surface water movement and circulation were predominantly driven by winds from the east (36%) and southwest (32%). Dashed lines represent 95% confidence interval.

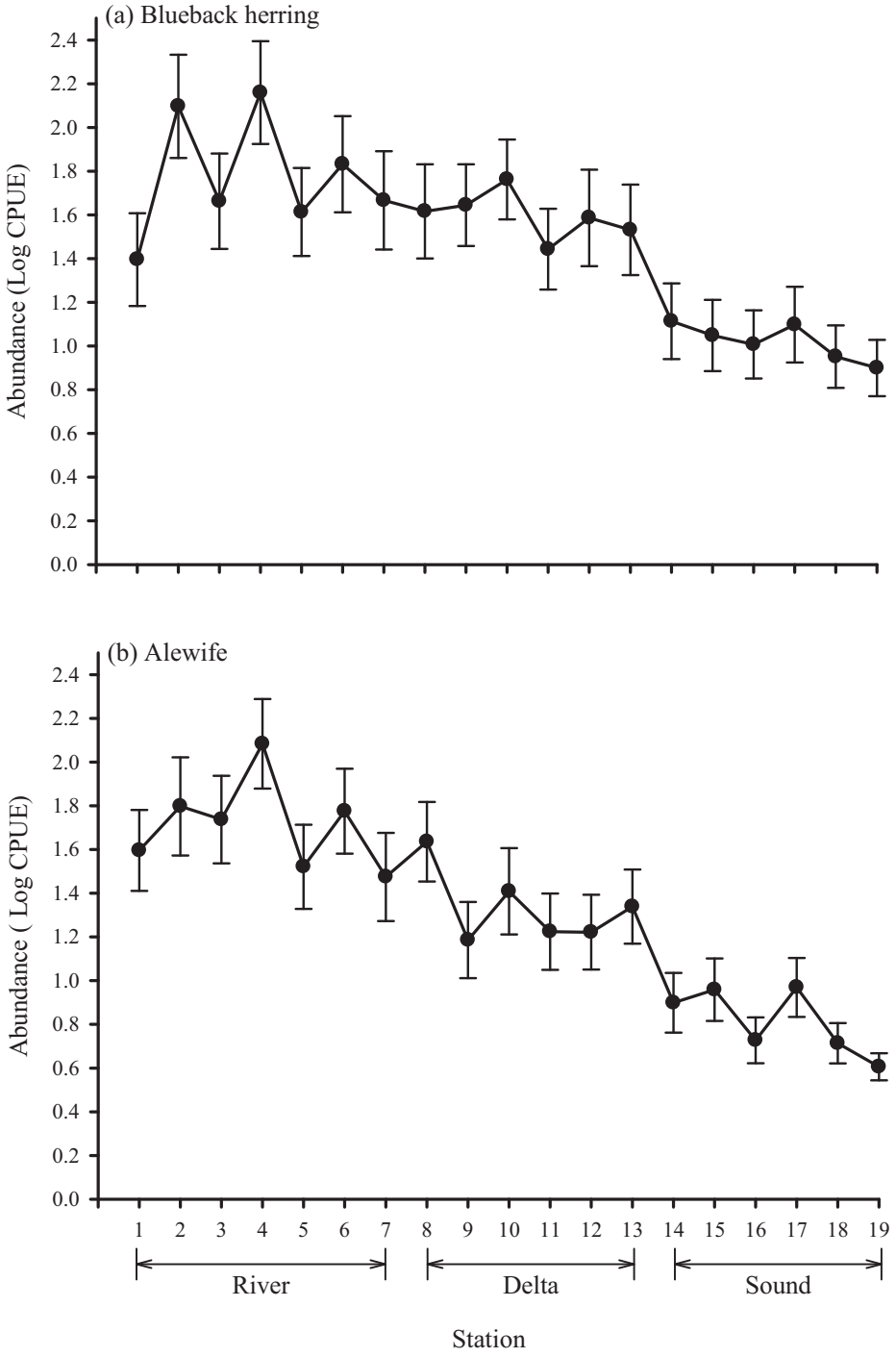

Figure 2.6. Abundance and distribution of blueback herring (a) and alewife (b) at fixed stations within the lower Roanoke River and western Albemarle Sound. The highest abundance of blueback herring and alewife was consistently observed in Warren Neck Creek (Station 4), a small tributary off the mainstem of the Roanoke River. Values represent means (±SD).

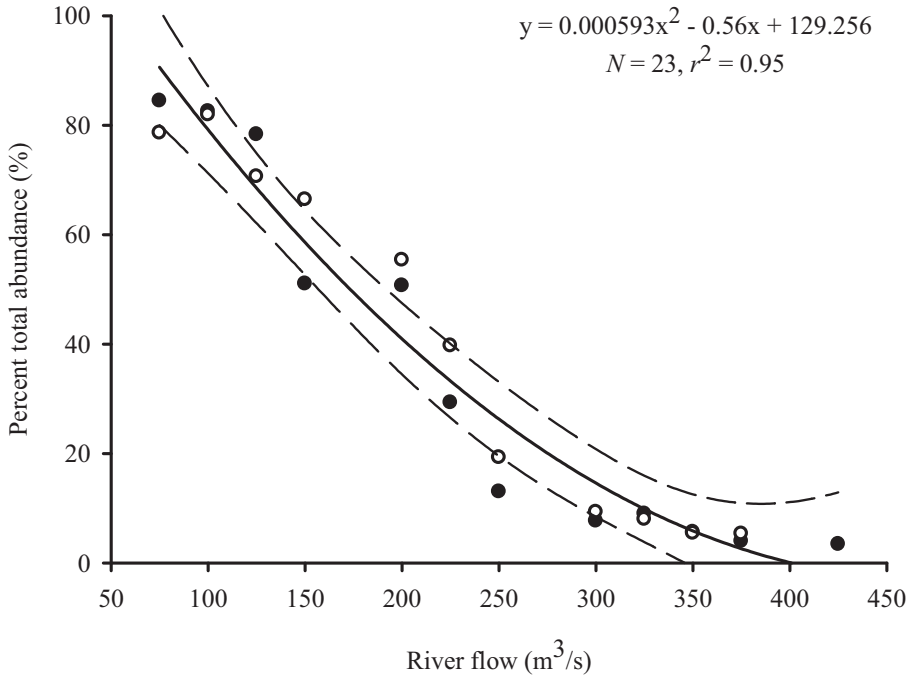

Figure 2.7. Advection of river herring from Roanoke River mainstem to distributaries was predictable and was not significantly different between Thoroughfare and Middle River. During periods of low river flow, larval advection from the mainstem channel was high and was not correlated with proportional rates of water loss from mainstem channel. Values represent proportions of river herring in Thoroughfare (filled circles) and Middle River (empty circles) compared to Roanoke River.

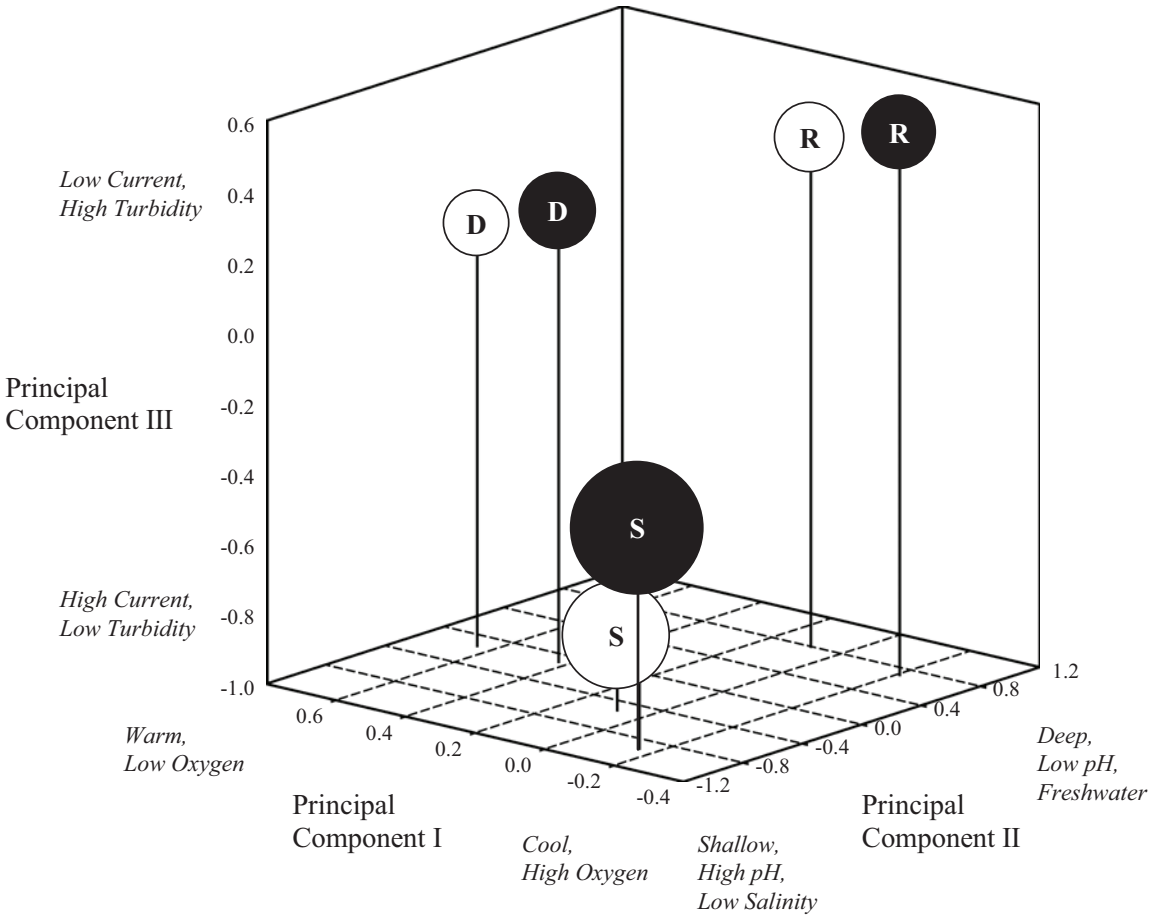

Figure 2.8. Distribution and habitat use patterns of larval blueback herring (black circles) and alewife (white circles) in three-dimensional principal component space. Balloons indicate the location of centroids, with balloon radii representing two standard errors about the mean. Eigenvalues and eigenvectors explain 77% of the variance from the components. Area codes are: R = Roanoke River, D = Delta, and S = Albemarle Sound.

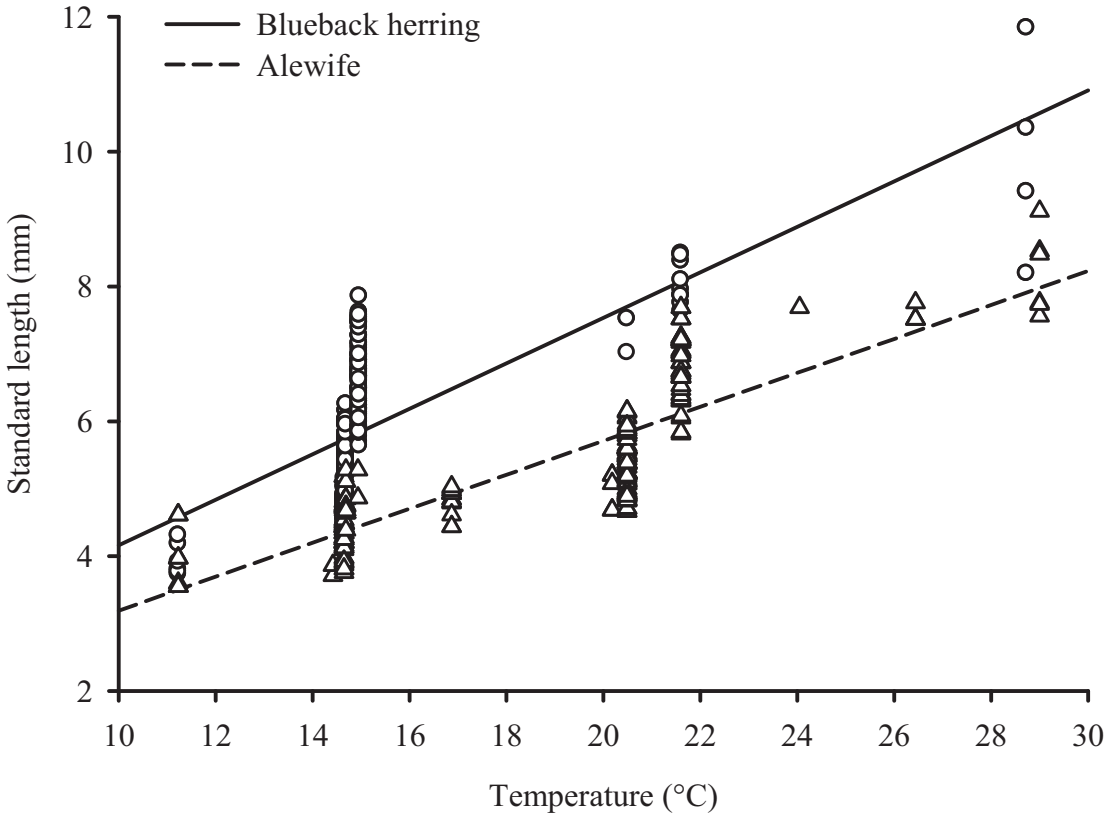

Figure 2.9. Standard length of blueback herring (circles) and alewife (triangles) was positively correlated with water temperature. Significant differences were observed between species (ANCOVA; $F = 20.36$, $N = 798$, $P < 0.001$).

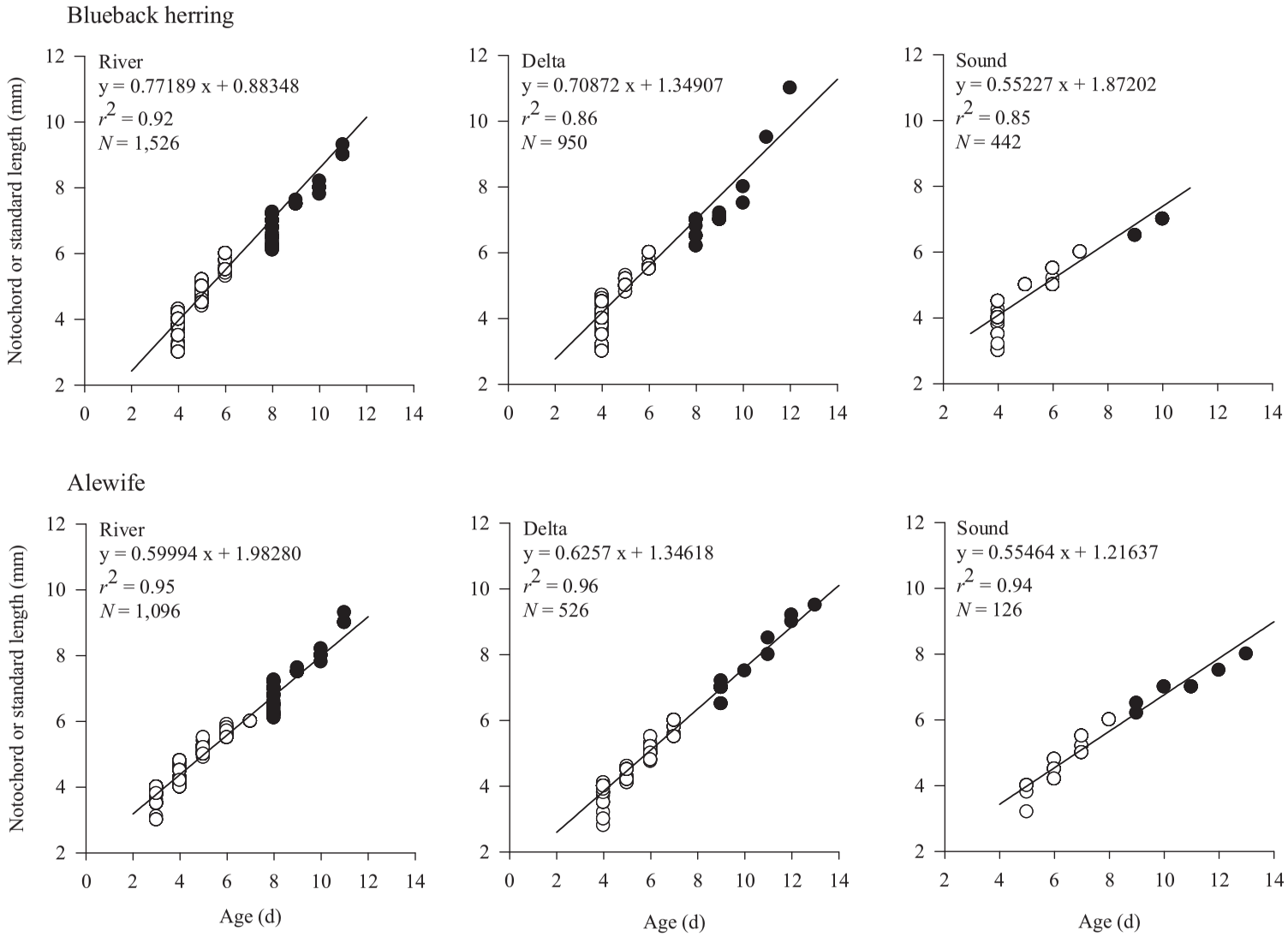

Figure 2.10. Length-at-age relationships for larval blueback herring and alewife within lower Roanoke River and Albemarle Sound, North Carolina. Regression coefficients represent larval growth within three separate nursery areas. Larvae retaining a yolk-sac are designated with white circles.

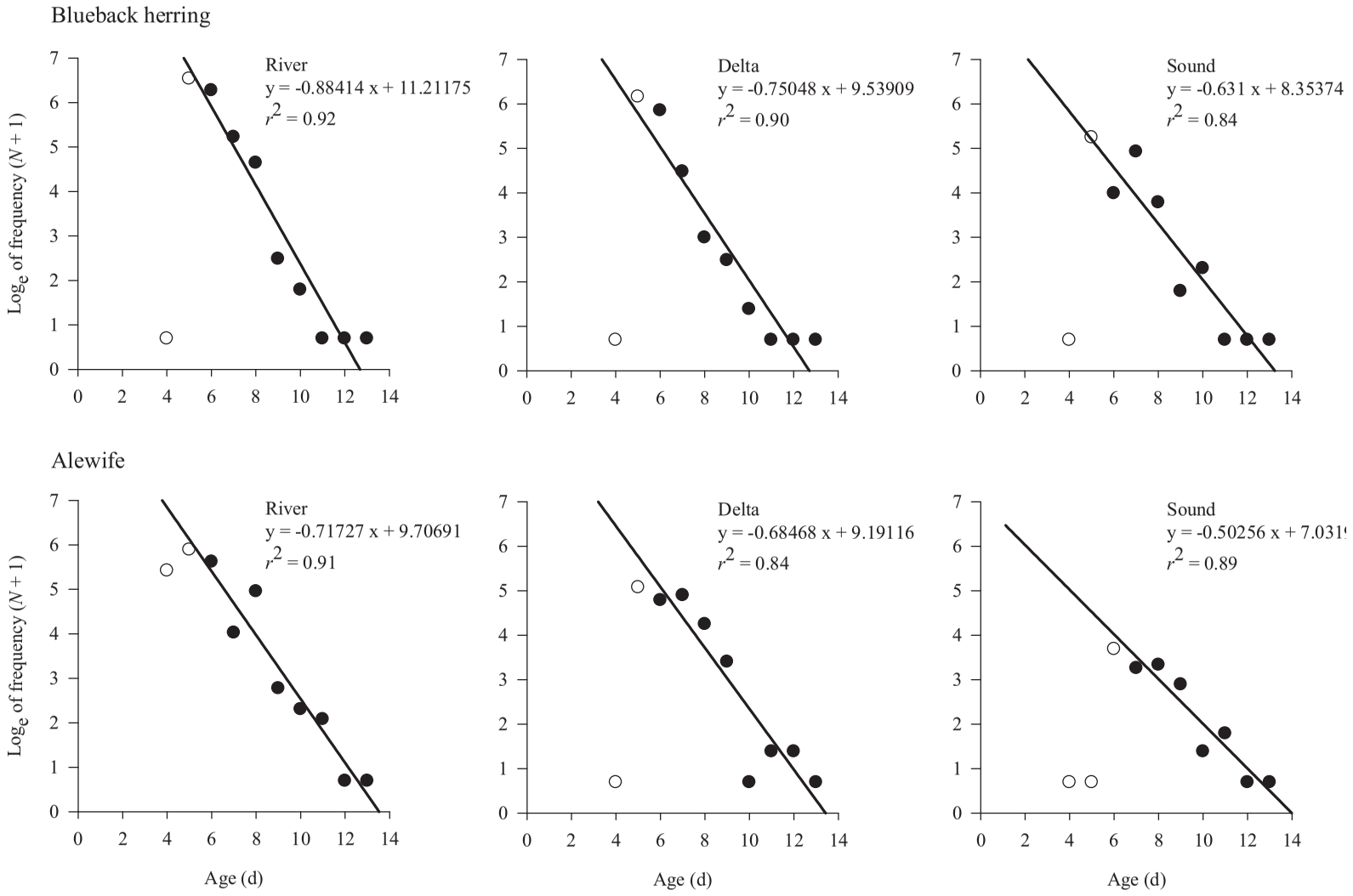

Figure 2.11. Abundance at age plots for larval blueback herring and alewife during peak periods of recruitment to lower Roanoke River and Albemarle Sound, North Carolina. Regression coefficients represent total instantaneous mortality (*Z*) within three separate nursery areas. Regressions were adjusted to only include fish fully recruited to the gear (black circles).

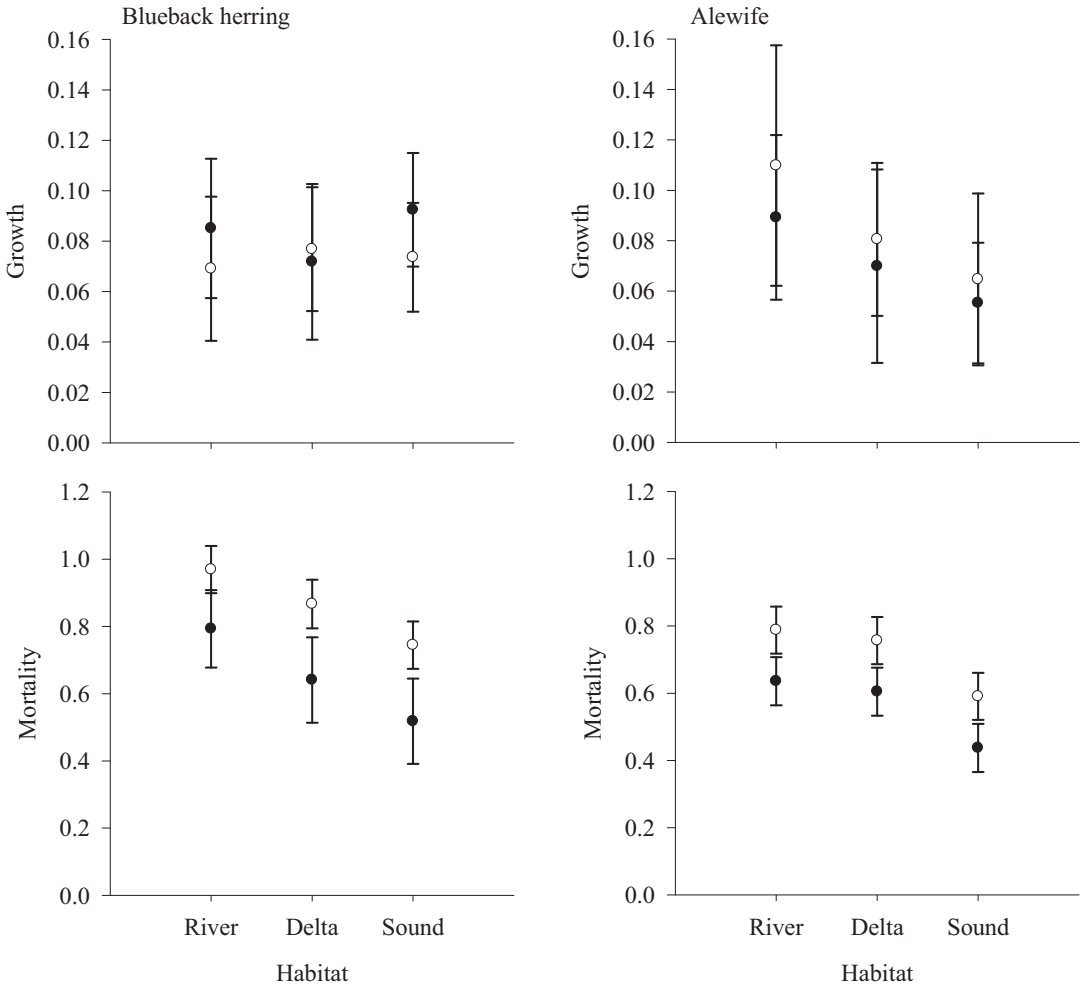

Figure 2.12. Instantaneous daily growth and mortality for larval blueback herring and alewife collected from lower Roanoke River and Albemarle Sound, North Carolina in 2008 (black circles) and 2009 (white circles). To evaluate habitat-specific growth, marginal increment analysis was used to back calculate growth within 2 d of capture. Values represent means (±SD).

CHAPTER 3. DISTRIBUTION, FEEDING ECOLOGY, AND CONDITION OF LARVAL BLUEBACK HERRING AND ALEWIFE IN TRANSITIONAL AREAS OF A FLOW-REGULATED RIVER SYSTEM

Abstract

Spatiotemporal overlap between larval fish and their prey is thought to have important effects on growth, survival, and recruitment success. The aim of this study was to investigate the ecological processes that influence recruitment of river herring (blueback herring *Alosa aestivalis* and alewife *A. pseudoharengus*) to lower Roanoke River and Albemarle Sound, North Carolina. Weekly sampling of nursery habitats allowed for analyses of diets and diet variability. Blueback herring were the most abundant species caught (78%) and their abundance (number/100 m^3 ± SD) was significantly higher in April (47.7 ± 15.6, $F_{2,91} = 3.87$, $P = 0.02$). Blueback herring abundance peaked during week 14 with 121.8 ± 54.1. The catch of alewife was low for all months, but peaked in May during week 19 with 24.4 ± 8.5. River herring abundances were not significantly different among the areas sampled. Most river herring larvae were small (3.2 – 10.8 mm) and many retained a yolk-sac (45%) or were at the first-feeding stages (20%). Larvae do not appear to be food limited in this system as indicated by diet analyses and the spatiotemporal overlap between river herring and zooplankton. Diets varied little with early ontogeny, and the smallest taxa (copepod nauplii and rotifers) accounted for over 85% of the diet. Blueback herring and alewife strongly selected for bosminids and copepod nauplii in areas where these prey were available. Because of a high-level of dietary overlap, intraspecific and interspecific competition is substantial for anadromous alosines.

Introduction

Anadromous clupeids (shads and herring) have complex lifecycles where individuals migrate great distances offshore along the continental shelf and then return to their natal rivers to spawn. Along the east coast of the United States, the distribution for most alosines is similar and the anadromous life cycle of these species differs only in the specific timing of their migration to spawn in freshwater (Cooke and Leach 2003). Timing of migration varies with latitude and is strongly correlated with water temperature (Mansueti 1962; Leggett and Whitney 1972; Loesch 1987; Limburg et al. 2003; Murauskas and Rulifson 2011). Sexually mature adults begin migrating in late winter and early spring leaving the open ocean for protected inshore coastal bays and sounds. During brief residency in estuaries, these fish use productive waters to build energy reserves and then migrate through coastal rivers to their spawning grounds (Bigelow and Schroeder 1953). In North Carolina, American shad *Alosa sapidissima*, hickory shad *A. mediocris*, and river herring (blueback herring *A. aestivalis* and alewife *A. pseudoharengus*) historically migrated to the headwaters of the Cape Fear, Neuse, Tar, Roanoke, and Chowan (Rulifson et al. 1982). Adults would navigate through thousands of kilometers of inland waterways, ascend hundreds of meters in elevation, and traverse natural obstacles to reach spawning grounds at the headwaters of these rivers. Although shad and river herring continue to use many of the same routes, inland migrations have become restricted because dams and barriers exist on nearly all rivers and coastal streams in North Carolina (Collier and Odom 1989; Beasley and Hightower 2000). Without access to upstream reaches, fish spawn at select habitats within the dam tailrace, river channel, distributaries, and adjacent flooded hardwood forests.

Characterization of riverine spawning and nursery habitats has become an important objective for the management and restoration of American shad and river herring (Greene et al.

2009). Recent studies in Roanoke River, North Carolina have focused on identifying specific spawning sites (Sparks 1998; Harris and Hightower 2010) and nursery habitats for early life stages (Walsh et al. 2005). This coastal river system has received increasing attention, because it once supported artisanal fisheries and large-scale industrial operations in Albemarle Sound (Chestnut and Davis 1975). Unfortunately, over the past thirty years American shad and river herring abundances in Roanoke River and Albemarle Sound have declined to levels far below historical records (Rulifson 1994; Hightower et al. 1996; Cooke and Leach 2003), while in the same river system the recovery of striped bass *Morone saxatilis* has become a regional success story for management of diadromous fishes (Haeseker et al. 1996; Field 1997; Richards and Rago 1999).

Understanding factors related to declining populations of American shad and river herring is complex. Declines are largely influenced by human activities in the coastal zone resulting in habitat alteration and degraded ecological conditions (Waldman and Limburg 2003; Limburg and Waldman 2009). Because most alosines exhibit relatively short generation times, high natural mortality, and low number of ages exposed to harvest, restoration and protection of dwindling populations requires measures that extend beyond a reduction in fishing mortality (Boreman and Friedland 2003). Restoration requires a concerted effort to advance fish passage and access to spawning habitats, preserve water quality, provide adequate river flow, and bolster recruitment through identification and protection of nursery habitat.

This study represents part of a large-scale project using laboratory and field-derived data to identify blueback herring and alewife nursery habitats used in lower Roanoke River and western Albemarle Sound, North Carolina. Information on nursery habitats for production of river herring in this coastal river system is limited. The habitats and environmental conditions

supporting production of striped bass larvae are well documented and believed to differ from river herring only in the temporal distribution of larvae (Rulifson and Manooch 1990a; Rulifson et al. 1992; Cooper 1996). Most research with river herring in Roanoke River has focused on techniques to document the presence or absence of eggs or larvae. During peak spawning, blueback herring and alewife larvae have been collected throughout much of the river below the hydroelectric dam located 221 km upstream from the river mouth (Street et al. 1975; Hayman and Holloman 1996; Harris and Hightower 2010). Within a small section of the river 100 km below the dam, Walsh et al. (2005) observed that blueback herring and alewives use a variety of habitats including backwater tributary systems and flooded bottomland hardwood forests. Habitat use was significantly affected by fluctuations in river flow and periods with high flow increased connectivity between habitats. Within the lower river (10 km upstream from river mouth), Rulifson and Overton (2005) observed a similar relationship with river flow. River herring exhibited a preference for small distributaries despite high flows that would typically concentrate and transport larvae in the mainstem of the river.

The goal of this study was to evaluate production of larval blueback herring and alewife within transitional areas of a flow-regulated river system. To build upon previous studies and gain a better understanding of riverine habitats available, 108 km^2 within the lower Roanoke River watershed were sampled. The specific objectives were (1) to determine the spatiotemporal distribution of alewife and blueback herring during peak periods of larval production; (2) to examine how physical properties and prevailing environmental conditions, especially river flow, influence retention or advection of larvae and prey resources, and (3) to compare diet and food selectivity among larvae at various habitat types. This study is the first to compare feeding ecology and dietary overlap with first-feeding blueback herring and alewives.

Methods

Study Area

The Roanoke River drains an expansive watershed (25,000 km^2) that originates in the mountains of Virginia and flows southeast through the piedmont and coastal plain of North Carolina to Albemarle Sound. Flows in the watershed were unregulated until 1950; since then six dams have been constructed for flood control, hydroelectric power generation, water supply, and recreation. None of the dams constructed included provisions for fish passage. The most downstream facility on the river, Roanoke Rapids Dam, has restricted fish migrations since completion in 1955 (Zincone and Rulifson 1991). Flow patterns in the lower river (below Roanoke Rapids Dam) are controlled by the release schedules of upstream dams (Giese et al. 1985). Flows within this region are also seasonally regulated from April through mid-June to maintain the river's natural flow regime, which presumably provides migratory and spawning cues for striped bass and increases access to spawning or nursery areas. During striped bass spawning season, water is discharged from Roanoke Rapids Dam to maintain river flow within the range of 167 to 240 m^3/s and mimic preimpoundment (1912-1950) flow characteristics (Rulifson and Manooch 1990b; Rulifson and Manooch 1990a).

Study sites were selected by use of a random stratified sampling technique. The study area within the lower Roanoke River and western Albemarle Sound was stratified into three areas (*e.g.*, River, Delta, Sound), which were delineated using a geographic information systems database and records of historical sampling programs. The selection of these three areas was designed to provide broad scale information on temporal and spatial abundance of alosine larvae. The habitats within these areas support river herring during a critical phase in their early life history and represent transitional areas that connect the river with the estuary. The distribution

of stations followed the riverine gradient from the 22-km reach within the main channel of Roanoke River to the open water of Batchelor Bay, located on the western boundary of Albemarle Sound (Figure 3.1).

Field Sampling Procedures

Water quality, ichthyoplankton, and zooplankton samples were collected at weekly intervals during spring 2009 between March 9 and May 27, when larval river herring were abundant. Two stations from each strata were randomly selected for each week sampled. Sampling was conducted during the day (10:00-16:00) and at night after sunset (19:00-04:00). Strata and stations were sampled in random order sequence to minimize the variance related to temporal variation inherent to ichthyoplankton and zooplankton communities. Sampling gear efficiencies were assumed to be equal in all areas.

Ichthyoplankton were collected using paired surface pushnets supported from an aluminum frame mount on the bow of a 5.8-m boat. Each net had a 0.5-m square opening and a mouth-to-tail ratio of 1:5. Nets were constructed of 505-µm nitex mesh with a Dacron® collar sewn at the mouth. The net mesh size was selected because it allowed comparative analysis with long-term ichthyoplankton sampling programs and the size prevented excessive clogging of nets with detritus and floating debris (Zincone and Rulifson 1991; Overton and Rulifson 2007). Each net was equipped with a calibrated mechanical flowmeter (Model MF315, SeaGear Corp., Melbourne, Florida) mounted inside the mouth of the net allowing for a calculation of the volume of water filtered. The surface nets were pushed at a uniform speed of 1.5 m/s for 120 s. The contents of each net were washed down, condensed in a 1-L plastic collection jar, and preserved with 5% buffered formalin.

Zooplankton samples were collected at each station using a vertical haul technique that sampled the entire water column. This technique was selected because it allowed comparisons of the planktonic community without the temporal effects of vertical migratory behavior exhibited by some planktonic species. Zooplankton were collected using a conical net constructed of 90-µm nitex mesh material, with a 0.5-m diameter mouth opening and a 1:3 mouth-to-tail ratio. The contents of the net were washed down and condensed in a 1-L sample jar and preserved with 5% buffered formalin. The depth from which the net was pulled was recorded for calculating abundance estimates.

Several environmental and hydrographic parameters were recorded for each area and station. These parameters were selected based on their relationship with habitat, water quality, and food resources. Air temperature (°C) and wind speed (m/s) were measured using a portable digital anemometer (Skymate Model SM-18, Campbell Scientific, Inc., Logan, UT). Water quality was measured 1 m below the surface and 1 m above the bottom substrate using a multiparameter dissolved oxygen probe (Model 85, YSI, Inc., Yellow Springs, OH). Water flow was measured at each station from an anchored position. Current velocity (m/s) and direction were measured 1 m below the surface using a portable electromagnetic flow meter (FLO-MATE 2000, Marsh-McBirney, Inc., Frederick, MD). Surface water samples (100 ml) were collected for analysis of pH (Model 98128, Hanna Instruments, Woonsocket, RI) and turbidity (Model DRT15, HF Instruments, Ltd., Bolton, Ontario, Canada).

To determine long-term trends in water temperature, data loggers were deployed within each region (IBCod Type 22L, Alpha Mach, Inc., Mont St-Hilaire, Quebec, Canada). Data loggers were attached to a fixed mooring station, and water temperatures were recorded 1 m below the surface and 1 m above the bottom. Temperatures were recorded at 15-min intervals for the

duration of the project. Precipitation and air temperature data were obtained from a 2-m weather station located at Tidewater Research Station in Plymouth, North Carolina. The State Climate Office of North Carolina operates the weather station and data are maintained by the National Climatic Data Center. Daily water discharge rates were obtained from Roanoke Rapids Dam water monitoring gage, located 4.5 km downstream of the dam and 221 km upstream from the study area (SCONC 2009). The gage is maintained by US Geological Survey and Dominion Power Company and records hourly discharge rates and river height data (USGS 2009).

Laboratory Processing of Samples

Larval fishes

Ichthyoplankton samples were transferred to 95% ethyl alcohol after 24 h. Fish larvae were separated from debris, counted, and identified using a dissecting microscope (Olympus SZX-ILLD100, Tokyo, Japan) and a variety of larval taxonomic keys (Lippson and Moran 1974; Auer 1982; Sismour 1994a; Walsh et al. 2005). Intact alosines were identified to species, whereas degraded fish were classified as either "*Alosa* species" (< 0.05% of total) or "river herring" (< 0.05% of total) based on length measurements and meristic characters. The abundances of larval fish were standardized as the number of fish sampled per 100 m^3. Abundance estimates within each strata were calculated by averaging the catch at each station.

The standard length (SL) and total length (TL) of all alewife and blueback herring were recorded to the nearest 0.25 mm using a dissecting microscope equipped with an ocular micrometer. From each sample, a subsample of 5 alewife and blueback herring were used for measurement of selected anatomical features, diet analysis, gut fullness, and dry weight. Specimens were randomly selected to ensure that observations of size, body condition and recent

feeding history were well represented. Larvae were digitally photographed using a dissecting microscope at 40-x 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 were measured and analyzed using image analysis software (Image-Pro Discovery software version 4.5, Media Cybernetics, Inc., Silver Spring, MD). All measurements were recorded to the nearest 0.001 mm and calibration errors were maintained at less than 1 μm (≤0.1% of 1 mm).

Body lengths were recorded as SL and TL (Snyder 1983). For each larva, size of the yolksac, gut length, and gut fullness were recorded. Yolk volume was determined by using the equation for a prolate spheroid:

$$\textit{Yolk volume} = 4/3\ \pi\ [\textit{yolk-sac length}]\ [\textit{yolk-sac depth}]^2. \quad (1)$$

Gut fullness was measured as presence or absence of food in proportion to the length of the entire alimentary canal (*i.e.*, gut length). Gut contents were examined by carefully dissecting prey items from the alimentary canal using fine dissecting needles. Prey were counted and identified to the lowest taxonomic level and life stage possible. Predominant and intact prey classified as bosminid, copepod, daphnid, dipteran, ostracod, and rotifera were measured in length and width using the same methods previously described for digital photography and image analysis.

A feeding ratio, or mean number of prey per larval gut, was calculated for each diel period and area. The ratio was used as an index of recent feeding activity. Changes in prey size use patterns with ontogeny were examined using quantile regression procedures (Scharf et al. 2000; Costa 2009). This procedure was selected because the ontogenetic shift to larger prey sizes was slow and river herring throughout their early life stages continued to consume small prey. Niche

breadth (the relative variance in prey size) was calculated as the standard deviation of log-transformed mean prey widths (Young et al. 2010). Data from gut contents and zooplankton sampling were used to evaluate prey selectivity and feeding peculiarities. The Manly-Chesson preference index (Chesson 1978; Chesson 1983) was used to compute prey selectivity for blueback herring and alewife. The index is one of the most widely accepted mathematical indexes for prey selectivity (Manly 2002; Chipps and Garvey 2007) because it is possible to test the apparent selectivity against a random model (Manly 1974). The index is also amenable to parametric statistical analyses because selectivity measures are approximately normally distributed.

Selectivity was defined as the difference between the proportion of prey type in the diet and the proportion of prey type in the forage base (*i.e.*, plankton community). The Manly-Chesson index was computed as:

$$\alpha_i = \frac{r_i}{n_i} \frac{1}{\sum(r_j/n_j)} \qquad i = 1, \ldots, m \tag{2}$$

where α_i is Manly's alpha for prey type i; r_i and r_j are proportion of prey type i or j in the diet; n_i and n_j are 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 $1/m$.

The dry weight (DW) of larvae was used with length measurements to assess the morphometric condition of larvae. Dissected larvae, including gut contents, were dried overnight in aluminum pans at 60 °C to a constant weight (24 h). Samples were transferred and temporarily held in a desiccator after drying. Fish were individually weighed to the nearest µg using a Cahn microbalance (Thermo Electron Corporation, Beverly, MA). The relationship between length and weight was evaluated using regression analysis with

logarithmically transformed data (log_{10}) for SL and DW. Evidence of different growth trajectories was interpreted as a significant interaction effect with habitat. Analysis of covariance (ANCOVA) was used to compare slopes of length-weight regressions for blueback herring and alewife from each area.

Fulton's condition index was used to quantify the overall condition of the larvae (Bolger and Connolly 1989). The index is the condition factor, K:

$$K = (W / L^3) \text{ x } 100, \quad (3)$$

where W is dry weight (μg), L is standard length (mm), and 100 is a scaling constant. Fulton's condition index has proven most useful when coupled with other growth and condition indices for larval fishes (Lochmann et al. 1997; Suthers 1998).

Zooplankton

Within 24 h of sampling, zooplankton samples were condensed to known volumes and transferred to 95% ethyl alcohol. Zooplankton were identified using a dissecting microscope and taxonomic keys for freshwater zooplankton (Balcer et al. 1984; Thorp and Covich 2001; Haney 2010). Prey were counted and identified to the lowest taxonomic level or life stage practical. At least 50 individuals were identified from each subsample. Abundances were determined by counting all organisms within 5-ml subsamples taken with a Hensen-Stempel pipette. The average of two replicates was used to calculate abundance. Zooplankton abundance estimates were standardized (number/m^3) by dividing total number of zooplankton per sample by the volume of water filtered. The size distribution of zooplankton was determined using digital image analysis. From each sample, up to 10 individuals representing each prey taxa were randomly selected and measured. Body length and width (appendages excluded) of zooplankton

were measured according to Culver et al. (1985). For the cyclomorphic forms of cladocerans, length was measured from the anterior margin of the helmet to the base of the tail spine. Copepods were measured from the head to the base of caudal spines. In determining forage base and prey selectivity, ichthyoplankton and other large organisms (> 1 mm in length or width) were removed from the zooplankton dataset.

Statistical analysis

The general linear model function in SAS (SAS 9.2; SAS Institute, Cary, NC, USA) was used for all analyses unless otherwise noted. Exploratory statistical analysis was conducted to determine whether area, diurnal period, or environmental parameters accounted for a significant amount of variability in the spatiotemporal distribution of river herring and zooplankton. To satisfy assumptions of parametric tests and univariate normality, Shapiro-Wilk's *W*-test and residual plots were used to analyze the distribution of each data series (Shapiro and Wilk 1965; Royston 1992). When necessary, data were logarithmically transformed ($\log_{10}$) before statistical analysis to normalize observations and stabilize the variance. Fish and abundance data with zero values were transformed by using lognormal data and adding 0.01 to account for zeros. An arcsine-square root transformation was applied to proportional data for gut fullness and prey frequency of occurrence.

Environmental parameters including river discharge, depth, water flow, water temperature, dissolved oxygen, salinity, pH, and precipitation were analyzed using independent samples *t*-test for diurnal period and analysis of variance (ANOVA) for week of year, month, and location. ANOVA was also used to statistically compare data that included abundance estimates, predator and prey size, number of prey in gut, gut fullness, prey selectivity, and indices of larval

condition. If the ANOVA was significant, the Ryan-Einot-Gabriel-Welch (REGWQ) test was used to determine if significant differences existed among treatment means. This post-hoc test, based on the studentized range statistic, holds family wise alpha at 0.05.

A one-way multiple analysis of variance (MANOVA) was used to evaluate diet composition and test for an overall location effect. Wilks' lambda was used to test the hypothesis that prey types within river herring diets have identical means among areas (McGarigal and Cushman 2000). Wilks' lambda ranges from 0 to 1, with 0 indicating strong differences between groups (McGarigal and Cushman 2000) . Within the MANOVA, individual ANOVAs compared prey type by area. Because ANOVAs were completed a posteri, appropriate alpha levels for pairwise comparisons were obtained using a Bonferroni correction (Chipps and Garvey 2007). Alpha levels were adjusted downward based on the number of treatments (α / n) and differences were considered significant at $P \leq 0.005$.

In order to explore relationships within the zooplankton community and river herring diets, PRIMER v6 (Primer-E Ltd, Plymouth, UK) was used to conduct multivariate analysis and derive similarity matrices based on Bray-Curtis similarity coefficients (Clarke and Warwick 2001). This software package has been used to reveal patterns in zooplankton community structure (Wishner et al. 2008) and study diet overlap among fishes (Sampson et al. 2009). Prior to analysis, data were checked for multicolinearity, outliers, normality, and homogeneity of variance. Abundance data were fourth-root transformed ($\sqrt[4]{x}$), with abundant species being down-weighted allowing mid-range and rare species to exert some influence on the calculation of similarity. A one-way analysis of similarity (ANOSIM) was used to evaluate spatiotemporal variability with data for zooplankton composition and dietary overlap for blueback herring and alewife.

The ANOSIM procedure uses randomization techniques to determine the average of all ranked dissimilarities among and within groups (Global *R*; Sampson et al. 2009). A *P*-value is derived using random permutations of the similarity matrix, and is calculated as the probability that a greater *R* could be achieved from random combinations of the data (Clarke and Warwick 2001). Post-hoc pairwise comparisons were computed when the Global *R* was significant, and were adjusted for experiment-wise Type I error using a Bonferroni correction ($P \leq 0.005$). Species contributing the most to the similarities within categories and differences between categories were identified with the Similarity Percentages (SIMPER) procedure. SIMPER decomposes Bray-Curtis dissimilarity values and transforms them into percentage contributions from each taxon, listing them in decreasing order of contribution. Results from ANOSIM and SIMPER were corroborated and visualized using a non-metric, multidimensional scaling (NMDS) ordination plot. NMDS ordination used the Bray–Curtis coefficients with 50 restarts to determine the lowest stress, preferably ≤ 0.2 (Clarke and Warwick 2001). Within the two-dimensional ordination plot, the distance between points correlates with the similarity among samples (*i.e.*, points close together represent samples that are similar in composition).

Results

Habitat and environmental data

Sampling was completed at weekly intervals throughout the study period except during week 16 when severe weather prevented sampling within the Sound. Stations located in the River were significantly deeper (4.4 ± 0.3 m) than stations in Delta (3.1 ± 0.1 m) and Sound (3.2 ± 0.1 m). Environmental data and water quality parameters were within ranges expected for shad and river herring migration, spawning, and larval development (Greene et al. 2009). There were no

significant differences among the environmental and water quality parameters recorded within the River and Delta. Salinity, current velocity, and wind speed were significantly higher in the Sound. Salinity within the Sound ranged from 0.1 – 1.0 psu and was significantly higher than other areas ($F_{2,91} = 5.49$, $P = 0.006$). Water within the River and Delta flowed downstream and surface currents were similar in both areas, ranging from 0.02 – 0.45 m/s, with a mean velocity of 0.2 ± 0.1 m/s. Surface flow measurements were not significantly different from week to week in the River or Delta. Surface flow within these regions was also not correlated with river discharge or rainfall. Inland stations along the River and Delta were generally protected from prevailing winds from the east (46%) or southwest (38%). These winds affected the open waters of the Sound causing wave action, wind rows, and visible signs of circulation patterns (*i.e.*, Langmuir circulation). Surface currents were strongly correlated with wind speed (Figure 3.2; $r^2 = 0.76$, $F_{1,22} = 68.8$, $P < 0.001$). Surface currents were significantly higher ($F_{2,91} = 6.46$, $P = 0.002$) in the Sound (0.3 ± 0.2 m/s), ranging from 0.0 – 0.8 m/s, and currents most frequently originated from the west (46%). Flow measurements within the Sound were significantly higher for week 14 (0.5 ± 0.1 m/s) and lower for week 15 (0.1 ± 0.01 m/s) as compared to other weeks ($F_{6,17} = 3.64$, $P = 0.01$).

Seasonal trends were observed for dissolved oxygen, water temperature, pH, and turbidity. Dissolved oxygen declined steadily throughout March, April, and May (Figure 3.3). Dissolved oxygen levels were rarely observed below 5.0 mg/L and hypoxic conditions (≤ 3.0 mg/L) were never detected. Water temperatures increased throughout the sampling period from 10.5 °C in March to 25.3 °C in May. The difference between surface and bottom temperature was minimal (0.3 ± 0.1 °C) and not significantly different for time of day, week, or area. Water temperatures were 15.0 ± 0.5 °C during the peak capture periods for blueback herring in April and 21.6 ± 0.3

°C during the peak capture periods for alewives in May. As water temperatures increased, measurements of pH generally decreased for stations within the River and Delta and increased for stations within the Sound. Although not significantly different, the lowest pH levels were recorded for stations located in the Delta at the confluence of Cashie River and Roanoke River. Within this region, pH ranged from 5.2 to 6.8. Turbidity decreased from 100 ± 31 ntu during the first week of sampling to 5 ± 1 ntu during the last week of sampling, although the correlation was weak ($r^2 = 0.25$, $F_{1,71} = 23.7$, $P < 0.001$).

Mean daily discharge from Roanoke Rapids Dam was 240 ± 88 m^3/s and ranged from 80 – 546 m^3/s (Figure 3.4). In response to episodes of heavy rains throughout the watershed, flows peaked in March and April with maximum instantaneous discharge rates ranging from 430 – 592 m^3/s. Flows were > 200 m^3/s for 80% of the sampling period and never exceeded 600 m^3/s. During striped bass spawning and recruitment, flows were maintained within management guidelines for 93% of April and May.

Larval abundance

A total of 27,364 larvae were collected in 94 pushnet samples and primarily consisted of fishes belonging to six families: Moronidae (striped bass, white perch), Percidae (yellow perch), Cyprinidae (minnows), Centrarchidae (sunfish and bass), Clupeidae (shads and herring), and Engraulidae (anchovies). Clupeid larvae were present throughout the sampling period; however, the numbers of larvae varied by area (Table 3.2). Stations 2, 4, and 6 located within the River comprised 49% of the catch, while station 10 located in the Delta comprised 13% of the catch.

The remaining 15 stations across all areas comprised 5% of the catch. Among the alosines identified to species, blueback herring (51%) were the most abundant species followed by hickory shad (34%), alewife (14%), and American shad (1%).

Differences in blueback herring and alewife abundance (number/100 m^3 ± SD) and size distribution were observed between diel period and area (Table 3.3). The mean abundance of blueback herring caught at night (43.5± 109.5) was significantly higher than fish caught during the day (8.5 ± 19.4, $t_{92} = 2.16$, $P = 0.03$, $g = 0.45$). In contrast, there was no significant effect of diel period on alewife abundances (6.8 ± 15.0, $t_{92} = 0.39$, $P = 0.70$). Blueback herring had significantly higher abundances in April (47.7 ± 107.8) than the other months (4.5 ± 11.2, $F_{2,91} = 3.87$, $P = 0.02$), and the catch peaked during week 14 with 121.8 ± 187.3. Alewife abundance was not significantly different among months (6.8 ± 15.0, $F_{2,91} = 0.84$, $P = 0.43$). The catch of alewife peaked in May during week 19 with 24.4 ± 24.2. While the abundance of blueback herring was generally higher in the River (37.1 ± 122.2) as compared to the Delta (17.7 ± 30.4) and Sound (21.0 ± 40.1), these abundances were not significantly different ($F_{2,91} = 0.57$, $P = 0.57$). Similarly, the abundance of alewife was not significantly different among areas ($F_{2,91} = 2.10$, $P = 0.13$); although, the catch was highest in the River (10.8 ± 21.5) as compared to the Delta (4.5 ± 6.9) and Sound (4.2 ± 10.1).

Zooplankton abundance and taxonomic composition

Zooplankton abundances (number/m^3) were highly variable across broad spatial and temporal scales. Abundance within the river was positively correlated with average weekly discharge from Roanoke Rapids dam (Figure 3.5, $r^2 = 0.66$, $F_{1,10} = 19.06$, $P = 0.001$). When zooplankton abundances were combined for all areas, a significant temporal effect was detected for month

($F_{2,90}$ = 5.37, P = 0.006) and week of year ($F_{8,84}$ = 2.63, P = 0.01); however, there was no significant effect of diel period (t_{91} = 0.21, P = 0.83). Mean abundances (± SD) were significantly higher for March (11,360 ± 13,563) than April (6,324 ± 3,122) and May (4,635 ± 5,385). Zooplankton abundance peaked in March during weeks 11 (12,520 ± 14,406) and 12 (13,601 ± 17,883). The lowest abundances were observed in May during weeks 19 (3,325 ± 2267) and 20 (2,055 ± 1231), in which, 68% of samples (N = 13) had abundances < 2,000 zooplankton / m^3. There was no significant effect of area on zooplankton abundance ($F_{2,90}$ = 1.76, P = 0.18); although, the highest abundances were observed in the River (8,104 ± 10,105) followed by Sound (6,314 ± 4,028) and Delta (5,002 ± 2,848). The widest range of abundance estimates were in the River (1,044 - 49,430).

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, Bosminiidae, Sididae, Chydoridae, and Leptodoridae. These five taxa account for 98% of the composition for each area. Dipteran insect larvae (*e.g.*, flies, midges, mosquitoes) were collected in 3.2% of samples and represented < 1% of the composition for each area. Some of the other less common taxa (≤ 1%) included ostracods, gammarid amphipods, and harpacticoid copepods. Oligochaetes (0.03%) were unique to samples collected from the River and bivalve veligers (0.07%) were unique to samples collected from the Delta.

Zooplankton community structure varied significantly by month (ANOSIM, Global R = 0.266, P = 0.001). Bray Curtis average similarity was 72.0 ± 4.7 for March, April, and May. In March, zooplankton communities in the River were dominated by bosminids (39%) and daphniids (21%). Cladocerans (18%) were less abundant in April as the community structure

transitioned to rotifers (55%). In May, zooplankton communities in the River primarily consisted of rotifers (34%), cyclopoid copepods (33%), and copepod nauplii (16%). In the Delta, rotifers (50%) and bosminids (30%) were dominant in March. The zooplankton community diversified in April to include rotifers (42%), copepod nauplii (24%), cladocerans (15%), and cyclopoid copepods (14%). In May, rotifers (55%) and copepod nauplii (22%) remained high in the Delta. The zooplankton community in the Sound was similar in March and April with cladocerans (29%), rotifers (29%), copepod nauplii (26%), and cyclopoid copepods (11%). Cladocerans (2%) were less prevalent in May as rotifers (60%) and copepod nauplii (25%) dominated the zooplankton community in the Sound.

Although statistically weak (ANOSIM Global $R = 0.111$, $P = 0.001$), zooplankton community structure varied significantly by area (Figure 3.6). Bray Curtis average similarity was 70.8 ± 0.9%. The abundance of rotifers (26.5 ± 0.1%) and copepod nauplii (22.9 ± 2.6%) contributed to the similarity of zooplankton among areas. Pairwise comparisons revealed significance within the ANOSIM was primarily driven by the community structure of the River and Sound, which were significantly different (Global $R = 0.224$, $P = 0.001$). Post-hoc tests showed the Delta may serve as a transitional or mixing zone as this area was not significantly different from the River (Global $R = 0.047$, $P = 0.31$) or Sound (Global $R = 0.071$, $P = 0.26$). SIMPER analysis comparing the River and Sound showed 50% of the dissimilarity was attributed to bosminids, daphniids, calanoid copepods, and harpactacoid copepods.

Trends in river herring and zooplankton abundance

There was spatial and temporal overlap between river herring and zooplankton (Figure 3.7). Zooplankton abundance was greatest in March when water temperatures approached 12.0 °C and

when river herring were least abundant. In April, declines in zooplankton abundance (31 ± 1%) during weeks 13, 14, and 15 coincided with peaks in river herring abundance (*i.e.*, blueback herring). Similar trends were observed throughout the study and abundances of zooplankton and river herring generally showed an inverse relationship. The data suggests a match:mismatch relationship may occur (Figure 3.7a); however, linear regression between zooplankton abundance and river herring abundance fell short of statistical significance ($r^2 = 0.16$, y = -0.187x + 9.253, $F_{1,34} = 4.0$, $P = 0.058$). When a 2-week time lag was applied to river herring abundance data, linear regression analysis yielded a statistically significant result ($r^2 = 0.70$, y = 0.004x – 6.335, $F_{1,34} = 23.4$, $P < 0.001$). Declines in zooplankton abundance were correlated with larval abundance, and these results suggest foraging by larval alosines could negatively alter the abundance and structure of the zooplankton community especially when river herring abundance exceeds 25 fish/100 m^3.

Larval condition

Length measurements for blueback herring and alewife were not significantly different between species (TL, $t_{670} = 1.12$, $P = 0.26$; SL, $t_{670} = 1.16$, $P = 0.24$); however, dry weights were significantly higher for blueback herring ($t_{670} = 3.83$, $P = 0.0001$). The standard length of blueback herring ranged from 3.2 to 10.8 mm and weights ranged from 5 to 107 µg. Significantly larger blueback herring were collected in the River and Delta compared to fish collected in the Sound ($F_{2,276} = 4.80$, $P = 0.009$). Alewife SL ranged from 3.3 to 9.7 mm and weights ranged from 4 to 102 µg. Although the largest fish were collected in the River and Delta, length measurements were not significantly different among areas ($F_{2,276} = 0.27$, $P = 0.76$). Regression analysis revealed that growth and weight were highest for blueback herring and alewife caught in the River, especially for individuals > 5.0 mm SL (Table 3.4; Figure 3.8).

The results of an ANCOVA based on dry weight as the response variable and length as the covariate, showed a significant interaction with area (Blueback herring, $F_2 = 19.55$, $P = 0.001$; Alewife, $F_2 = 7.07$, $P < 0.0001$).

Among the blueback herring collected, 43% had a yolk-sac and measured 4.5 ± 0.6 mm SL, while 47% of alewives had a yolk-sac and measured 4.6 ± 0.7 mm SL (Table 3.5). The volume of yolk was not significantly different between species ($t_{481} = 1.32$, $P = 0.19$) and recently hatched fish (≤ 4.0 mm SL) had a yolk-volume of 0.41 ± 0.06 mm^3. The volume of yolk exhibited by larval river herring was not significantly different among areas ($F_{2,480} = 0.40$, $P = 0.67$) or time of day ($t_{481} = 1.04$, $P = 0.30$). Approximately 20% of fish collected during the day and 5% of fish collected at night had remnants of a yolk-sac while transitioning to exogenous feeding (*i.e.*, yolk-sac and food present in gut).

Fulton's condition index ranged from 7.7 to 87.6 for blueback herring and 6.3 to 49.3 for alewife (Table 3.6); and larval condition was not influenced by the time of day that sampling occurred ($t_{481} = 0.80$, $P = 0.42$). A comparison of condition indices between species indicated that blueback herring had a significantly higher condition index ($t_{481} = 2.94$, $P = 0.003$). Blueback herring and alewives with the highest measures of condition were collected in the River (21.3 ± 8.9) followed by the Delta (19.5 ± 6.8) and Sound (18.5 ± 7.2). Larval condition for blueback herring was not significantly different among areas ($F_{2,276} = 1.05$, $P = 0.35$); however, the condition of alewives collected from the River was significantly higher than the Delta or Sound ($F_{2,201} = 13.93$, $P < 0.001$).

Feeding and prey selectivity

Prey were observed and identified in 76% of river herring collected and a maximum of 8 prey were identified in larvae less than 11.0 mm SL (Figure 3.9). Neither gut fullness (t_{481} = 0.25, P = 0.80) or feeding ratios (t_{280} = 0.61, P = 0.54) were significantly different between species. River herring gut fullness was 37 ± 32% and feeding ratios were 2.5 ± 1.5. Gut fullness and feeding ratios were influenced by time of day fish were sampled (Tables 3.5 and 3.6). Blueback herring and alewife gut fullness were significantly higher for fish collected during the day (blueback herring, t_{277} = 12.68, P < 0.0001; alewife, t_{202} = 8.78, P < 0.0001). Similarly, blueback herring and alewife feeding ratios were significantly higher for fish collected during the day (blueback herring, t_{41} = 3.44, P = 0.001; alewife, t_{43} = 2.25, P = 0.03). Gut fullness was significantly higher for fish collected in the River as compared to the Delta and Sound (blueback herring, $F_{2,276}$ = 11.30, P < 0.0001; alewife, $F_{2,201}$ = 20.05, P < 0.0001); however, feeding ratios were not significantly different among larvae collected from select habitats (blueback herring, $F_{2,42}$ = 0.94, P = 0.40; alewife, $F_{2,42}$ = 0.54, P = 0.59). Although no significant differences were detected for gut fullness compared to week of sampling ($F_{8,273}$ = 1.79, P = 0.08), gut fullness peaked in week 19 for blueback with 49 ± 32% and week 17 for alewife with 65 ± 42%. Feeding ratios peaked during the same periods with no significant difference in the presence of prey across a temporal scale ($F_{8,273}$ = 1.89, P = 0.09).

Of the 684 prey items extracted from larvae, the smallest taxa including copepod nauplii and rotifers accounted for over 85%. Frequencies of occurrence for copepod nauplii (49 ± 8%), rotifers (41 ± 13%), and bosminids (13 ± 7%) suggest these were the most abundant prey types for both blueback herring (Table 3.7) and alewife (Table 3.8). Other less common prey observed were cyclopoid copepods, calanoid copepods, daphnia, ostracods, and dipterans. Bivalve

veligers were observed only in April. Dipteran insect larvae were consistently among the largest prey (0.3 – 0.8 mm) collected from the guts of river herring. Other large prey collected (> 0.6 mm) included daphniids and bosminids.

There was overlap between the types and size of prey extracted from larvae and those within the zooplankton community (Figure 3.10). The results of a one-way MANOVA suggested area effects could explain the majority of variance in diet for blueback herring (η^2 = 78%, Wilk's Λ = 0.22, $P < 0.0001$) and alewife (η^2 = 87%, Wilk's Λ = 0.13, $P < 0.0001$). With an adjusted alpha level ($\alpha = 0.005$), individual ANOVAs for larval diets indicated bosminids, copepod nauplii, cyclopoid copepods, and rotifers varied significantly with area (Table 3.9). A one-way ANOSIM indicated weak (Global $R = 0.162$), but significant ($P = 0.001$) differences in the diets of blueback herring and alewife caught in the River. Rotifers (75.6 ± 3.5%) contributed the most similarity to river herring diets in the River. SIMPER analysis showed 80% of dissimilarity was attributed to the abundance of bosminids, rotifers, ostracods, and daphnids (Table 3.10). The diets of blueback herring and alewife were not significantly different for fish caught in the Delta (Global $R = 0.007$, $P = 27.3\%$) or Sound (Global $R = 0.037$, $P = 13.2\%$). The similarity of river herring diets in the Delta and Sound were 35.5 ± 0.4 % and 58.6 ± 0.4 %, respectively. Copepod nauplii (49.3 ± 16.0%) and rotifers (35.3 ± 15.6%) contributed to river herring diet similarity in the Delta, whereas copepod nauplii (81.5 ± 9.9%) contributed the most similarity to river herring diets in the Sound.

The composition of river herring diets changed little with early ontogeny (Figure 3.11). First feeding larvae within the 3 to 5 mm SL class primarily consumed bosminids and rotifers in the River, while cohorts fed on copepod nauplii and rotifers in the Delta. In the Sound, first feeding larvae consumed copepod nauplii and cyclopoid copepods. Rotifers were consistently consumed

by all fish in the River and Delta. Copepod nauplii and to a lesser extent ostracods, cyclopoid copepods, and bosminids were a staple of diets from fish collected in the Delta and Sound. Larger fish (7 – 12 mm SL) in the River consumed proportionally more copepod nauplii than smaller cohorts. When available, dipterans were consumed by larger fish in the River and Delta.

Prey selectivity was highly variable by area for blueback herring (Table 3.7) and alewife (Table 3.8) and reflected proportional distributions of prey and trends in consumption. Across all areas, both blueback herring and alewife displayed positive selection for copepod nauplii and negative selection for calanoid and harpactacoid copepods. Both fish species strongly selected for bosminids within the River. Within the Delta, blueback herring selected for copepod nauplii and alewives selected for cyclopoid copepods. Copepod nauplii were positively selected by blueback herring and alewives within the Sound.

The range of prey sizes consumed expanded with increasing size of blueback herring and alewife. Prey size was positively correlated with fish length (Figure 3.12) and niche breadth increased linearly ($y = 0.224\ x + 0.017$) with prey size ($r^2 = 0.74$, $F_{1,8} = 19.58$, $P = 0.003$). Quantile regression models based on prey length and width were statistically significant (Table 3.11). While models indicated upper-bound slopes ranged from 0.02 to 0.06, lower bound slopes were not variable and had a slope of 0.01. Although rarely consumed, large prey types were responsible for driving the upper-bound slopes of prey size models. The lower bound slopes of models were less variable because the smallest size fractions of prey were preferentially eaten by all size classes (*i.e.*, copepod nauplii and rotifers).

Discussion

Feeding has been the most studied facet of larval fish ecology (Miller and Kendall 2009). Many studies have demonstrated that planktivorous fish can alter freshwater zooplankton communities by size-selective grazing (Hansson et al. 2007; Nicolle et al. 2010). The majority of work has focused on 'top-down' effects of fish on zooplankton in large lakes; most notably the introduction of alewives in the Laurentian Great Lakes ecosystems (Wells 1970; Scavia et al. 1986; Hewett and Stewart 1989; Miller et al. 1990; Evans 1992). Zooplankton communities of many rivers vary in composition, but are generally dominated by rotifers and small-bodied crustaceans, such as bosminids (Jack and Thorp 2002). Zooplankton abundances in rivers are often lower than those seen in lakes and reflect seasonality, forage base, and hydraulic retention (Hynes 1970; Obertegger et al. 2007; Dickerson et al. 2010). The results of the present study demonstrate river herring production in Roanoke River coincides with a significant reduction in zooplankton abundance. The continuous overlap in alosine production in the river does not provide a temporal refuge for zooplankton. Gut contents confirm size-selective grazing by blueback herring and alewife larvae. Prey in guts were not proportional to the organisms of the same size in the water where the larvae were collected. These results suggest a high-level of interspecific competition between coexisting alosines in Roanoke River. Crecco and Blake (1983) observed a similar phenomena with larval American shad and blueback herring in Connecticut River. They documented a high-level of dietary overlap contributing to intraspecific and interspecific competition.

Food limitation and starvation have long been considered threats to recruitment of anadromous species in Roanoke River (Rulifson et al. 1988). Zooplankton production within this region has historically been low and long-term investigations concluded zooplankton

abundances were between 1-2 orders of magnitude lower than other North Carolina river systems (Rulifson et al. 1992; Coggins 2005; Binion et al. In press). We tested hypotheses of match:mismatch regulation by comparing zooplankton abundance with the distribution of larval river herring. Blueback herring spawning and larval production were correlated with peaks in zooplankton abundance. For late spawning alewife, a mismatch was induced by the arrival of blueback herring in nursery habitats early in March and April. It is doubtful that intense grazing by blueback herring affected production of alewife or other fishes spawned late in the season because most fish were observed with food in their guts. Therefore, we concluded larvae do not appear to be food limited. Interpretation of dry weight and condition indices confers a recruitment advantage to blueback herring spawned early in the season. Blueback herring larvae would have more food resources available and substantially more time to grow to larger sizes. Alewives with lower dry weights and condition indices probably reflect subtle differences in recent feeding history and growth. Small fish with slow growth rates could have been selectively preyed upon and experienced high mortality. Unfortunately, the relationship between growth and survival is not well established.

Dietary overlap between blueback herring and alewives has not been previously reported. Regardless of size or stage of larval development, small copepod nauplii, rotifers, and bosminids contributed the most similarity in diets of blueback herring and alewife. Prey selectivity reflected spatiotemporal patterns in zooplankton abundance. Throughout this study, small zooplankton remained an important component in larval diets (Figure 3.12). Similar to the observations of Crecco and Blake (1983) with blueback herring, it is difficult to explain why

minimum prey sizes remained nearly constant with larval ontogeny. Selectivity for larger cyclopoid copepods and ostracods by alewives in late spring probably reflects a consequence of competition with a limited forage base.

Differences in diel patterns of feeding and larval abundance should be considered in designing an ichthyoplankton sampling program targeting alosines. As evidenced by feeding ratios and gut fullness, feeding was significantly higher during the day and probably relates to activity level and the ability to detect prey. Results from sampling at night might lead researchers to infer high rates of starvation or low incidences of feeding. In actuality, starving fish are seldom observed in ichthyoplankton collections. It is believed starving larvae die or are vulnerable to predation. Larval abundance estimates for each species were influenced differently by diel period. Significantly more blueback herring were caught at night than during the daytime. Conversely, there was no effect of diel period on collection of larval alewives. Using the same gear and sampling techniques in Roanoke River, Overton and Rulifson (2007) did not detect differences in abundance of river herring based on time of day; however, species level interactions probably masked any differences that existed. In contrast with the present study, Cole and MacMillan (1984) demonstrated that catches of larval alewives were higher (up to 20:1, night:day) during night than daytime. These researchers found larval alewives (≤ 30 mm TL) in Lake Erie evade capture through vertical migration. They also noted yolk-sac larvae avoid capture by remaining at the lake bottom until transition to exogenous feeding. The high proportion of yolk-sac larvae (45%) caught in this study suggests extensive mixing in the water column resulting from the high flow rates and relatively shallow depths of Roanoke River and Albemarle Sound. The collection of several species of benthic invertebrates in push-net samples further supports this finding (*e.g.*, Amphipods *Gammarus tigrinus;* Clams *Rangia* sp.).

Although this study covered a large portion of the lower Roanoke River and includes flows that drain tributaries throughout the watershed, few eggs were caught in ichthyoplankton and zooplankton samples, and none of the eggs were identified as *Alosa* spp. The high proportion of yolk-sac larvae caught indicated that fish had been carried downstream from spawning grounds. Yolk-sac and first-feeding larvae were present throughout the habitats sampled in the River, Delta, and Sound. In recent years, river herring have been observed spawning in habitats adjacent to the tailrace of Roanoke Rapids Dam, located 221 km from Albemarle Sound and approximately 200 km upstream of this study (Harris and Hightower 2010). Viable river herring eggs and yolk-sac larvae have also been collected in backwater tributary systems distributed 100 km downstream of the dam (Walsh et al. 2005). The age distribution of blueback herring and alewife collected in this study was not determined; however, estimates for time of travel (4 - 9 d) and advective transport (1.5 - 2.3 km/h) from the dam tailrace correspond closely with hatching, stage of development, and the onset of first feeding (Edsall 1970; Fay et al. 1983; Herrmann 1993; Sismour 1994b). Drift of larvae in April and May should be similar because discharge from Roanoke Rapids Dam is regulated between 113 and 388 m^3/s. High flows in March would have produced strong advective forces affecting predators and prey within the river. Unless mechanisms exist for retention of larvae in upstream habitats, these findings suggest a large proportion of larvae drift downstream in narrow, channelized river reaches until they are entrained in low-velocity habitats at the mouth of the river or dispersed into the sound.

River flow and estuarine circulation patterns can have negative effects on larvae by transporting them to unfavorable environments, physically damaging them, and diluting their food resources. In a previous study on Roanoke River, alosine larvae were less abundant in the main river channel compared to backwater habitats (Walsh et al. 2005). Larval abundances in

the river increased during low flow periods when swamps drained and concentrated fish in the river. In the present study, there was no significant difference in the abundance of blueback herring or alewife among the areas sampled. The abundance of larvae in Albemarle Sound suggests open water habitats are important if physical processes exist to control advective losses. Much like daily mortality from starvation and predation, dispersal losses from failed retention in nursery habitats can severely impact the larval population (Houde 1989).

Albemarle Sound does not exhibit an estuarine turbidity maxima or other known hydrographic feature that represents an important nursery area for larval fishes (Schubel 1968; North and Houde 2003). The sound is a shallow estuary (3.5 m average depth) with a surface area of about 1,820 km^2, volume of 6.5 km^3, and a salinity that is < 5 psu (Roelofs and Bumpus 1953; Giese et al. 1985). The estuary is well mixed as vertical gradients in temperature and salinity have rarely been observed. The astronomical tidal effect in the sound is minimal, and because of its east-west orientation, wind stress comprises the primary forcing mechanism for water movement and hydraulic residence time (Copeland et al. 1983). During this three-month study, wind-forced circulation patterns in the sound caused fluctuations in salinity, dissolved oxygen, turbidity, surface flow, and water level. Wind events may have had an indirect, but perhaps significant, effect on ichthyoplankton and zooplankton composition by influencing the direction and strength of gravitational circulation. Evidence supporting this observation was provided by temporal changes in zooplankton community composition and river herring diets. These results illustrate the potential for varying circulation patterns to structure communities of larval fish and their prey.

Duration of wind stress and variability of magnitude largely influenced surface currents. During periods of westerly winds, river flow and sound currents resulted in a net flow of water

seaward and produced a positive correlation between zooplankton abundance and river flow (Figure 3.5). Throughout the study, zooplankton communities in the River were dominated by rotifers; however, under these conditions cyclopoid copepods, daphniids, and other taxa were flushed from backwaters in the watershed (Casper and Thorp 2007). These species typically aggregate in protected backwater environments with submerged and emergent vegetation providing refuge (Saunders and Lewis 1989; Garner et al. 1996). Cyclopoid copepods and daphniids that usually avoid open water habitat were transported downstream and became a valuable and preferred component in river herring diets.

Easterly winds were responsible for causing surface currents within Albemarle Sound to collide and mix with river flow at the mouth of the Roanoke, Middle, and Cashie Rivers. Surface flow within the Delta was recorded moving upstream (0.05 – 0.13 m/s) on a few occasions ($N = 3$) when strong winds (> 3.0 m/s) originated from the east-southeast. Sustained winds from the east reduced downstream surface flow in the river and concentrated fish and zooplankton in the lower reaches of Roanoke River. Mixing and water exchange between the Delta and Sound were evident because distributions of calanoid copepods, harpactacoid copepods, and amphipods were similar and were not representative of zooplankton contributions from the River. While copepods were abundant under these conditions, blueback herring and alewife exhibited negative selection for all forms of calanoid and harpactacoid copepods except naupliar stages.

Over the long-term, large losses of larvae from advection and aberrant drift can lead to low recruitment and failed year-classes. While our data demonstrate that habitats within the lower Roanoke River do not currently support river herring spawning, these habitats are clearly important in larval transport and serve as transitional areas linking nursery habitats. Although

much remains unknown about advective losses from Roanoke River and availability of nursery habitats in Albemarle Sound, the results from this research suggest that riverine habitats with abundant sources of food may be more conducive to larval production than previously assumed. Growth trajectories and condition indices for fish that transitioned to exogenous feeding in the River were consistently higher than fish in the Delta or Sound. More detailed knowledge on the contiguous distribution of eggs and larvae from spawning sites to nursery areas would improve dispersion models and estimates of retention in nursery areas. Species-specific estimates of instantaneous growth and mortality would help elucidate questions about habitat quality throughout the watershed. Discharge and flow regimes should be revised if retention of larvae in riverine habitats is a management objective.

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Table 3.1. Mean values (±SD) for environmental parameters from each sampling area in lower Roanoke River and Albemarle Sound, North Carolina. Means sharing a letter in their superscript are not significantly different at the 0.5 level according to a Ryan-Einot-Gabriel-Welch (REGWQ) procedure.

	Area					
Environmental parameter	River		Delta		Sound	
Current velocity (m/s)	0.1	$(0.1)^{A}$	0.2	$(0.1)^{A}$	0.3	$(0.2)^{B}$
Depth (m)	4.4	$(1.6)^{A}$	3.3	$(0.9)^{B}$	3.2	$(0.4)^{B}$
Dissolved oxygen (mg/L)	8.3	$(1.6)^{A}$	7.9	$(1.3)^{A}$	8.5	$(1.7)^{A}$
pH	6.6	$(0.3)^{A}$	6.5	$(0.3)^{A}$	6.6	$(0.4)^{A}$
Salinity (psu)	0.1	$(0.0)^{A}$	0.1	$(0.0)^{A}$	0.3	$(0.2)^{B}$
Turbidity (ntu)	28.5	$(53.0)^{A}$	27.9	$(48.6)^{A}$	27.9	$(53.2)^{A}$
Water temperature (°C)	17.2	$(4.4)^{A}$	17.8	$(4.2)^{A}$	18.5	$(4.1)^{A}$
Wind speed (m/s)	1.0	$(1.5)^{A}$	1.8	$(1.6)^{A}$	3.1	$(2.3)^{B}$

Table 3.2. Number and percent frequency of occurrence in samples of larval alosines identified from ichthyoplankton samples collected in lower Roanoke River and western Albemarle Sound, North Carolina during spring 2009.

	River		Delta		Sound	
Species	*N*	%	*N*	%	*N*	%
Blueback	407	27.1	188	12.5	170	11.3
Alewife	129	8.6	47	3.1	29	1.9
Hickory shad	318	21.2	164	10.9	24	1.6
American shad	5	0.3	1	0.1	2	0.1

Table 3.3. Number of ichthyoplankton samples collected, mean abundance (larvae / 100 m^3), minimum (min), maximum (max), and mean (SE) standard length of blueback herring and alewives collected in lower Roanoke River and western Albemarle Sound, North Carolina, during 2009. Mean abundances sharing a letter in their superscript are not significantly different.

			Abundance		Standard length					
					Blueback herring			Alewife		
Area	Diel period	*N*	Blueback herring	Alewife	Min	Max	Mean	Min	Max	Mean
River	Day	18	4.5^{A}	6.9^{A}	3.6	10.8	5.5 (0.2)	3.8	7.9	5.4 (0.2)
	Night	18	69.7^{B}	14.7^{A}	3.6	7.7	5.3 (0.1)	3.3	7.4	5.3 (0.2)
Delta	Day	18	13.8^{A}	4.4^{A}	3.3	8.6	5.5 (0.2)	3.8	7.8	5.2 (0.2)
	Night	18	21.2^{B}	4.5^{A}	3.7	8.7	5.2 (0.1)	3.8	9.7	5.5 (0.2)
Sound	Day	13	7.4^{A}	7.5^{A}	4.2	7.3	5.3 (0.2)	4.0	5.7	5.0 (0.1)
	Night	13	37.0^{B}	0.2^{A}	3.2	6.6	4.6 (0.1)	4.2	7.8	5.7 (0.3)

Table 3.4. Descriptive statistics and estimated parameters for river herring standard length (explanatory variable) and dry weight (dependent variable) at three different areas. Slope (B_1) and intercept (B_0) estimates were generated using linear regression techniques.

Species	Area	B_0	B_1	r^2	P	95% Confidence Interval
Blueback herring	River	-68.9574	18.89	0.79	0.0001	0.73 - 0.83
	Delta	-68.9384	19.08	0.89	0.0001	0.86 - 0.90
	Sound	-34.0809	12.49	0.79	0.0001	0.72 - 0.82
Alewife	River	-68.3323	18.50	0.79	0.0001	0.74 - 0.83
	Delta	-70.0944	18.02	0.73	0.0001	0.66 - 0.78
	Sound	-49.5101	14.17	0.66	0.0001	0.55 - 0.72

Table 3.5. Endogenous and exogenous feeding history of blueback herring and alewives collected in lower Roanoke River and western Albemarle Sound, North Carolina, during 2009. Values for yolk-sac, yolk-sac and food present, and food present represent mean (SE) percentage of occurrence. Values for gut fullness represent means (SE).

		Blueback herring								Alewife							
Area	Diel period	*N*	Yolk-sac		Yolk-sac and food present		Food present		Gut fullness		*N*	Yolk-sac		Yolk-sac and food present		Food present		Gut fullness	
River	Day	30	34	(18)	13	(7)	71.4	(19)	27	(5)	39	39	(9)	28	(7)	78	(8)	22	(4)
	Night	66	29	(7)	4	(2)	28.2	(8)	3	(1)	64	30	(11)	0	(0)	40	(16)	2	(1)
Delta	Day	46	34	(9)	25	(12)	77.7	(11)	44	(4)	27	9	(6)	9	(6)	79	(20)	49	(7)
	Night	65	32	(9)	8	(4)	48.5	(6)	7	(1)	35	28	(17)	5	(5)	53	(14)	7	(2)
Sound	Day	27	10	(6)	10	(6)	87.4	(10)	69	(8)	28	23	(14)	20	(12)	83	(7)	55	(8)
	Night	45	46	(6)	2	(2)	42.9	(4)	9	(2)	11	44	(30)	6	(6)	56	(30)	9	(2)

Table 3.6. Mean (± SD) condition of larval blueback herring and alewife collected from lower Roanoke River and western Albemarle Sound.

	Blueback herring				Alewife			
Area	*N*	Fulton's *K*	Feeding ratio	Feeding ratio (daytime)	*N*	Fulton's *K*	Feeding ratio	Feeding ratio (daytime)
River	96	21.5 (1.0)	2.3 (0.2)	2.8 (0.5)	103	21.2 (7.6)	2.9 (0.5)	3.2 (0.7)
Delta	111	19.9 (7.5)	2.8 (0.4)	3.8 (1.1)	62	15.9 (5.8)	2.3 (0.4)	2.0 (0.3)
Sound	72	21.3 (6.7)	2.2 (0.4)	2.5 (0.5)	39	16.3 (6.1)	2.8 (0.4)	4.0 (0.8)

Table 3.7. Ingested prey items summarized by numerical percentage (%N), frequency of occurrence in feeding larvae (%FO), and selectivity (Manly-Chesson index, α_i) for larval blueback herring collected from lower Roanoke River and western Albemarle Sound. Values of $\alpha_i > 0.25$ indicate preference by larvae for prey type *i*. Values significantly different ($P \leq 0.05$) are indicated by plus signs for positive selection and minus signs for negative selection. *N* is the total number of prey items excised.

				Selectivity (α_i)											
Prey	*N*	%N	%FO	River			Delta			Sound			Overall		
Bivalvia	5	1.3	2.5	0.200	(0.200)		0.210	(0.198)		0	(0)		0.158	(0.104)	
Bosminidae	71	19.0	38.0	0.596	(0.193)	+	0.074	(0.059)		0.022	(0.013)	-	0.263	(0.105)	
Calanoida	14	3.7	7.6	0	(0)		0.014	(0.014)	-	0.155	(0.081)		0.041	(0.025)	-
Copepod nauplii	108	28.9	54.4	0.003	(0.003)	-	0.440	(0.219)	+	0.420	(0.290)	+	0.268	(0.114)	+
Cyclopoida	50	13.4	26.6	0.009	(0.009)	-	0.093	(0.083)		0.184	(0.120)		0.082	(0.043)	
Daphniidae	21	5.6	11.4	0.017	(0.017)	-	0.020	(0.020)	-	0.117	(0.080)		0.041	(0.022)	-
Diptera	14	3.7	7.6	0.069	(0.046)		0.081	(0.081)		0	(0)		0.058	(0.035)	
Harpacticoida	4	1.1	2.5	0	(0)		0.027	(0.027)	-	0.102	(0.051)		0.034	(0.018)	-
Ostracoda	15	4.0	9.5	0.081	(0.070)		0.008	(0.008)	-	0	(0)		0.034	(0.027)	-
Rotifera	72	19.3	31.6	0.024	(0.011)	-	0.031	(0.017)	-	0	(0)		0.021	(0.008)	-

Table 3.8. Ingested prey items summarized by numerical percentage (%N), frequency of occurrence in feeding larvae (%FO), and selectivity (Manly-Chesson index, α_i) for larval alewife collected from lower Roanoke River and western Albemarle Sound. Values of $\alpha_i > 0.25$ indicate preference by larvae for prey type *i*. Values significantly different ($P \leq 0.05$) are indicated by plus signs for positive selection and minus signs for negative selection. *N* is the total number of prey items excised.

				Selectivity (α_i)											
Prey	*N*	%N	%FO	River			Delta			Sound			Overall		
Bivalvia	2	0.6	0.8	0	(0)		0.2	(0.2)		0	(0)		0.071	(0.071)	
Bosminidae	47	15.2	26.6	0.436	(0.142)	+	0.115	(0.084)		0	(0)		0.197	(0.075)	
Calanoida	10	3.2	7.3	0.032	(0.032)		0	(0)		0.015	(0.015)	-	0.016	(0.012)	-
Copepod nauplii	98	31.6	46.8	0.009	(0.009)	-	0.085	(0.045)		0.351	(0.222)	+	0.134	(0.071)	+
Cyclopoida	33	10.6	20.2	0.003	(0.003)	-	0.318	(0.152)	+	0.113	(0.113)		0.147	(0.069)	
Daphniidae	18	5.8	14.5	0.026	(0.016)	-	0.034	(0.034)		0.269	(0.185)		0.098	(0.058)	
Diptera	6	1.9	4.8	0.016	(0.016)	-	0.054	(0.054)		0.25	(0.25)		0.096	(0.072)	
Harpacticoida	1	0.3	0.8	0	(0)		0.089	(0.089)		0	(0)		0.032	(0.032)	-
Ostracoda	7	2.3	5.6	0.373	(0.159)		0	(0)		0	(0)		0.133	(0.072)	+
Rotifera	88	28.4	48.4	0.104	(0.018)		0.105	(0.041)		0.001	(0.001)	-	0.075	(0.020)	

Table 3.9. Analysis (ANOVA) of which prey types are consumed by river herring in varying habitats. Because tests were a posteri, alpha level was adjusted using the Bonferroni inequality. Tests were significant at $P \leq 0.005$.

		Blueback herring				Alewife			
Prey item	Source of variation	df	Sums of squares	F-value	*P*	df	Sums of squares	F-value	*P*
Bivalvia	Area	2	0.014	1.48	0.23	2	0.002	0.71	0.49
Bosminidae	Area	2	6.155	39.95	0.0001	2	3.035	23.94	0.0001
Calanoida	Area	2	0.125	11.50	0.62	2	0.110	11.50	0.0001
Copepod nauplii	Area	2	7.369	44.69	0.0001	2	8.078	47.53	0.0001
Cyclopoida	Area	2	1.489	18.70	0.0001	2	0.386	6.77	0.0016
Daphniidae	Area	2	0.048	0.91	0.40	2	0.104	1.68	0.19
Diptera	Area	2	0.062	1.98	0.14	2	0.034	1.57	0.21
Harpacticoida	Area	2	0.030	2.00	0.14	2	0.001	0.71	0.49
Ostracoda	Area	2	0.081	4.48	0.01	2	0.058	6.10	0.003
Rotifera	Area	2	1.890	13.76	0.0001	2	3.810	14.63	0.0001

Table 3.10. Average dissimilarity (%) of diet composition between blueback herring and alewife collected from Roanoke River and Albemarle Sound, North Carolina. Only significantly different pairwise comparisons of fish diet are reported. Rank order of importance of the prey type dissimilarity is reported in parentheses.

Area	Average dissimilarity (%)	Percent contribution in diet differences							Cumulative dissimilarity (%)
		Bosminidae	Calanoida	Copepod nauplii	Cyclopoida	Daphniidae	Ostracoda	Rotifera	
River	61.19	30.9 (1)	-	6.9 (5)	-	10.1 (4)	11.0 (3)	30.6 (2)	89.5
Delta	64.79	11.6 (4)	-	23.6 (2)	15.0 (3)	11.1 (5)	-	24.0 (1)	85.4
Sound	43.09	10.6 (4)	16.6 (3)	22.4 (2)	34.1 (1)	7.2 (5)	-	-	91.0

Table 3.11. Regression equations relating median, maximum, and minimum prey size to larval fish length. Slope (B_1) and intercept (B_0) estimates for prey size were generated using quantile regression techniques. Compared to least-squares regression, this procedure consistently estimates the upper and lower bounds of prey sizes for larval river herring.

	Prey length (mm)				Prey width (mm)			
Quantile	B_0	B_1	Sum of residuals	*P*	B_0	B_1	Sum of residuals	*P*
0.5	-0.1587	0.06	50.81	0.0002	-0.0219	0.02	19.64	0.0002
0.95	-0.0446	0.07	114.24	0.0002	-0.0134	0.03	45.67	0.0002
0.05	0.0336	0.01	81.19	0.0002	0.0165	0.01	28.08	0.0002

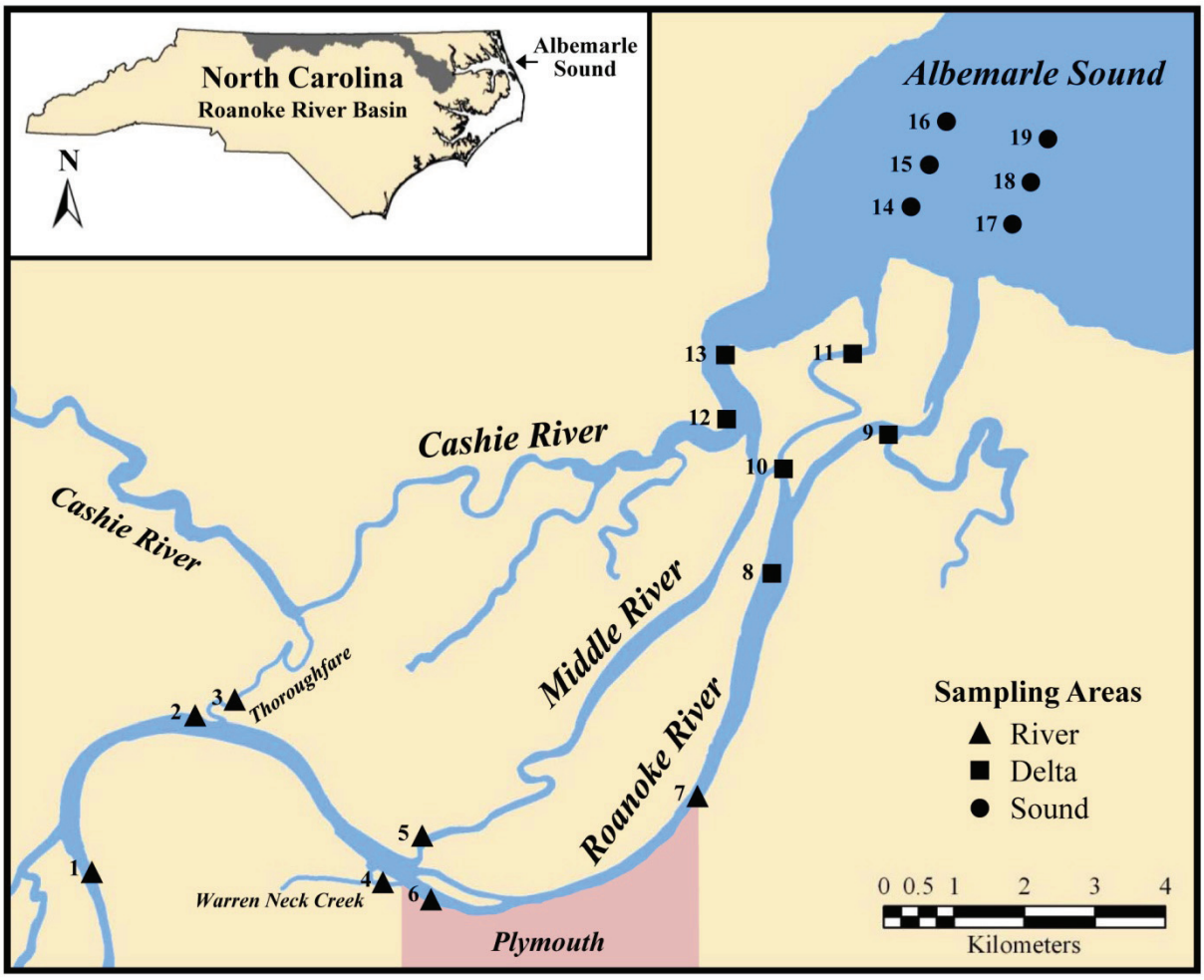

Figure 3.1. Map of study sites for sampling water quality, ichthyoplankton, and zooplankton in lower Roanoke River and western Albemarle Sound, North Carolina.

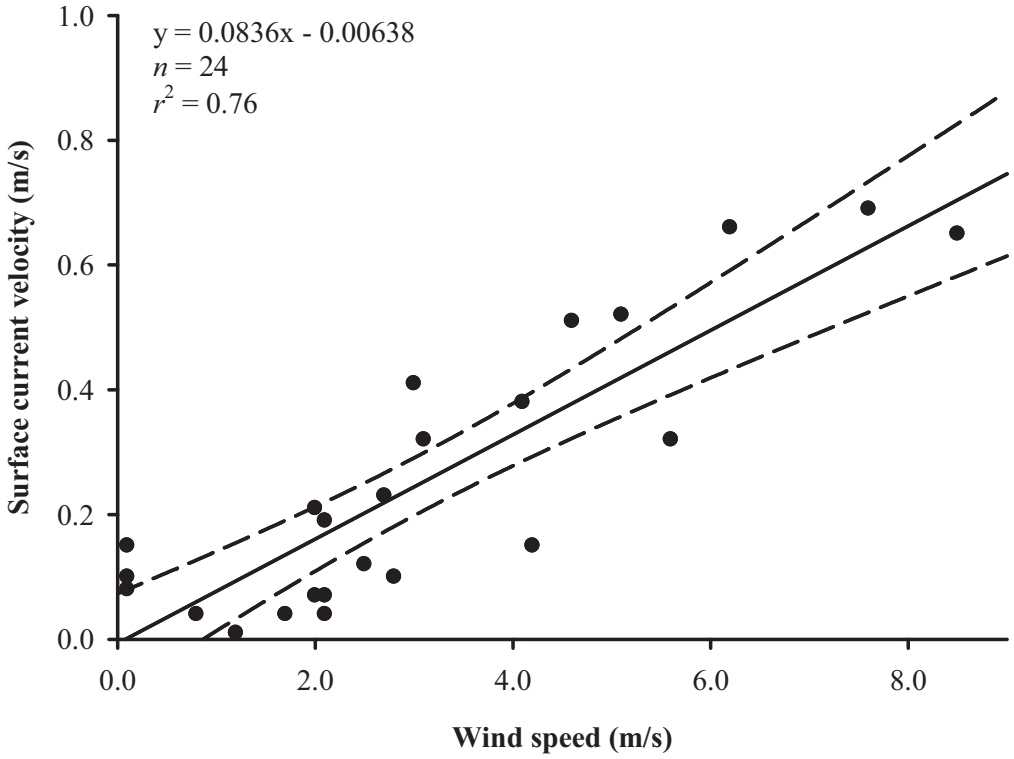

Figure 3.2. Linear regression analysis of wind speed and surface water currents in Albemarle Sound during spring 2009. Because of the east-west orientation of the Sound that spans 1,300 km^2, surface water movement and circulation were predominantly driven by winds from the east (46%) and southwest (38%). Dashed lines represent 95% confidence interval.

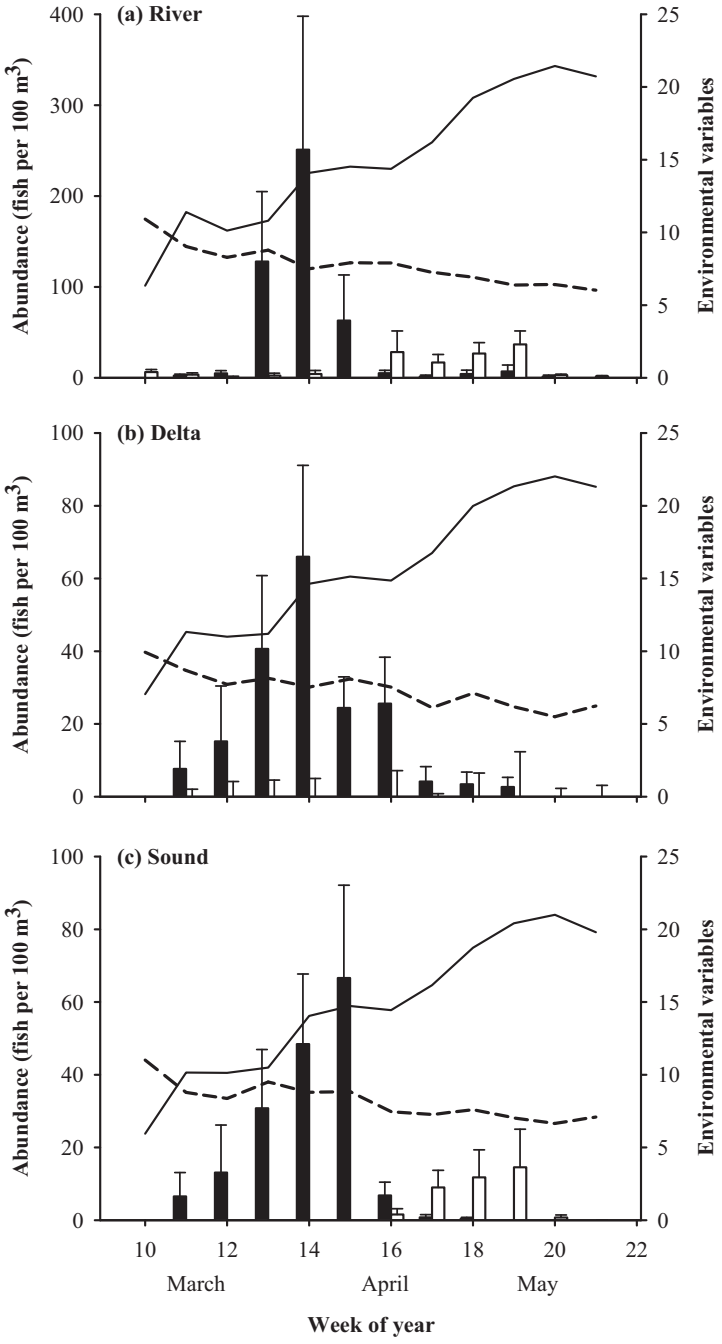

Figure 3.3. Abundance and distribution of blueback herring (solid bars) and alewife (empty bars) from lower Roanoke River and western Albemarle Sound for 2009. During the study period from March through May, water temperatures (solid line) generally increased while dissolved oxygen concentrations (dashed line) decreased. Values represent means (±SD). Note change in scale of abundance.

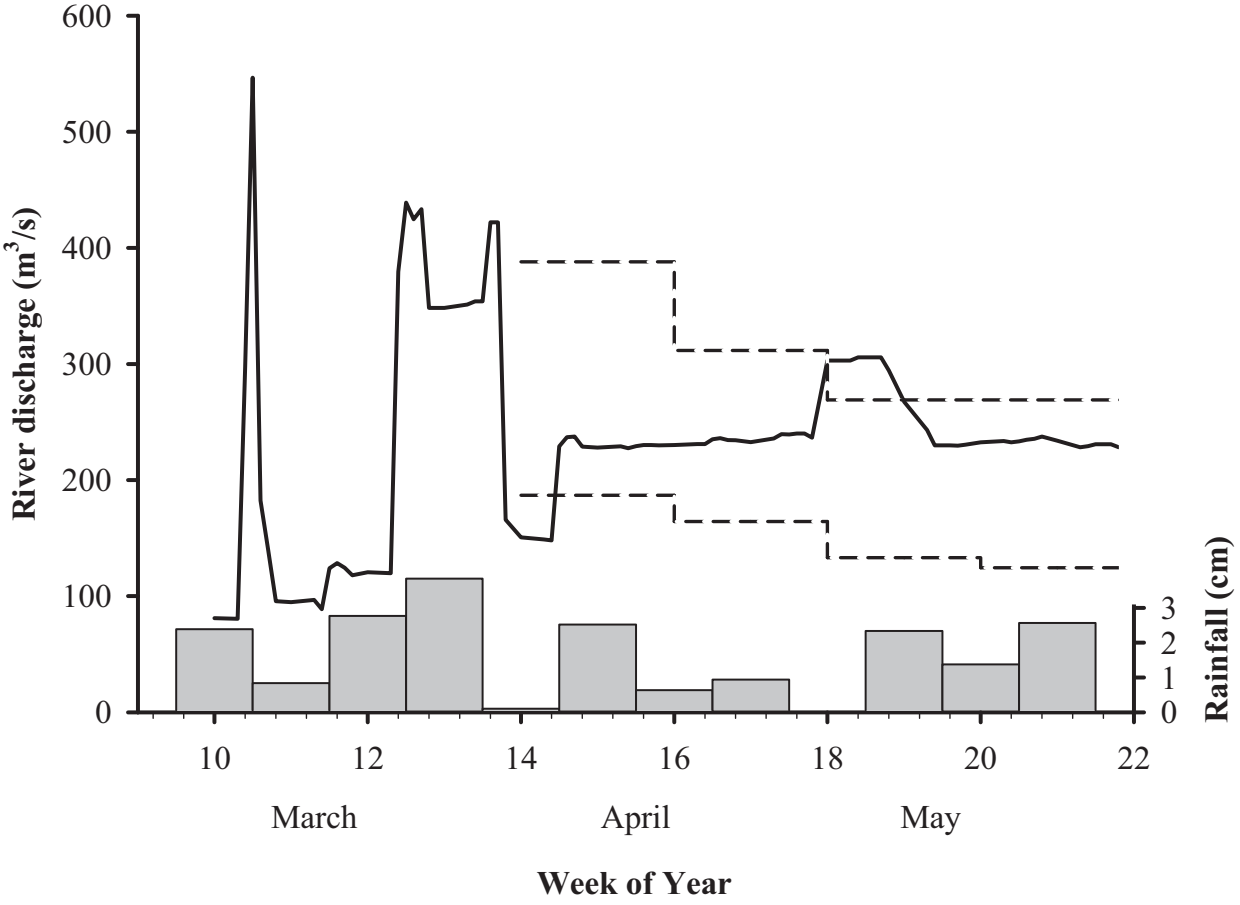

Figure 3.4. River flow (solid line) recorded by gage located 4.5 km downstream of Roanoke Rapids Dam and 221 km upstream from the study area. Dashed lines indicate the lower and upper regulated flow rates for conservation and management of striped bass, *Morone saxatilis*. In addition, outflow from the dam is limited to 42 m^3/s flow differential per hour. Rainfall data were obtained from a weather station located within the study area in Plymouth, North Carolina.

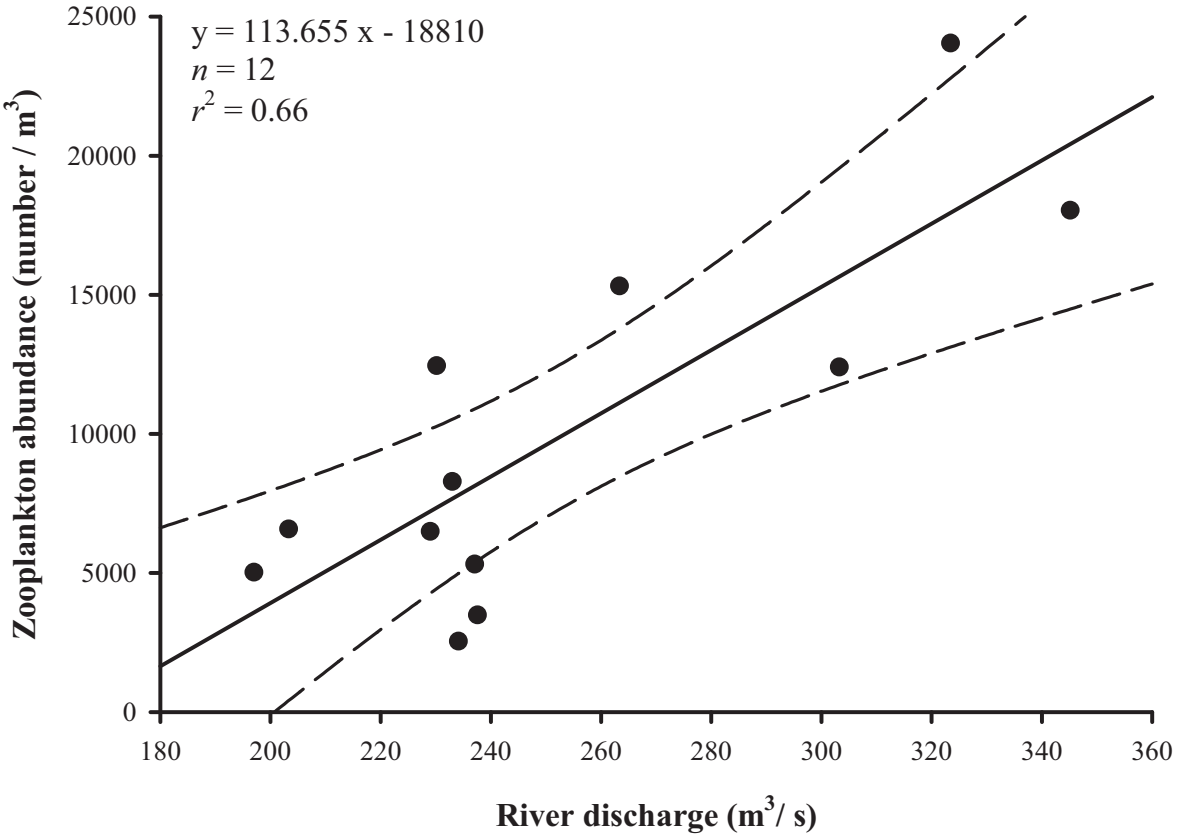

Figure 3.5. Zooplankton abundance in the lower Roanoke River was positively correlated with average weekly discharge from Roanoke Rapids dam ($F_{1,10} = 19.06$, $P = 0.001$). A 95% confidence interval for r^2 extends from 0.25 to 0.78. Zooplankton abundance estimates represent the average of four samples collected each week during March, April, and May 2009.

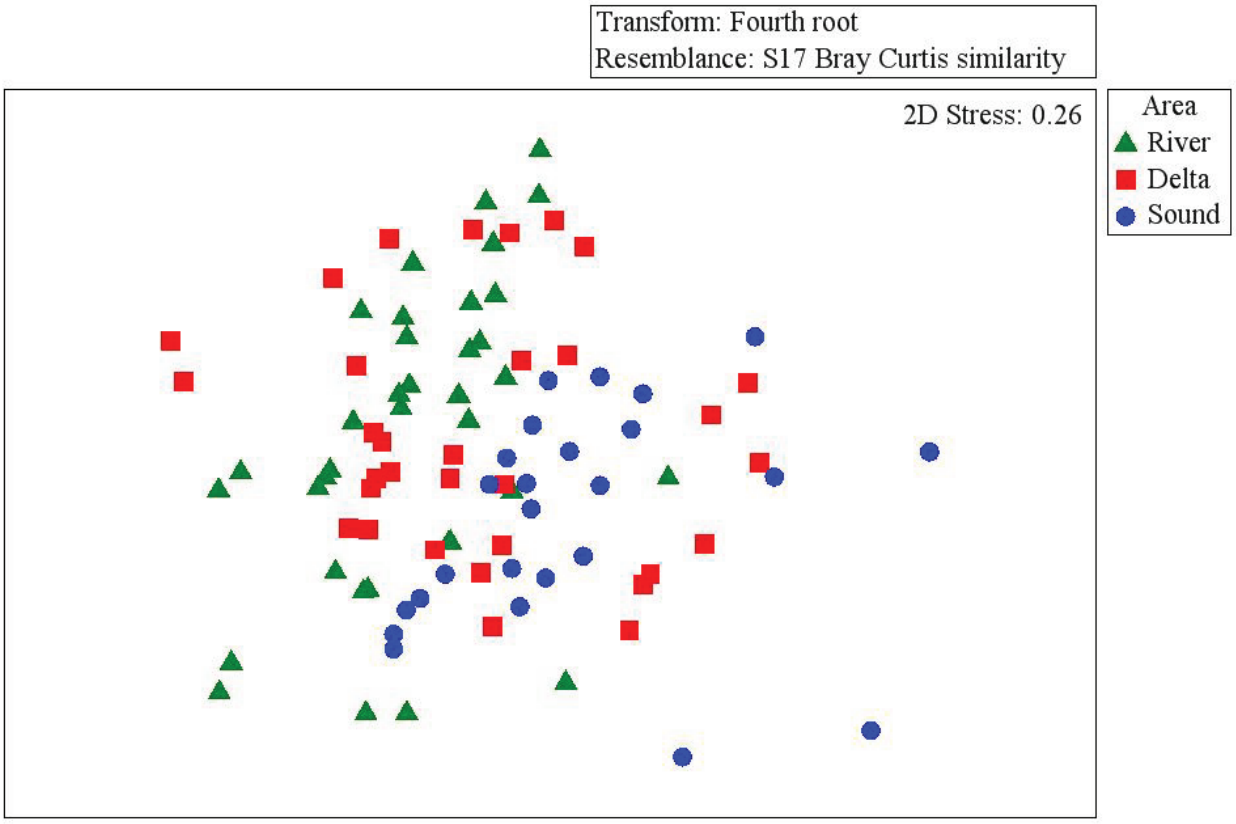

Figure 3.6. A 2-D, non-metric multidimensional scaling (MDS) ordination plot used to define groups of zooplankton samples based on species occurrence and abundance. Data in matrix (N = 1,598) were fourth-root transformed, with rare species being down weighted. Symbols closer together have greater similarity in zooplankton community structure than symbols that are farther apart.

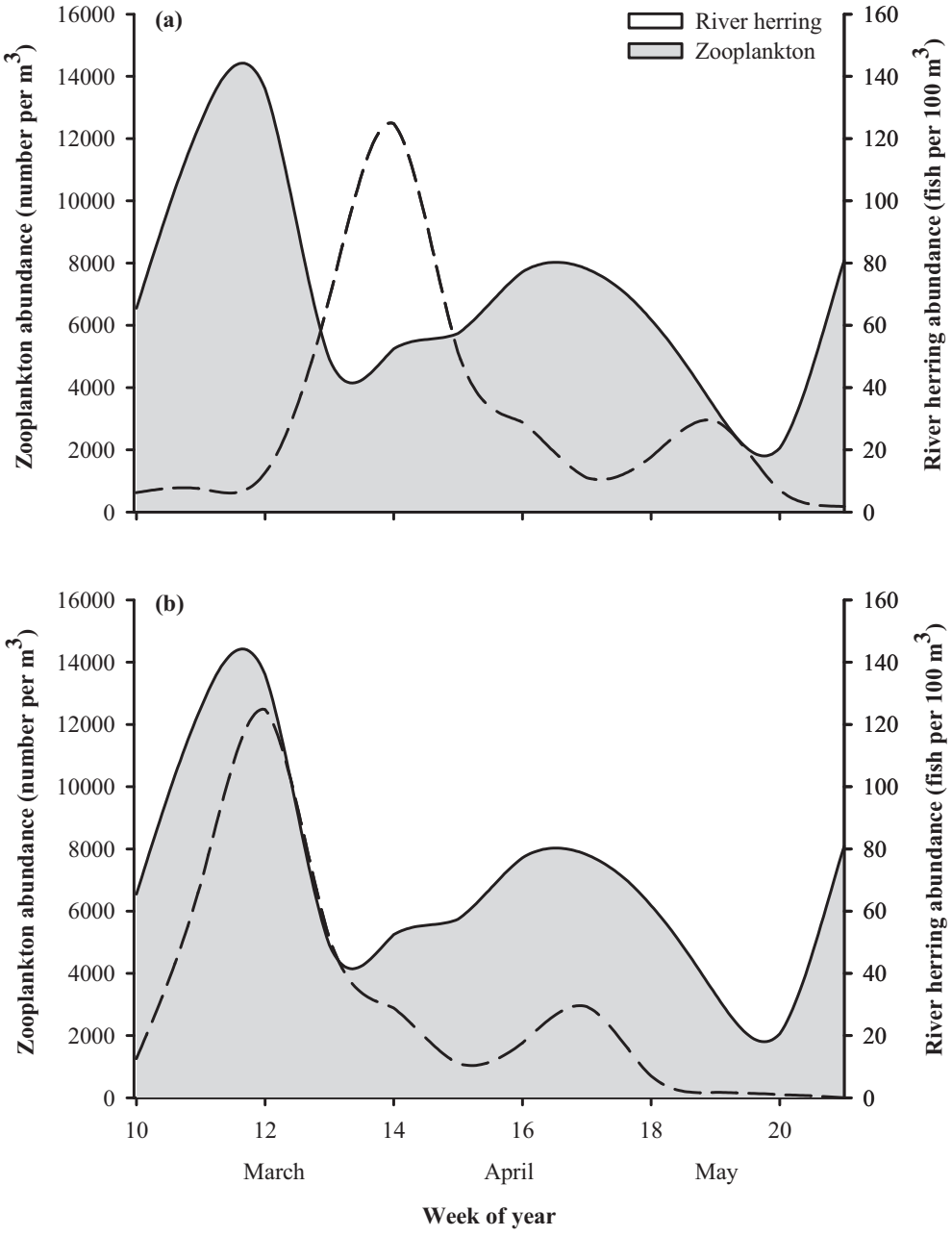

Figure 3.7. Hypotheses of match:mismatch regulation were tested by comparing zooplankton abundance (solid line) and river herring abundance (dashed line). Values represent weekly mean abundance of fish and zooplankton. A mismatch was induced by river herring feeding on zooplankton (a). When a 2-week time lag was applied to river herring abundance (b), the data actually suggests a match occurred with a temporal overlap of predators and prey.

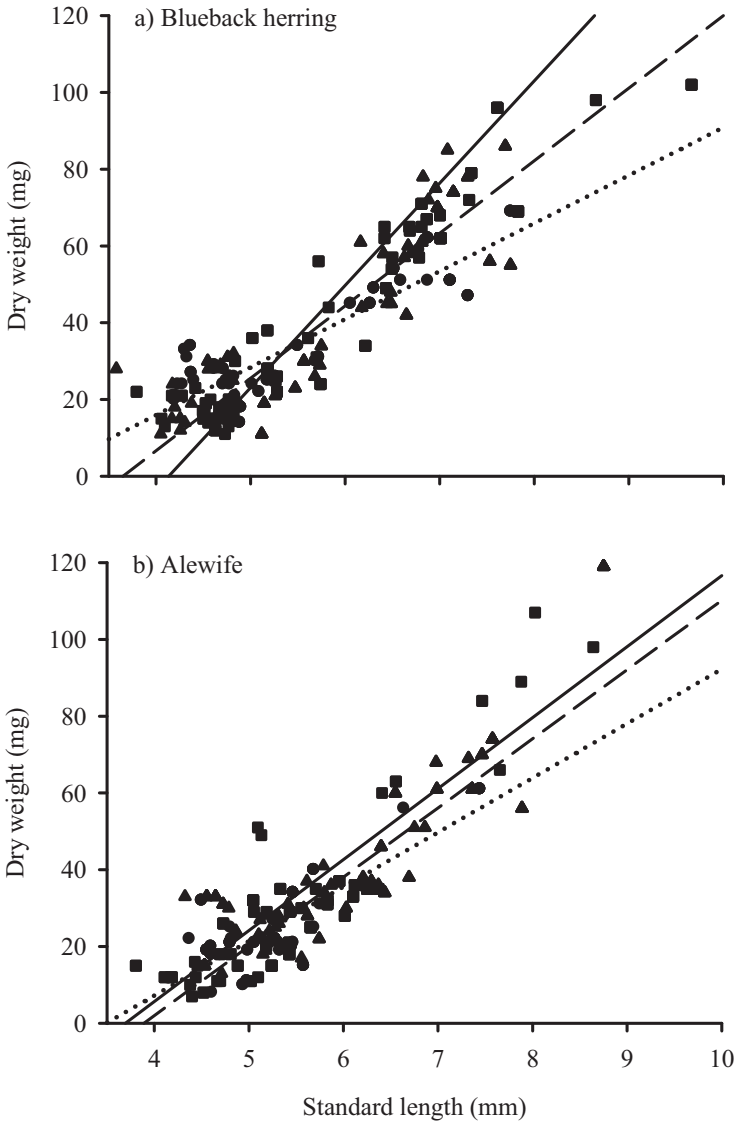

Figure 3.8. Regression of blueback herring and alewife length and weight by area. For both species, growth was higher in the River (triangle, solid line) as compared to the Delta (square, dashed line) and Sound (circle, dotted line).

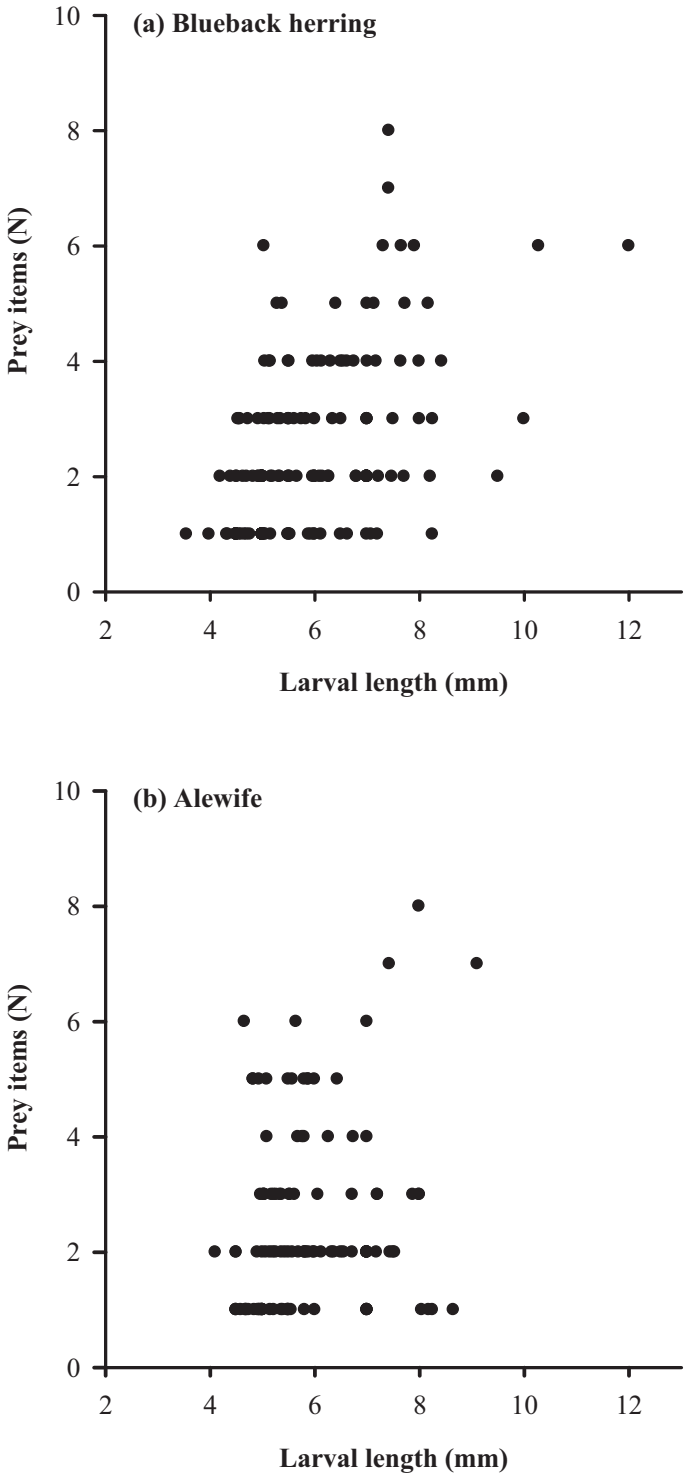

Figure 3.9. Relationship between the number of prey items consumed per larva and larval predator length for (a) blueback herring and (b) alewife.

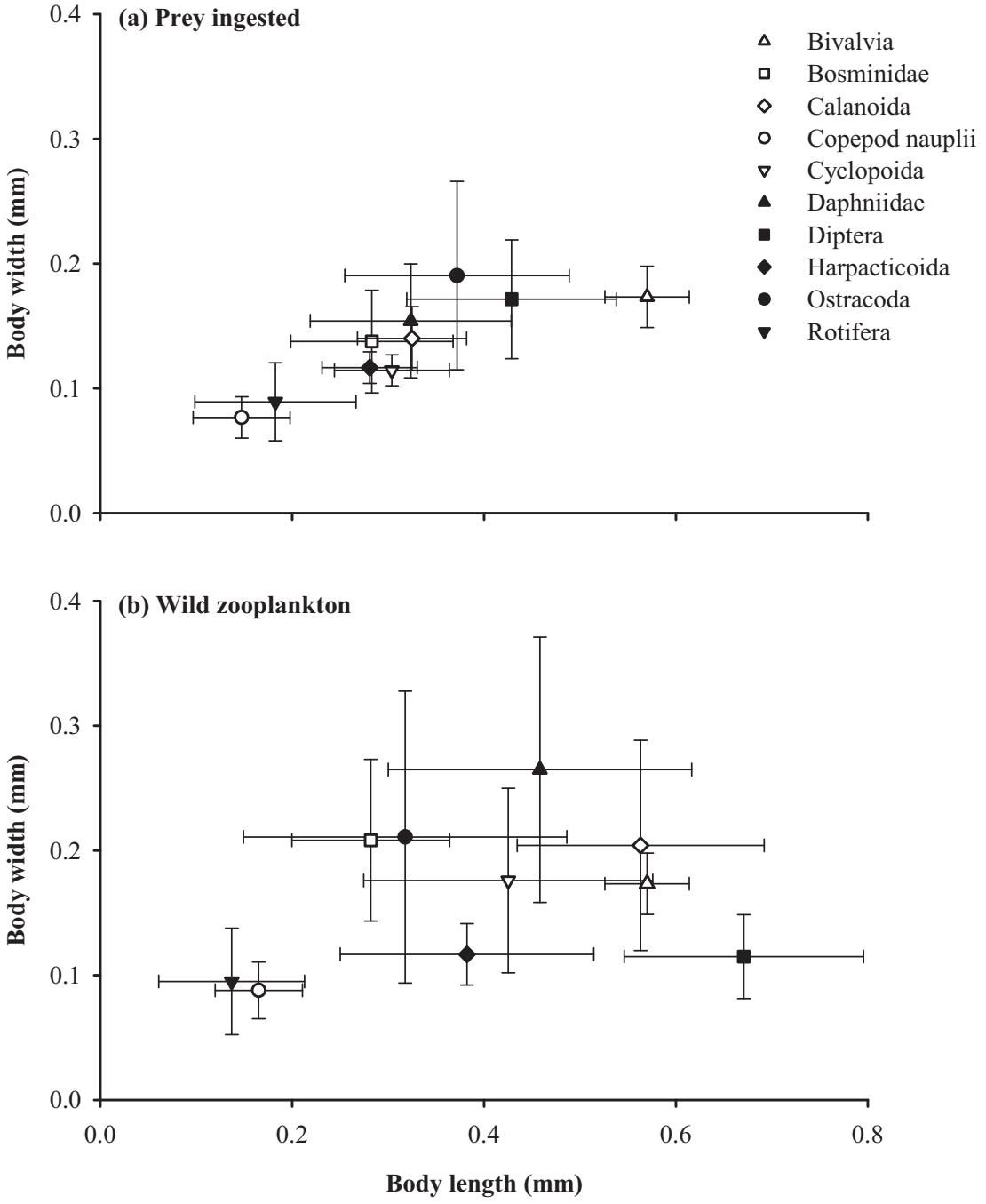

Figure 3.10. Body lengths and widths for the prey identified from the guts of river herring (a) and zooplankton (b) collected concurrently from the lower Roanoke River and Albemarle Sound. Values represent means (±SD). Data for wild zooplankton were trimmed to include individuals that measured less than 0.8 mm in length. As a result, large dipterans were removed.

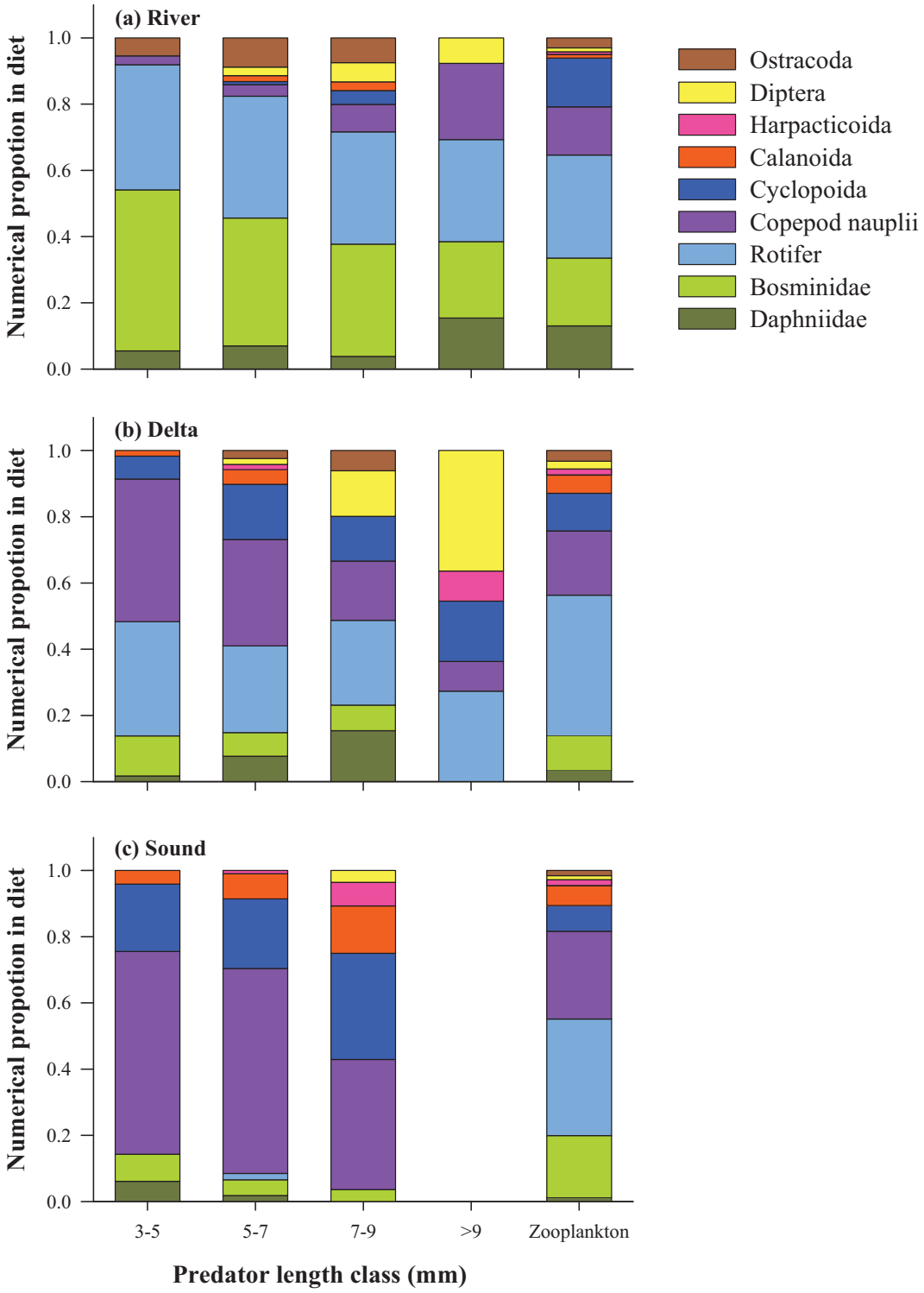

Figure 3.11. Numerical proportions of zooplankton and prey ingested by river herring within lower Roanoke River (a), Roanoke River delta (b), and Albemarle Sound (c), North Carolina.

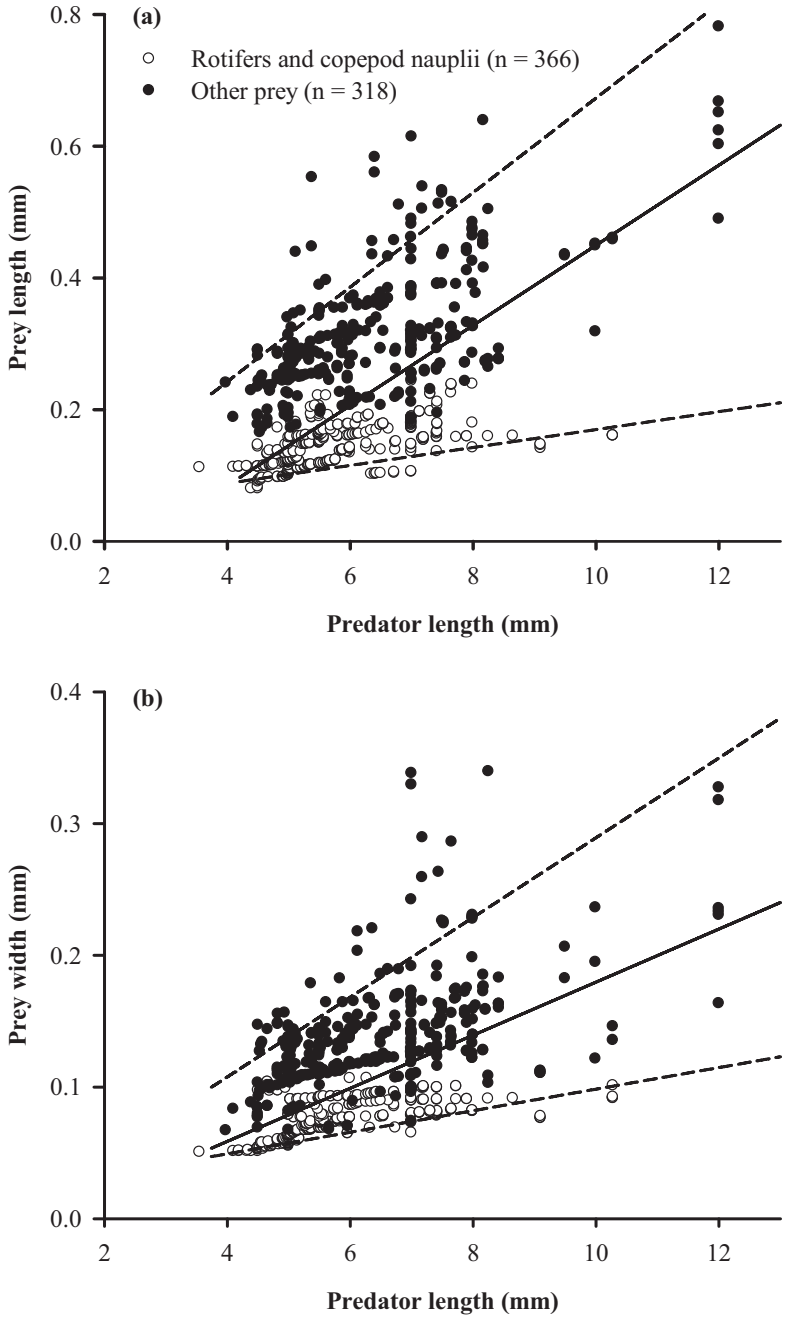

Figure 3.12. Relationship between individual ingested prey size and river herring standard length. Quantile regression (Scharf et al. 1998) was used to characterize the median (solid line) and the upper and lower bounds for prey size (5^{th} and 95^{th} percentile, dashed lines). Regression models based on prey length (a) and width (b) were both statistically significant. Regression equations are presented in Table 3.11.

CHAPTER 4. ESTIMATING THE FOOD REQUIREMENTS AND PREY SIZE SPECTRA OF LARVAL AMERICAN SHAD

Abstract

Widespread declines in American shad *Alosa sapidissima* along the Atlantic Coast have been attributed to overfishing, decrease in water quality, and loss of habitat. Recent surveys along Roanoke River and Albemarle Sound, North Carolina suggest stocks are continuing to decline despite extensive management and stock enhancement efforts. Laboratory experiments were conducted to evaluate the effect of prey density on 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 days after hatching in five treatments: (1) no food; (2) low (1 prey/L), which simulated prey densities in Roanoke River; (3) medium (50 prey/L), which simulated prey densities typical of coastal watersheds; (4) high (500 prey/L), and (5) *Artemia* spp. (500 prey/L). Larval survival was 35 ± 7% and was not significantly different among treatments. Treatments with starved fish had lowest survival (22 ± 12%), while highest fish survival was observed in treatments with high densities of wild zooplankton (46 ± 18%) and *Artemia* (40 ± 16%). Length-specific growth rates were 0.017 for starved treatments, 0.024 for low-prey, 0.029 for medium-prey, 0.034 for high-prey, and 0.039 for *Artemia*. Larval growth as a function of length was not significantly different between *Artemia* and high-prey; however, these treatments were significantly higher than lower prey densities (ANOVA; $P < 0.0001$). Weight-specific growth rates (G_w) were significantly higher for *Artemia* ($G_w = 0.129$; $P < 0.0001$) and were lower for all other treatments ($G_w = 0.081$). Analysis of gut contents indicated

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Riley, K. L., S. M. Binion, and A. S. Overton. *In press.* Estimating the food requirements and prey size spectra of larval American shad. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science.

American shad were selectively feeding on the smallest zooplankton (80 – 250 μm) and larvae exhibited a strong preference for copepod nauplii and rotifers. These results suggest spatial and temporal overlap between larvae and zooplankton is important for larval growth and survival.

Introduction

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 survival and growth of fish larvae has become a fundamental paradigm in fishery science (Bergenius et al. 2002; Rakocinski et al. 2006; Jenkins and King 2006).

During the past century, a number of hypotheses have been developed to explain recruitment variability. These hypotheses largely attribute larval mortality to a lack of food resources leading to starvation or resulting 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 suitable prey must be available during the first feeding stage of larvae 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., phytoplankton as a proxy for zooplankton) and larval fish abundance. Considerable

evidence to support these hypotheses has resulted from field observations with 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 prey size spectrum, prey mobility, patchiness of prey distribution, and prey density (Kamler 1992; Horn and Ferry-Graham 2006). Energy spent searching and capturing prey can have severe consequences if a larva is not successful at feeding. At first feeding, most larvae have limited abilities 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 the presence or absence of 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 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 in a steady proportion to their own growth (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 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. Fish used in experiments were cohorts of the same age and had undergone the same treatments as shad larvae stocked into Roanoke River, North Carolina. Wild-caught broodstock that were of Roanoke River origin were spawned on 04 May 2008. Larvae obtained for use in experiments were of the same age, but were mixed progeny. Within the hatchery, larvae were reared using standard production methods with *Artemia* spp. as a 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 to 22.0 $^{\circ}$C, salinity was 2.0 psu, and pH levels were >7.5.

General Experimental Conditions

Fish were obtained at 9 days after hatching (DAH) and approximately 5 days after transitioning to live feeds. Fish were transported to East Carolina University's Aquatic Animal

Research Laboratory (ECU-AARL) in an insulated cooler with supplemental oxygen. Upon arrival at the ECU-AARL, fish were allowed to equilibrate in temperature and salinity prior to transfer into two large (80 L) holding tanks. Fish were held for 24 h and fed *Artemia* spp. nauplii before stocking experimental systems. Experiments were conducted in a temperature-controlled laboratory under cyclic photoperiod conditions (14L : 10D).

Larvae were reared in freshwater to simulate water quality characteristics of Roanoke River, NC. To produce freshwater for 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, OH, USA). Total hardness was adjusted to 140 mg/L with calcium carbonate, and total alkalinity was adjusted to 220 mg/L with sodium bicarbonate.

Experiments were conducted using 21-L cylindrical plastic tanks ($N = 35$) that were transparent and colorless. Tanks were wrapped in black plastic to simulate downwelling light, as a more natural condition, and to provide a 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 to 4.84 μmol photons s^{-1} m^{-2} provided by overhead fluorescent light fixtures. Each tank was stocked with a total of 84 larvae at 10 DAH. The goal of stocking was to select a low enough density (4 larvae/L) to accurately project growth and survival, while not masking the effects of treatment variables (Chesney 1989). Larvae that died within the first 24 h were replaced.

Larvae were reared from 11 to 20 DAH in five treatments: (1) no food; (2) low-food (1 prey/L), which simulated prey densities in Roanoke River; (3) medium-food (50 prey/L), which simulated prey densities typical of coastal watersheds; (4) high-food (500 prey/L), and (5) *Artemia* spp. (500 prey/L), which served as an experimental control. The latter treatments also

simulated 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 harvested three tanks from each treatment at 16 and 20 DAH. Fish were harvested from tanks by siphoning water and concentrating fish on a 53-µm mesh Nitex sieve.

With exception of treatments without food and those fed 24-h-old nauplii of *Artemia* spp., fish were fed size-sorted wild zooplankton (53-800 µm) collected from a series of oxbow lakes adjoining Tar River in Greenville, NC (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 size frequency distribution. Body length and width of zooplankton were measured on up to 25 individuals per taxa.

Fish were observed at least twice daily at 09:00 and 15:00, 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 through measurement of temperature, dissolved oxygen, salinity, pH, and total ammonia nitrogen (TAN). 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 < 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-x 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, IL, USA). 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:

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

where a is mouth gape, b is upper jaw length, c is lower jaw length, and α is a measure of the angle that forms the degree of mouth opening. Calculations were based on the assumption that during active feeding the mouth of larvae opens to an angle ranging from 90° to 120° to capture prey (Shirota 1970; Krebs and Turingan 2003). Optimal prey sizes were estimated at 30% and 50% of 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 TL and NL measurements. Estimates of prey size used with the regression model were based on measures that optimal prey dimensions are 50% of mouth gape.

Linear regression was used to examine larval growth and mortality rates. Mortalities were tallied from the daily removal of dead larvae from each experimental tank and compared to surviving larvae at the time of harvest. The relationship 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. The comparison between these plots allowed assessment of somatic growth pattern 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 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 and used to evaluate gut contents and gut fullness. Larvae were dissected on glass slides using forceps and fine-point needle. A dissecting microscope at 40-x magnification was used to identify ingested prey removed from the foregut of 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; Chesson 1983) was used to measure prey selectivity in 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 prey type in the diet and the proportion of prey type in the culture tank. We used a derivation of the Manly-Chesson index (Chesson 1983) for controlled laboratory experiments with constant prey abundance:

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

where α_i is Manly's alpha for prey type i; r_i and r_j are proportion of prey type i or j in the diet; n_i and n_j are 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 parameters including temperature, dissolved oxygen, salinity, pH, and TAN were assessed using ANOVA. The general linear model function in SAS (SAS 9.2; SAS Institute, Cary, NC, USA) 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 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 HSD post-hoc multiple range tests were used to determine if significant differences existed among treatment means. Differences were considered significant at $P \leq 0.05$. Results are expressed as the means ± SE 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. Overall survival of American shad larvae reared through 20 DAH was 35 ± 7% and was not

significantly different among treatments. The highest survival occurred with fish fed high densities of zooplankton (46 ± 18%) followed by *Artemia* (40 ± 16%) and medium densities of zooplankton (37 ± 22%). The lowest survival was observed with low densities of zooplankton (31 ± 18%) and starved fish (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 (G_{TL}) based on total length measurements were 0.039 ± 0.003 for *Artemia*, 0.034 ± 0.003 for high-prey, 0.029 ± 0.005 for medium-prey, 0.024 ± 0.002 for low-prey, and 0.017 ± 0.001 for treatments with no food. Length-specific growth rates (G_{NL}) based on notochord length measurements were 0.036 ± 0.002 for *Artemia*, 0.034 ± 0.001 for high-prey, 0.034 ± 0.001 for medium-prey, 0.025 ± 0.001 for low-prey, and 0.022 ± 0.001 for treatments with no food. Separate growth equations were developed for each treatment because of significant differences in growth (Table 4.1). Larval growth as a function of length was not significantly different between *Artemia* and high-prey (Figure 4.1); however, these treatments were significantly higher than the lower prey densities at 16 and 20 DAH (ANOVA; df = 5, 163; $P < 0.0001$).

Variability in length was less pronounced with notochord measurements (CV 6%) as compared to total length measurements (CV 12%). Because freshly killed larvae were used for measurements, this variability was not a result of sample storage or shrinkage. Variance was most likely an indicator of larval condition and stage of development. The presence of intact fins and fin rays indicated that 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 (G_w) were 0.128 ± 0.011 for *Artemia*, 0.082 ± 0.018 for high-prey, 0.025 ± 0.006 for medium-prey, -0.016 ± 0.004 for low-prey, and -0.020 ± 0.027 for treatments with no food. Separate growth equations were developed for each treatment because significant differences in growth were observed (Table 4.2). At 16 DAH, larval growth as a function of dry weight was significantly different between *Artemia* and all treatments (ANOVA; df = 4, 95; $P < 0.0001$). In contrast, at 20 DAH dry weights were not significantly different among treatments with *Artemia*, high-prey, and medium-prey (Figure 4.1); however, these treatments were significantly higher than 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 4.3). The mouth gape of larvae at 20 DAH were not significantly different among treatments with *Artemia*, high-prey, and medium-prey; however, these treatments were significantly higher than 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 4.2). Prey size based of larval mouth gape estimates of 30% (min) and 50% (max) ranged from 0.229 to 0.585 mm at 12 DAH, 0.248 to 0.587 mm at 16 DAH, and 0.271 to 0.606 mm at 20 DAH. With exception of small copepod nauplii (< 0.100 mm) and large cladocerans (> 0.600 mm), these values correspond closely with the size of zooplankton and *Artemia* spp. nauplii used as a food in experiments.

Prey Composition and Size Spectra

Zooplankton samples collected during this study were uniform in composition and primarily consisted of cladocerans, copepods, and rotifers (Figure 4.3). Cladocerans and adult copepods were among the largest prey types, while copepod nauplii and rotifers were the smallest. Insects, with exception of chironomid larvae, were absent from samples as a result of the sieving process. Minimal overlap in size was observed among the different prey types (Table 4.4). Variation of prey densities within each treatment was not pronounced, with coefficients of variation (CV) ranging from 49-68% among treatment replicates.

Larval Behavior

Larvae were observed actively searching for prey in all treatments at the initiation of experiments. Search and feeding behavior was typical of larval American shad and other clupeids with larvae assuming the S-flex position in anticipation of capturing prey (Blaxter and Hunter 1982; Ross and Backman 1992; Ross et al. 1996). Larvae that were not feeding or 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 four days 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, 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 four days 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.

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 4.4). Chironomids and gastropods were the only prey taxa observed in plankton samples, but not observed in the guts of larvae. American shad displayed strong selection for copepod nauplii and rotifers in all treatments with wild zooplankton (Table 4.5). Larvae had 5.1 ± 2.7 prey in their guts in high density treatments and 0.8 ± 0.7 prey in their guts in medium density treatments. Gut fullness was not significantly different among treatments with *Artemia* (90 ± 12%), high prey (78 ± 19%), and medium prey (63 ± 19%), but these treatments were significantly higher than the treatment for low prey density (12 ± 12%; ANOVA; df = 5, 117; $P < 0.0001$).

Discussion

The abundance and distribution of food is critically important for growth of fish larvae and results from this study suggest 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 feeding conditions typical of coastal rivers in North Carolina, and more specifically conditions observed in 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 populations of anadromous fish species (Hassler et al. 1981; Rulifson et al. 1993).

While it is well known rivers are not highly productive systems for zooplankton (Hynes 1970; Chick and Van Den Avyle 1999), abundance and distribution of zooplankton in Roanoke River is the lowest of 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 Roanoke River are historically low and often 1 to 2 orders of magnitude lower than adjacent watersheds (Table 4.6). In these studies, zooplankton abundances never exceeded 1000 individuals/m^3 during critical periods (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 temporal asynchrony of predators and prey results in starvation of fish larvae.

In laboratory experiments, increases in growth using length and dry weight measurements were positively correlated with increasing densities of prey. These findings are consistent with studies suggesting American shad larvae exhibit high rates of growth when *Artemia* spp., a proxy for naturally occurring plankton, are fed at densities ≥ 500 nauplii/L (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 zooplankton distributions in Roanoke River and Albemarle Sound (Rulifson and Manooch 1993; Binion 2011). Using discrete methods for feeding larvae, we found growth was highest when larvae were fed at densities ranging from 50 – 500 prey/L and when larvae were able to forage on the smallest species of zooplankton.

The results of this study suggest an optimal prey size exists for larval American shad and that prey size is a function of mouth gape (Figure 4.2). 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 larvae can capture and consume. We observed 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 < 50% of mouth gape, and American shad larvae are dependent upon vision for prey detection (Blaxter 1986) or other non-visual senses for prey selectivity (Batty and Hoyt 1995; Salgado and Hoyt 1996).

Although fish in all treatments demonstrated a preference for small zooplankton (80 - 250 μm), prey size was correlated with growth rate suggesting fish behavior or experience ensures a high rate of success for prey capture and feeding. Our work differs from other published findings with American shad because fish showed strong preference for small 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 if 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 analysis of dry weight is a more appropriate measure of growth as compared to length. While fish in treatments with low densities of prey and no food continued to grow in length (0.25 ± 0.06 mm/d), fish in the same treatments 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 < 50 prey/L were undergoing a loss of body condition, the onset of starvation, and lagged their cohorts in development as evidenced by weight loss and appearance. These results build upon 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 four days of the experiment. This suggests larvae undergo a transitional period from feeding on *Artemia* nauplii to 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 a temporal overlap or weaning period is required in transitioning fish from an environment with 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. Survival of fish among tanks and treatments (35.3 %) was similar to previous studies with the early life history of American shad (Limburg and Ross 1995; Ross et al. 1996; Leach and Houde 1999). Unlike the work of Johnson and Dropkin (1995) 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 (Rogers and Westin 1981; Eldridge et al. 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 stocks of American shad along the Atlantic Coast have been attributed to overfishing, 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 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 upon studies that indicate: (1) migration and spawning is 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 effects (Rulifson 1994; Hightower and Sparks 2003; Walsh et al. 2005). Cultured fish are released to supplement natural recruitment and assist in recovery of populations to historical levels.

Since 1998, *c.* 26.4 million American shad larvae have been stocked into Roanoke River, North Carolina (NCWRC 2009). Larval fish (12 to 18 DAH; 8 to 16 mm TL) are used in shad restoration programs because of 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 (≤ 1000 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 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 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 varies with season, temperature, water quality, primary productivity, and predation. The presence of adequate densities of suitable prey is essential for 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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Table 4.1. Linear relationships for total length (G_{TL}) and notochord length (G_{NL}) for American shad larvae reared at 24 °C. Experiments evaluated the effects of different feed types and concentration on larval growth.

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 Age + 10.9	0.57	0.20
		8.1 - 13.9	G_{NL} = 0.4 Age + 9.4	0.72	0.13
High prey	136	9.7 - 17.2	G_{TL} = 0.4 Age + 10.9	0.62	0.15
		8.1 - 12.8	G_{NL} = 0.4 Age + 9.2	0.78	0.10
Medium prey	110	9.7 - 16.6	G_{TL} = 0.3 Age + 10.7	0.38	0.18
		8.1 - 12.7	G_{NL} = 0.4 Age + 9.2	0.63	0.15
Low prey	121	9.7 - 16.6	G_{TL} = 0.3 Age + 10.7	0.29	0.20
		8.1 - 12.7	G_{NL} = 0.3 Age + 9.3	0.42	0.16
No food	125	9.7 - 16.6	G_{TL} = 0.2 Age + 10.9	0.17	0.22
		8.1 - 12.0	G_{NL} = 0.2 Age + 9.3	0.44	0.14

Table 4.2. Linear relationship for dry weight (G_w) and age of American shad larvae reared at 24 °C. Experiments evaluated the effects of different feed types and concentration on larval growth.

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

Table 4.3. Mouth gape size of American shad larvae reared at 24 °C. Values represent measurements (means ± SE) for larvae sampled from treatments feed *Artemia* spp. and high densities of zooplankton (500 prey/L). Mouth gape estimates were based upon calculations assuming the mouth opens 90° (min) to 120° (max) during feeding and prey capture.

Days after hatching	Lower jaw length (mm)	Upper jaw length (mm)	Min mouthgape (mm)	Max mouthgape (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

Table 4.4. Size (mean ± SD) of zooplankton used in feeding experiments with American shad larvae.

Prey type	Body length (μm)	Body width (μm)
Daphniidae	1406 ± 198	655 ± 179
Bosminidae	287 ± 49	142 ± 10
Cyclopoida adult	1031 ± 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

Table 4.5. Mean preference index, α_i, values (Chesson 1983) for American shad larvae reared from 11 to 20 days after hatching. Larvae were fed size-sorted wild zooplankton at three different densities: (1) low density (1 prey/L), (2) medium density (50 prey/L), and (3) high density (500 prey/L). Values of $\alpha_i > 0.25$ indicate preference by the larvae for a 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

Table 4.6. Comparison of mean zooplankton abundance (number/m^3) for coastal rivers and estuaries in North Carolina, South Carolina, and Virginia.

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

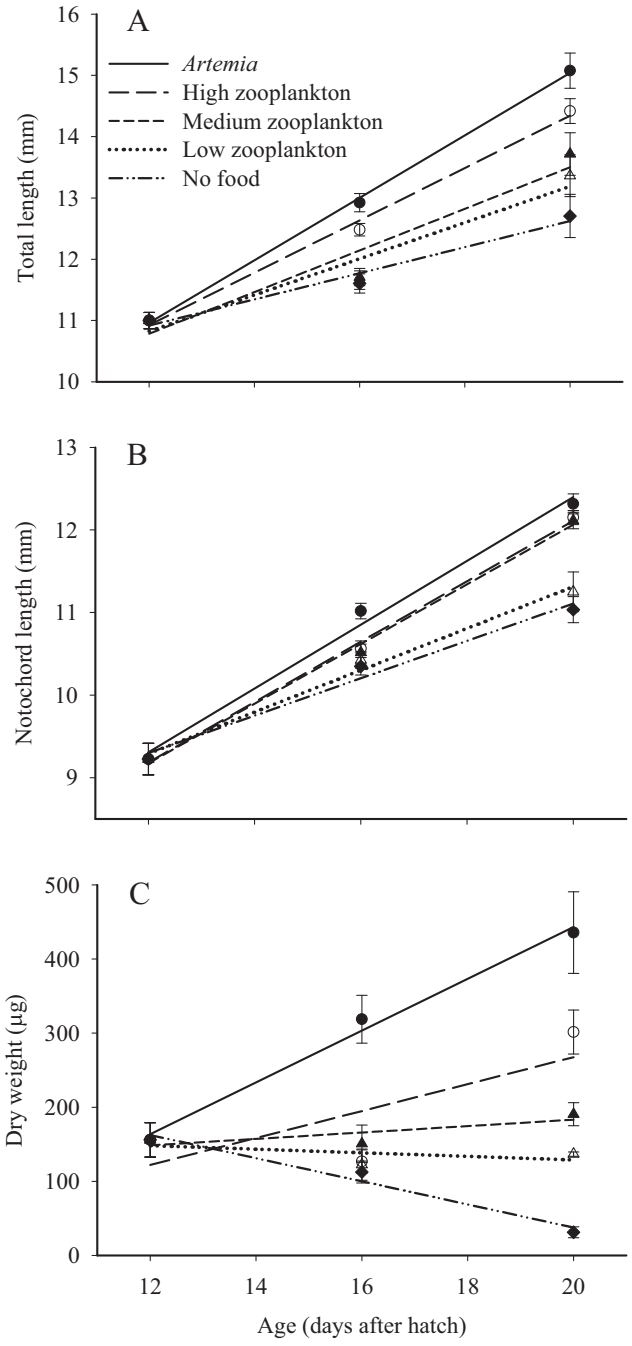

Figure 4.1. Total length (A), notochord length (B), and dry weight (C) of American shad larvae reared from 12 days after hatching (DAH) to 20 DAH. Experiments evaluated the effects of food availability on larval growth. Regression lines are plotted with mean ± SE values for treatments *Artemia* (filled circle), high zooplankton (open circle), medium zooplankton (filled triangle), low zooplankton (open triangle), and no food (diamond).

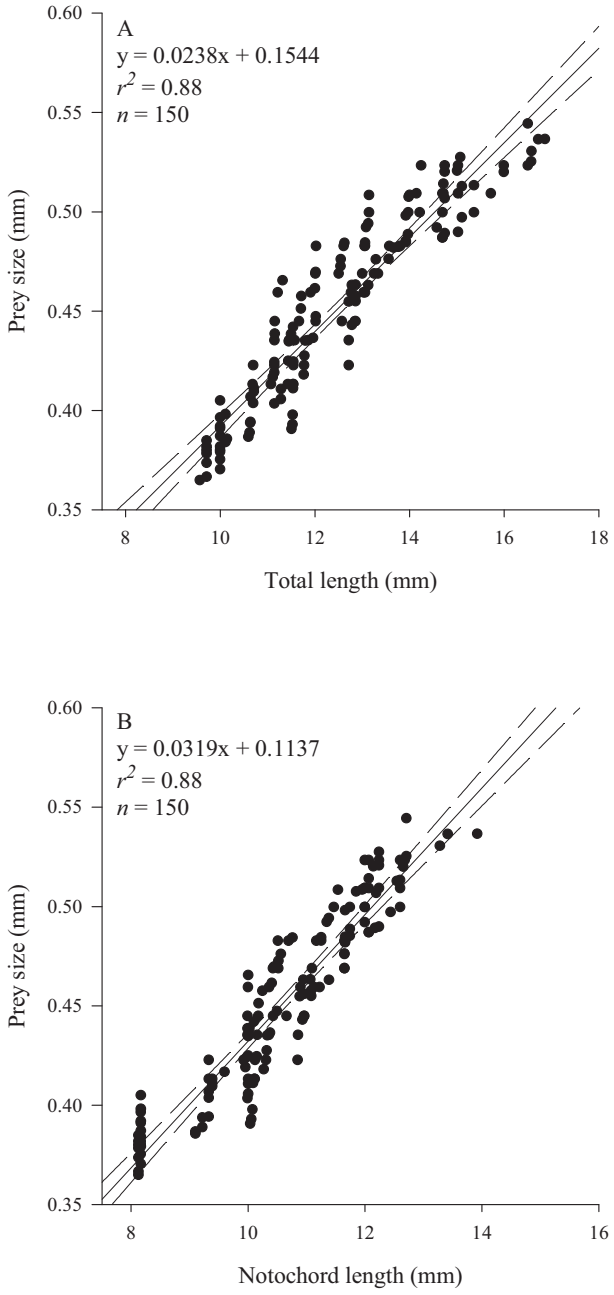

Figure 4.2. Regression (solid line) with 95% confidence limits (dashed line) of theoretical prey size on total length (A) and notochord length (B) measurements for American shad larvae. Prey size was estimated at 50% of mouth gape for larvae. Data represent combined measurements of three feeding treatments (*Artemia*, high prey, medium prey) that were not significantly different (ANOVA; df = 2, 27; $P = 0.18$).

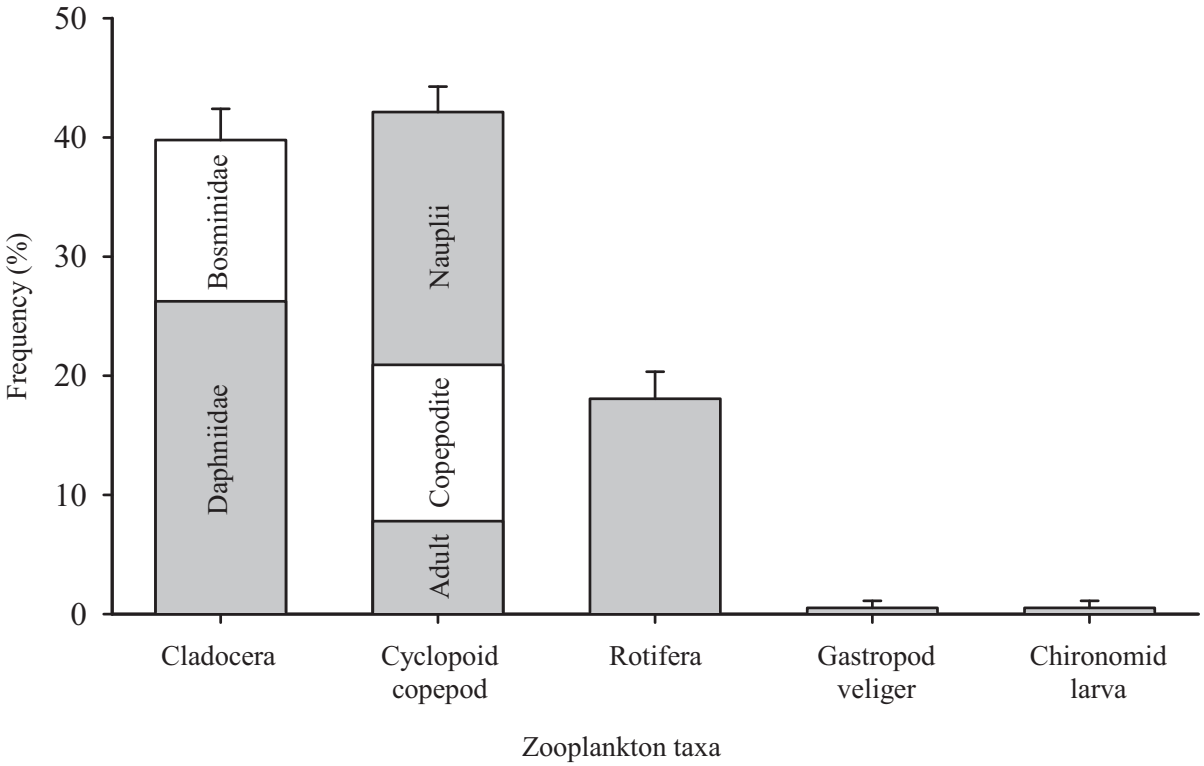

Figure 4.3. Frequency distribution of size-sorted, wild zooplankton collected and used as food in larval rearing trials with American shad. Samples were washed through an 800-µm mesh sieve to prevent the introduction of ichthyoplankton, insects, and other predatory species. Data represent the mean distribution of invertebrate taxa among daily samples collected from the field.

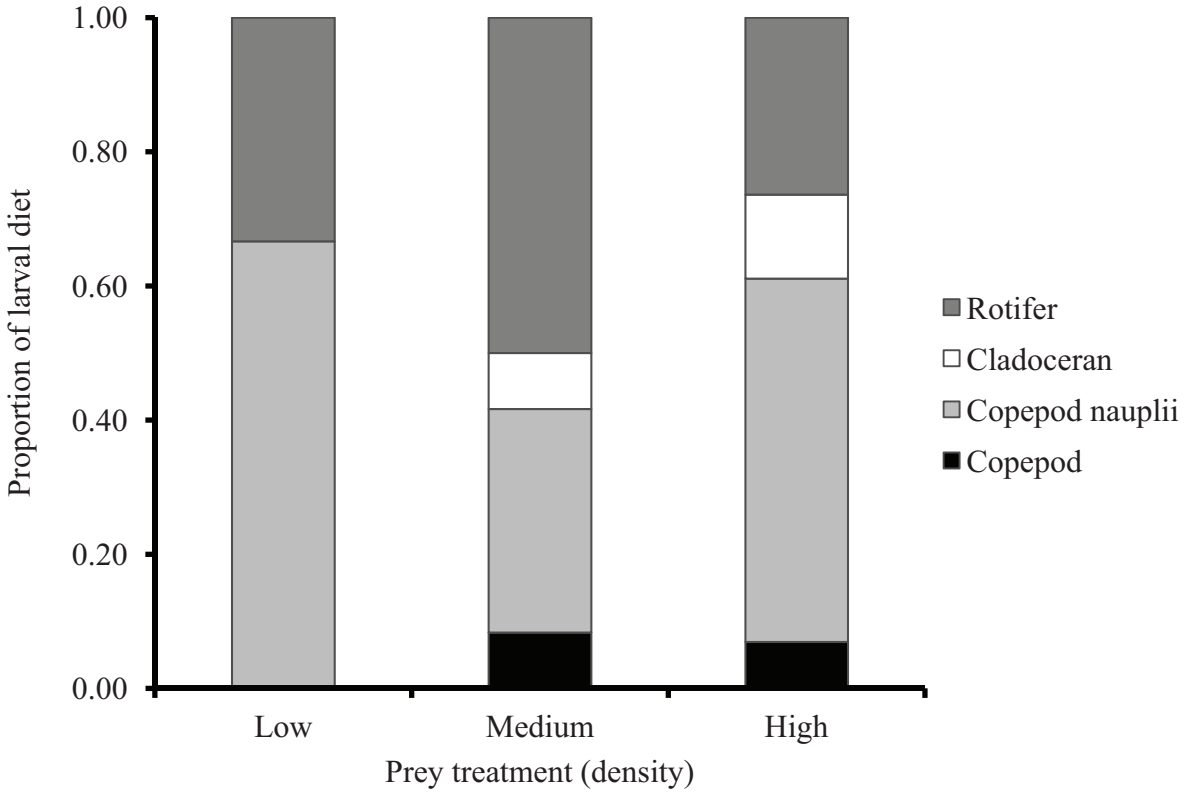

Figure 4.4. Diet composition of American shad reared 12 to 20 days after hatch in three treatments with varying densities of food. Replicated treatments consisted of low-density zooplankton (1 prey/L), medium-density zooplankton (50 prey/L), and high-prey (500 prey/L).

CHAPTER 5. INTERANNUAL VARIABILITY IN ESTUARINE RECRUITMENT, GROWTH, AND MORTALITY OF RIVER HERRING IN NORTH CAROLINA, USA

Abstract

Interannual variation in patterns of abundance, growth, and mortality were examined to determine the causes of recruitment variability in river herring (blueback herring *Alosa aestivalis* and alewife *A. pseudoharengus*). Long-term datasets from 1984 to 2009 were used to quantify the relationship between larval recruitment in Roanoke River and juvenile recruitment in Albemarle Sound. Synchrony was not observed in recruitment of larvae and juveniles. River herring yolk-sac larvae were prevalent throughout samples and clearly comprise an important component of the ichthyoplankton assemblage. Larval abundances peaked during the latter part of April (564 ± 191 number / 100 m^3) and declined steadily through June. Juvenile recruitment was strong for June, July, and August. Emigration of alewives was clearly evident in September and October. With exception of a strong year-class in 1985, we failed to observe any other strong year-classes. Instantaneous larval growth (G; 0.005 – 0.043) and mortality (Z; 0.006 – 0.067) were low, but were comparable with other studies. Juvenile growth (0.001 – 0.005) and mortality (0.001 – 0.0214) were both lower than larval estimates and differed by an order of magnitude. Larval fish production was negatively affected by spring river flow (r^2 = 0.62). High flows resulted in larval advection from Roanoke River. Low flows and drought conditions coincided with high larval abundances. Spring river flow was highly correlated with juvenile abundance (r^2 = 0.90). Stepwise multiple regression was used for detailed assessment of the relationship among river herring abundance, river flow, and wind stress. The results suggest that density-independent and density-dependent processes work in concert to regulate recruitment.

Introduction

The early life history for most anadromous species is complex and intertwined with natural variability in biotic and abiotic factors. Fish movement and distribution patterns are often governed by physics, ontogeny, food abundance, and predation (Leggett and Deblois 1994; North and Houde 2003a). River flow and circulation features contribute to the dispersal of eggs and larvae. Temperature and other environmental conditions exert major influences on growth and mortality. Because growth and mortality are linked processes, they are important determinants of recruitment success (Houde 2008). Relatively small variations in mortality rates, growth rates, or stage duration in the early life of fishes can have fluctuations that vary by one or two orders of magnitude in recruitment (Houde and Hoyt 1987). As a result, understanding the processes that regulate recruitment has become central focus of fisheries science (Heath 1992).

River herring are two small anadromous alosines (blueback herring *Alosa aestivalis* and alewife *A. pseudoharengus*) that are collectively managed as a single stock along the Atlantic coast. Widely known for their economic value to commercial and recreational fisheries (Hightower et al. 1996; Schmidt et al. 2003), river herring also serve as an important forage base for predators throughout their range (Hartman and Margraf 2003; Walter et al. 2003). Upon reaching sexual maturity (age 3-6), river herring undertake spawning migrations through estuaries and coastal rivers (Marcy 1969; Loesch 1987). Spawning is assumed to occur in natal rivers and streams near headwaters or to the extent that dams and obstructions limit migrations (Meador et al. 1984; O'Connell and Angermeier 1997; Cooke and Leach 2003; Harris and Hightower 2010). After spawning, eggs and larvae drift downstream through a variety of habitats (Walsh et al. 2005). Retention in specific nursery habitats is mediated by local hydrography, precipitation and weather, and river flow.

Effective conservation and management of river herring depends on the ability to predict and forecast recruitment for a given year. While it is presumed that adult stock abundance plays a role in regulating recruitment, the relative size and contribution of parental stocks does not guarantee the emergence of a strong year-class (Walton 1987; Wood and Austin 2009). Few studies with anadromous alosines have been able to establish a relationship between abundances of adults and juveniles (Leggett 1976; Jessop 1990; Kosa and Mather 2001). This observation is not unique to anadromous species and extends to many marine fish populations where recruitment varies strongly and can be independent of adult stock abundance (Iles 1994; Myers and Barrowman 1996). Most studies with alosines report a failure to detect the relationship between adult and juvenile abundance, because recruitment variability is driven by climate-scale forcing events (Crecco and Savoy 1984; Henderson and Brown 1985; Jessop 1994). Owing to the difficulties in establishing a stock-recruit relationship, an approach to understanding population dynamics is to compare the relationship between successive stages of the recruitment process.

Few datasets allow for long-term correlations between production of larvae and juveniles. Since their precipitous decline in the latter part of the 20th century, river herring in Roanoke River and Albemarle Sound, North Carolina have been included in monitoring programs for conservation of anadromous species (Rulifson 1994; Carmichael 1999). The present study examines a 25-year dataset that includes juvenile river herring collected by the North Carolina Division of Marine Fisheries (NCDMF). The study also includes ichthyoplankton samples collected and summarized by the authors for 13 years. Anadromous fish production within this estuary and coastal river system has received considerable attention because conservation efforts have led to the recovery striped bass *Morone saxatilis* (Reinert et al. 2005; Greene et al. 2009).

Anadromous fish populations in Roanoke River have been affected by changes in streamflow, water quality, and habitat heterogeneity caused by construction of dams for hydropower generation and flood control (Rulifson and Manooch 1990a). Roanoke River is straddled by six major dams, none include provisions for anadromous fish passage. The most downstream facility on the river, Roanoke Rapids Dam, has restricted fish migrations since completion in 1955 (Zincone and Rulifson 1991). The dam is located 100 river kilometers (rkm) upstream from the river mouth. Flow patterns within this region are controlled by release schedules of upstream dams (Richter et al. 1997). Flows are seasonally regulated from April through mid-June to support striped bass production (Table 5.1). Spring river flow approximates historical pre-dam conditions (1912-1950), and dam discharge is managed to produce flow regimes that provide the necessary migratory and spawning cues for striped bass (Rulifson and Manooch 1990b; Rulifson and Manooch 1990a). Flows are kept within the twenty-fifth (Q1) and seventy-fifth (Q3) percentiles for the pre-dam period. The flow regime adopted in recent years includes provisions to manage daily flow magnitudes (150 – 240 m^3/s) and rates of change in flow levels ($\leq$ 42 $m^3/s \cdot h$). Because of stringent measures to protect river flow supporting striped bass production, recruitment of striped bass has returned to historical levels and the adult stock has increased eightfold since 1990s (Carmichael 2003; Rudershausen et al. 2005).

The primary goal of this study was to use long-term datasets to determine if a relationship exists between larval recruitment in Roanoke River and juvenile recruitment in Albemarle Sound and to determine how the relationship between these early life stages is influenced by environmental factors. The specific objectives were: (1) to test for synchronous patterns of abundance, growth, and mortality among early life stages and (2) to describe effects of interannual variability in hydrography, precipitation and weather, and river flow on river herring

production. In contrast to the classical definition in fisheries management that defines fisheries recruitment as the amount of fish added to the exploitable stock each year through growth or migration (Beverton and Holt 1957), the term recruitment in this study refers to the arrival of larval and juvenile stages of fishes to nursery habitats within a coastal ecosystem.

Methods

Larval River Herring Abundance

Ichthyoplankton data used for this study were collected as part of a long-term project to characterize fishery resources within Roanoke River, North Carolina. Data were extracted from three separate studies (1984 – 1991; 2001 – 2003; 2008 – 2009) and summarized for samples collected at weekly intervals from 15 April through 15 June. These months represent the bulk of anadromous fish production in Roanoke River and permit the collection of fish at various stages between hatching, yolk-sac absorption, and juvenile transformation (Rulifson and Overton 2005). Ichthyoplankton were collected at five fixed stations located in the lower Roanoke River watershed (Figure 5.1). Sampling was conducted at night because several studies indicate daytime sampling produces negatively biased abundance estimates for alosines (O'Gorman 1984; Höök et al. 2007). Sampling gears varied for each study and a statistical comparison was used to generate a corrective factor and standardize CPUE. Ichthyoplankton samples collected during the time period extending from 1984 to 1991 were obtained by towing paired conical nets in an oblique manner for 6 min against the current (Rulifson et al. 1992). Nets were constructed of 505-µm nitex mesh material with a 0.20-m^2 mouth opening and a tail-to-mouth ratio of 5:1. The same net configuration was used for samples collected in 2001, 2002, and 2003 (Rulifson and Overton 2005). Paired surface pushnets were introduced and used with oblique tows to collect

samples in 2002 and 2003 (Overton and Rulifson 2007). The paired pushnets were constructed of 505-µm nitex mesh material with a 0.25-m^2 mouth opening and tail-to-mouth ratio of 5:1. The nets were connected to an aluminum frame mounted on the bow of the boat and nets were lowered to sample 0.5-m below the surface. Surface nets were pushed into the prevailing water current for 2.0 min. Each net (oblique tow and pushnet) was equipped with a calibrated flowmeter mounted inside the mouth of the net to estimate the volume of water filtered. After collection, samples were condensed and preserved using either 95% ethanol or 10% buffered formalin. Water temperature and salinity were measured at each collection site.

Ichthyoplankton samples were transferred to fresh ethanol in the laboratory. Fish larvae were separated from debris, sorted, counted, and measured using a dissecting microscope equipped with an ocular micrometer. The stage of development was noted to differentiate yolk-sac larvae, feeding-stage larvae, and juveniles. Alosines were identified using a variety of larval taxonomic keys and criteria based on external morphological features (Lippson and Moran 1974; Auer 1982; Sismour 1994a; Walsh et al. 2005). Species identifications for the earliest study were limited to river herring because it was not within the scope of the study to separate blueback herring or alewife. Data on these species in more recent studies were consolidated to allow for statistical comparisons. To determine larval abundance, the catches between the two nets were averaged together. Abundances of larval fish were then standardized to catch per unit effort (CPUE; number of fish sampled per 100 m^3). Correction factors for differences between gears were applied to CPUE estimates for oblique tows.

Juvenile River Herring Abundance

To investigate how the abundance of juvenile river herring has changed over the last 25 years (1984 – 2009), data were extracted from the Albemarle Sound Juvenile Anadromous Fish Survey

conducted by NCDMF. This survey represents one of the longest-running independent fishery surveys in the United States and abundance indices developed from survey data are used in various stock assessment models for anadromous species (Rulifson and Manooch 1990a). The survey is extensive in its coverage of nursery habitats in Albemarle Sound and sampling is primarily conducted during the months of May through October. Data selected for this study spanned 1984 – 2009 and were chosen based on consistency of sampling methods, areas, and times. Data from May or earlier months were excluded from analyses because fish were not considered fully recruited to the seine gear until June. Data were summarized for 4 stations located within western Albemarle Sound and within close proximity of Roanoke River (Figure 5.1). These stations were selected based on their persistence in catch of juvenile river herring and their ability to serve as a sensitive indicator of long-term trends in abundance.

All fishes were captured using an 18.3-m bag seine constructed of 6.35-mm mesh body and 3.2-mm mesh bag (Rawls et al. 2010). For each sample, a single seine was pulled perpendicular to the shore starting from a depth of 1.0 – 1.5 m for a distance of 40 – 50 m. All fishes captured were identified and counted. The number of river herring captured per seine haul was used to estimate CPUE. Subsamples (≤ 70 fish) were measured for fork length (FL). Water temperature and salinity were measured during each sampling event.

Growth and Mortality

Annual growth and mortality rates for river herring larvae and juveniles were estimated using a length-based ageing method (Hackney and Webb 1978; DeAnglis et al. 1980). This method has produced comparable results with traditional ageing techniques using otoliths or bony structures (Zigler and Jennings 1993; Barfoot et al. 1999). Length-based ageing methods are also well suited for analysis of long-term datasets with persistent catch (Cada and Hergenrader

1980). To reduce bias, data were selected for fish that were equally vulnerable to each gear type. Catch curve analysis revealed larvae were vulnerable to ichthyoplankton nets at 4 mm total length (TL) and juveniles were vulnerable to seines at 35 mm FL. Growth and mortality were estimated for larvae between 5 and 15 mm TL and juveniles between 40 and 100 mm FL. For each year, an abundance-weighted mean date of capture was calculated for larvae grouped in 1-mm size-classes and juveniles grouped in 5-mm size-classes (Figure 5.2). The mean date of capture represents the day of year at which a given size-class is most abundant and was estimated with the equation:

$$D = (\sum LJ)/(\sum L), \quad (1)$$

where D is abundance-weighted mean date, L is the total fish abundance for each collection date and size-class, and J is the date of capture. Age (t) was calculated for each size-class by subtracting D for the smallest size-class from each of the subsequent size-classes. Instantaneous growth (G) was estimated with the equation:

$$L = ae^{Gt}, \quad (2)$$

where L is length of the lower limit of each size-class, a is the length axis intercept, G is the coefficient of instantaneous growth, and t represents age in days (Hackney and Webb 1978; Peterson and Jennings 2007). Instantaneous mortality (Z) was calculated based on catch-curve analysis using Ricker's (1975) model of exponential decline:

$$N_t = N_0 e^{-Zt}, \quad (3)$$

where N_t is the predicted number of fish at age t, N_0 is the abundance axis intercept at time zero, and Z is instantaneous mortality. This model assumes that once the members of a cohort have settled in Albemarle Sound, there is no emigration or immigration during the period in which mortality is being calculated (*i.e.*, June – October).

Meteorological and Hydrographic Data

To determine long-term trends in weather and climate, data were obtained from a 2-m weather station located at Tidewater Research Station in Plymouth, North Carolina. The State Climate Office of North Carolina operates the weather station and data are maintained by the National Climatic Data Center (SCONC 2009). Precipitation was recorded daily and summed to estimate total accumulation for the spring (March-June). Hourly records of wind speed and direction were used to calculate a mean daily average. Wind speed (m/s) and direction were then summed over each month for winds from each of 8 directional sectors (N, NE, E, SE, S, SW, W, and NW). To reduce the number of explanatory variables, data were summarized by four-month intervals (*e.g.*, March-June, July-October). These intervals correspond accordingly to larval and juvenile production periods.

Daily river discharge rates were obtained from Roanoke Rapids Dam water monitoring gage, located 4.5 km downstream of the dam and 221 km upstream from the study area (USGS 2011). The gage is maintained by US Geological Survey and Dominion Power Company and records hourly discharge rates and river height data. Daily river discharge (m^3/s) was averaged for each month and compared with larval and juvenile abundances. Daily river discharge was averaged over the same four-month intervals previously described and used for comparison with fish production. Finally, river discharge was summarized as the number of days between March and June with average flows greater than 300 m^3/s and less than 100 m^3/s. These values were used to assess larval and juvenile recruitment in relation to years with high or low river flow.

Data Analysis

River herring abundance data used for comparison of ichthyoplankton pushnets and oblique tows did not meet normality assumptions; nonparametric tests were used for comparisons of gears. Differences in sampling gear efficiencies were evaluated using the Mann-Whitney *U* test. A correction factor for CPUE estimates was developed using nonlinear regression analysis with untransformed CPUE data.

Juvenile CPUE data were first examined quantitatively to determine broad temporal patterns in recruitment of blueback herring and alewife. Data for blueback herring and alewife were then combined for subsequent analysis of river herring recruitment, growth, and mortality. Larval and juvenile abundance indices were calculated using arithmetic means of CPUE data ($\log_e [n + 1]$ transformed). Data were evaluated for normality and homoscedasticity using the Shapiro-Wilk and Levene tests. Temporal patterns of larval and juvenile abundance were examined relative to variation in water temperature, precipitation, wind speed and direction, and river discharge. Interannual patterns of fish abundance, instantaneous growth, and mortality were compared using simple linear regression with meteorological and hydrological variables. Stepwise multiple regression analysis based on a generalized linear model was used for detailed assessment of the relationship among river herring abundance, river flow, and wind. A *t*-test was used to examine the significance of the variable coefficients in the model ($P \leq 0.05$). To protect against multicolinearity and ensure that correlations between variables were not biasing results, collinearity diagnostics were used with variance inflation factors.

Analysis of variance (ANOVA) was used to statistically detect differences in growth and mortality between years. Data were evaluated for normality and homoscedasticity using methods previously described. If the ANOVA was significant, Tukey's HSD post-hoc multiple

range tests were used to determine if significant differences existed among means. Differences were considered significant at $P \leq 0.05$. Results are expressed as the means ± SE. All statistical analyses were conducted using SAS 9.2 (SAS Institute, Cary, North Carolina).

Results

Ichthyoplankton Gear Comparison

Gear type had a significant effect on mean abundance of larval river herring (Mann-Whitney U, $P = 0.01$). Pushnet abundances were generally 5 - 10 times higher than abundances for oblique tows as previously reported (Overton and Rulifson 2007). A polynomial regression best explained differences in catch efficiency ($r^2 = 0.95$, $F_{1,56} = 470.206$, $P < 0.001$), and the resulting quadratic equation ($y = 0.1099x^2 - 3.5165x + 35.144$) was used as a correction factor for CPUE estimates based on oblique tow samples.

Variation in River Herring Abundance and Distribution

Larvae and juveniles were collected through use of both ichthyoplankton sampling gears (Table 5.2). As a result of heavy rains and flooding in 1987, no larvae were caught for the entire year despite an extensive sampling effort. Length distributions were similar for each stage of development and year of collection. River herring yolk-sac larvae were prevalent throughout samples and clearly comprise an important component of the ichthyoplankton assemblage in Roanoke River. An unusually high proportion (70 ± 11%) of yolk-sac larvae and a low proportion (10.5 ± 1.6%) of feeding-stage larvae were caught in 2008 and 2009. With the exception of the most recent study, feeding-stage larvae were prevalent in most samples and represented the largest distributions of river herring collected. A low proportion (~5%) of yolk-sac larvae were caught in 1985 and 2002. The proportion of juveniles caught with oblique towed

nets was low (<5%) for the earliest study (1984-1991) and greatly increased (~15%) with oblique towed nets in 2001, 2002, and 2003. The proportion of juveniles caught with pushnets and oblique tows was similar and consistently high since sampling in 2001.

Larval abundances (267 ± 139 number / 100 m^3) were not significantly different between stations located within the Roanoke River mainstem channel or distributaries. River herring abundances generally peaked during the latter part of April (564 ± 191 number / 100 m^3) and declined steadily through June (Figure 5.3). For some years (1985, 2002, 2003, 2009), river herring abundances may have peaked before 15 April or coincided with the first week of sampling (Figure 5.4). Larval abundances were the highest on record in 1985 (28,872 ± 11,431 number / 100 m^3). Periods of low abundance occurred in 1987, 2001, and 2008 (Figure 5.5).

Juvenile river herring abundances (2.3 ± 1.1 fish) were generally low and were not significantly different among the stations sampled in western Albemarle Sound. Seasonal differences in recruitment of blueback herring and alewife juveniles were noticeable (Figure 5.6). Abundance of blueback herring and alewives was similar for June, July, and August. Alewife abundance sharply declined in September and October, while blueback herring remained abundant throughout the fall. Juvenile river herring abundances (2.3 ± 1.1 fish) were generally low and were not significantly different between the stations sampled in western Albemarle Sound. Seasonal differences in recruitment of blueback herring and alewife juveniles were noticeable (Figure 5.6). Recruitment of blueback herring and alewives was similar for June, July, and August. Length distributions for juvenile river herring were 55.1 ± 10.1 mm FL and ranged from 18 mm to 134 mm FL. Length distributions for blueback herring and alewife were similar (Figure 5.7). While fewer alewife were collected in the seine survey, alewife were significantly larger than blueback herring (Mann-Whitney test, $z = 27.33$, $P < 0.0001$).

Growth and Mortality

Instantaneous growth and mortality rates were highly variable for larvae (Table 5.3). Growth rates ranged from 0.043 ± 0.002 (r^2 = 0.40, P = 0.02) in 1985 to 0.005 ± 0.001 (r^2 = 0.31, P = 0.03) in 1986. Growth was significantly higher for 1985 and 1988 compared to all other years (ANOVA, $F_{10,33}$ = 160.21, $P < 0.0001$). Mortality ranged from 0.067 ± 0.006 (r^2 = 0.86, $P <$ 0.0001) in 1989 to 0.006 ± 0.001(r^2 = 0.21, P = 0.048) in 1985. Mortality was significantly higher for 1989 and 1986 than other years and was significantly lower for 2003 and 1985 than other years (ANOVA, $F_{10,33}$ = 78.92, $P < 0.0001$). Larval growth and mortality were not significantly different among stations in Roanoke River (ANOVA; $P > 0.05$); however, growth decreased and mortality increased along the river gradient.

While abundances of river herring juveniles were relatively low for Albemarle Sound (JAI 2.3 ± 1.1), instantaneous growth and mortality rates were calculated for all years included within this study (Table 5.4). The catch-curve mode varied among years in relation to the population size structure. Thus, it was important to analyze each year independently to estimate the abundance-weighted mean date on which fish achieved each size-class. Growth rates ranged from 0.005 ± 0.002 (r^2 = 0.36, P = 0.01) in 1986 to 0.001 ± 0.001 (r^2 = 0.23, P = 0.05) in 1985. Growth was significantly higher for 1986 and 2009 compared to all other years (ANOVA, $F_{12,39}$= 44.47, $P < 0.0001$). Mortality ranged from 0.021 ± 0.002 (r^2 = 0.90, $P < 0.0001$) in 1989 to 0.001 ± 0.001 (r^2 = 0.22, P = 0.048) in 1985. Mortality was significantly higher for 1989 than all other years (ANOVA, $F_{12,39}$= 163.43, $P < 0.0001$). Juvenile growth and mortality were not significantly different among the stations in Albemarle Sound (ANOVA; $P > 0.05$). Instantaneous growth rates were highest for stations located at the mouth of Roanoke River and

Chowan River. Growth rates decreased moving seaward away from the confluence of these rivers. The relationship between mortality and proximity of sampling location to river mouth was not as clear.

Direct comparison of instantaneous mortality between larval and juvenile stages indicated mortality rates were similar within a given year-class (Figure 5.8). Years with high larval mortality also experienced substantial juvenile mortality, although differences varied by an order of magnitude. Regression analysis showed an exponential model could be used to explain 80% of the variation in the relationship between stage-specific mortality ($r^2 = 0.80$, $F_{2,9}=59.0$, $P < 0.001$). In contrast with instantaneous mortality estimates, an inverse relationship was observed between growth rates for larvae and juveniles. Juvenile growth was lowest during years that supported high larval growth and an exponential growth model explained 83% of the variation in these growth rates (Figure 5.8, $r^2 = 0.83$, $F_{1,10}=172.8$, $P < 0.001$). This statistical significance and direction of the relationship between larval and juvenile growth led to the investigation of density dependence for each early life stage. Mortality estimates for larvae and juveniles were density independent. Similarly, larval instantaneous growth rates were density independent. Juvenile growth rates were density dependent and a negative correlation described the relationship between juvenile growth and abundance (Figure 5.9, $r^2 = 0.47$, $F_{1,10}=8.8$, $P = 0.01$).

Environmental Factors

Among the environmental and hydrographic variables examined, temperature was the most stable parameter measured with only slight variation from year to year (Table 5.5). Interannual distributions of larvae and juveniles were weakly correlated with air temperature ($r^2 < 0.20$). Years with warm temperatures showed an increasing trend for larval abundance ($r^2 = 0.18$, $P =$

0.16) and a decreasing trend for juvenile abundance (r^2 = 0.10, P = 0.31). Intraannual variability in water temperature was correlated with fish abundance and this relationship was similar for larval and juvenile river herring (Figure 5.10). Fish abundance was low during seasonally warm periods. Spring rainfall was especially high (> 8.0 cm) for 1984, 1989, 1990, and 2003 and was not directly correlated with a specific El Niño Southern Oscillation Pattern. Drought conditions, as evidenced by rainfall accumulation and river flow, were prevalent throughout 1985, 1986, 2002, and 2008.

Winds during the spring were generally stronger (~10%) and more sustained than those for the fall. Spring winds were predominantly from the southwest (32 ± 2%) and south (20 ± 2%). Fall winds were predominantly from the southwest (26 ± 2%) and northeast (21 ± 2%). Winds from most directions had minimal effect on larval distribution in Roanoke River. A notable exception was winds originating from the northwest significantly reduced the abundance of larvae in the river (r^2 = 0.86, $F_{1,11}$=31.37, P < 0.001). Spring winds from the south, northeast, and north had a significant influence on juvenile river herring abundance (Figure 5.11). The abundance of river herring in Albemarle Sound increased with sustained winds from the south (r^2 = 0.89, $F_{1,11}$=96.3, P < 0.001). Juvenile abundances declined with winds from the northeast (r^2 = 0.87, $F_{1,11}$=78.0, P < 0.001) and north (r^2 = 0.76, $F_{1,11}$=28.1, P < 0.001). Spring winds from other directions did not have a significantly effect on juvenile abundance. Late-summer and fall winds were weakly correlated (r^2 < 0.20) with juvenile river herring production in Albemarle Sound. Although not statistically significant, the general trend observed was winds from most directions, except west and northeast, were related to increased juvenile abundance in Albemarle Sound.

River Flow and Hydrographic Conditions

River flow was correlated with precipitation within the region ($r^2 = 0.45$, $F_{1,22} = 8.81$, $P = 0.01$); however, flow conditions were probably more related to management objectives for hydropower generation and maintenance of a negotiated flow regime for striped bass production (Table 5.6). Annual summaries of river flow were similar for spring and fall, and linear regression explained 61% of the variation in this relationship ($r^2 = 0.61$, $F_{1,11} = 16.9$, $P = 0.002$). River flow was exceptionally high (10^{th} percentile) for 2003, 1987, and 1984, and flow was exceptionally low (90% percentile) for 1988, 1986, 1985, and 2002. During the past 25 years, river flow was maintained within the Q1 – Q3 bounds for 47 ± 6% of time (Table 5.7). A good benchmark for determination of high flow years was the summation of days with average river discharge ≥ 300 m^3/s. Similarly, a benchmark for low flow years was the summation of days with average river discharge < 100 m^3/s.

Larval fish production was negatively affected by spring river flow (Figure 5.12, $r^2 = 0.62$, $F_{1,11} = 6.9$, $P = 0.02$). Low flows and drought conditions in 2002 and 1985 coincided with high larval abundances and relatively low concentrations of yolk-sac larvae (5.7 ± 0.7%). As a result of dispersal and advective processes in Roanoke River, low larval abundances were observed with high flow periods in 2003, 1987, and 1984. River flow had variable influence on recruitment of juveniles in Albemarle Sound. Spring river flow was highly correlated with juvenile abundance ($r^2 = 0.90$, $F_{1,11} = 109.3$, $P < 0.001$), whereas a relationship with river flow in the fall could not be detected. Instantaneous growth and mortality were not correlated with river flow for either the spring or fall.

Multiple regression analysis yielded a significant model [JA = 1.1 + (0.0016 x R) + (0.0058 x S) – (0.031 x N) – 0.0062 x NE)] for estimating juvenile abundance based on spring river flow and wind. The model indicates that juvenile abundance (JA) was positively related to river flow (R) and winds from the south (S), but negatively related to winds from the north (N) and northeast (NE). Analysis of the standardized partial regression coefficients (β) showed that river flow contributed the most toward predicting fish abundance. The contribution of winds towards predicting fish abundance was similar for all directions. The four predictor model was able to account for 92% of the variance in juvenile abundance ($r^2 = 0.92$, $F_{4,8} = 22.8$, $P < 0.001$, 90% CI [0.42, 1.78]). Multicolinearity among the predictor variables was not detected through correlation diagnostics and analysis of the variance inflation factors.

Discussion

The results of long-term data analysis for larval and juvenile river herring suggests Roanoke-Albemarle stocks are in decline as previously observed with fishery-dependent data and estimates of spawning stock biomass (Carmichael 1999; Schmidt et al. 2003). Historically, river herring exhibit distinct patterns in abundance reflected in the fishery age structure (Messieh 1977; Jessop 1990). Periods of abundance are attributed to the frequency and distribution of large, dominant year-classes. With exception of a strong year-class in 1985, we failed to observe a strong year-class for any other years included in this study. Persistent declines in abundance could be attributed to increased natural mortality occurring during the early life stages when year-class strength was established. Estimates of instantaneous mortality were high for larvae and juveniles and were not correlated with abundance. Similar to observations with American

shad *A. sapidissima*, river herring mortality rates decreased with age and size (Crecco et al. 1983; Houde 1997). Larval mortality was consistently an order of magnitude higher than juvenile mortality.

Larval mortality and growth rates estimated in this study were similar to published reports for blueback herring and alewife collected throughout their range (Essig and Cole 1986; Mansfield and Jude 1986; Sismour 1994b; Höök et al. 2007; Overton et al. In press). Working in an upstream reach of Roanoke River, Walsh et al. (2005) reported collecting a preponderance of yolk-sac larvae. Otolith-derived mortality and growth rates from these young fish (4-8 d) were comparable to those described herein. A few laboratory studies with blueback herring and alewife purport lower mortality rates for cultured larvae (Heinrich 1981; Sismour 1994b). Low mortality rates would be expected for fish living in an environment without predators. Estimates of American shad larval mortality (0.112 – 0.202) have been reported higher than our observations with river herring, but probably indicate subtle differences with fish size or temporal variation in recruitment (Crecco et al. 1983; Savoy and Crecco 1987).

Few publications present mortality and growth estimates for juvenile river herring. Mortality and growth rates in this study compare reasonably to Savoy and Crecco's (1988) observations with American shad in Connecticut River and estimates of mortality for Gulf menhaden *Brevoortia patronus*, a pelagic schooling clupeid (Loesch 1976; Deegan 1990). Estimates for juvenile river herring mortality and growth were lower than estimates for blueback herring in Rappahannock River (Dixon 1996) and American shad in Pamunkey River (Hoffman and Olney 2005). These rivers are important tributaries of Chesapeake Bay and are influenced by tidal exchange and saltwater intrusion. They are characterized by high total suspended solid concentrations, high light attenuation, and high densities of zooplankton and fish larvae.

Alosines in the Rappahannock and Pamunkey benefit from hydrologic conditions and environmental factors that are known to support anadromous fish production (North and Houde 2001; North and Houde 2003b).

Numerous authors have explored a wide range of processes contributing to density dependence in fishes (Cowan et al. 2000; Rose et al. 2001). Heath and Gallego (2000) identified several density-dependent processes that could affect growth and mortality of early life stages: (1) competition for refuge; (2) schooling behavior for protection from predators; (3) competition for food; (4) attraction of predators to local abundances of the target species, and (5) parasitism and disease. With river herring, slow growth and predation risk as a result of fish size or stage duration raises questions about why density dependence and compensatory effects were not observed with mortality (Litvak and Leggett 1992). While Savoy and Crecco (1988) documented density-dependent mortality in American shad eggs and larvae, this observation is rare for most fish species. We found larval mortality and growth were density independent. Density-dependent mortality was not detected for juvenile river herring, but may have been limited by population size or masked by high mortality rates. In a comprehensive review of marine fish with low stock abundance, Myers et al. (1995) found little evidence density dependence exists with mortality estimates. In this study, juvenile growth rates were density dependent and growth was slow during years with increasing abundance. Density dependence among juveniles was probably a consequence of competition and predation within the estuarine environment.

Obviously, the resurgence of striped bass populations has drawn attention of resource managers because predation is the agent of mortality for most young fishes (Houde 2008). Numerous studies have cited striped bass as a predator and a substantial cause for river herring

mortality (Nelson et al. 2003; Walter et al. 2003; Savoy and Crecco 2004). While Schmidt et al. (2003) attributed the initial decline of river herring stocks to overfishing and variability in environmental conditions, the authors caution that recovery of striped bass stocks and increases in striped bass abundance could make restoration of river herring stocks difficult. Within Albemarle Sound, the abundance of striped bass juveniles during recruitment periods and year-round presence of adults probably serves as a significant source of mortality for river herring. Predator-prey interactions with striped bass have been studied in this system and alosines contribute a major component (~20%) of the diet for age-1 fish (Tuomikoski et al. 2008). Consumption generally declines as river herring emigrate from coastal waters in late summer and fall. Striped bass consumption also declines with older individuals (age-2+) demonstrating preference for larger, more abundant clupeids (Rudershausen et al. 2005).

Throughout the recruitment period, river herring larvae and juveniles appear to be largely influenced by variability in hydrography, precipitation and weather, and river flow. Fluctuations in these environmental conditions can cause appreciable changes in fish abundance, growth, and mortality. Temperature was a critically important determinant of growth and abundance. Intraannual variability in water temperature was correlated with fish abundance. Operating on different spatiotemporal scales and mediated by seasonal selective processes, larval and juvenile abundances were low when during warm periods (Figure 5.10). Temperature also appeared to be important cue for emigration of juveniles in the fall. Alewife emigration occurred in September and October. While temperature was correlated with this event, juvenile abundance and competitive pressures with blueback herring may stimulate early emigration of alewives (Richkus 1975).

Analysis of interannual variability in temperature may provide insight on the effects of low-frequency climate change. Although the correlations were generally weak ($r^2 < 0.20$), years with warm temperatures showed an increasing trend for larval abundance and a decreasing trend for juvenile abundance. These findings concur with Kellogg's (1982) observations that warming trends would be beneficial to alewife populations because larval growth and survival is high at warm temperatures (20 – 26 °C). Similar observations have been reported for larval blueback herring, but are mostly based on field studies and have not been quantified in the laboratory (Klauda et al. 1991). The decline in juvenile abundance during warm years supports research that speculates climate change will cause a geographical shift in river herring spawning distributions and limit production within the southern extent of their range (Loesch 1987; Rulifson 1994). Because the results described herein were not consistent with different life stages, it suggests analysis of river herring population dynamics requires compilation of data for larvae, juveniles, and adults. Results indicate warm temperatures conducive for growth do not necessarily support good survivorship. While year class strength might be established during the larval stage, processes during late larval and juvenile stages could serve as a stabilizing mechanism regulating and dampening recruitment.

Models of meteorological forcing and water circulation across the Albemarle –Pamlico estuarine system have been widely used to study the mechanisms governing recruitment of estuarine-dependent fish (Pietrafesa and Janowitz 1985; Pietrafesa et al. 1986; Xie and Eggleston 1999). In these studies, recruitment models were based on larval transport from offshore spawning grounds through small inlets (≤ 1 km) along the North Carolina coastline (Tzeng et al. 2003; Sullivan et al. 2006; Taylor et al. 2009). Positive correlations exist between larval and juvenile abundances for three commercially important species (spot *Leiostomus xanthurus*,

southern flounder *Paralichthys lethostigma*, and Atlantic menhaden *B. tyrannus*) and with each species wind stress and river discharge were shown to significantly affect fish distributions (Pietrafesa et al. 1986; Taylor et al. 2009). Our study differs from previous work in the Albemarle-Pamlico estuarine system because river herring have contrasting life history patterns and spawning occurs in coastal rivers, the net movement of eggs, larvae, and juveniles is seaward (west to east). As previously noted by Taylor et al. (2010), the links between wind and river flow are not always clear, but these correlates of water current have a significant influence on river herring production.

Wind forcing was particularly evident in synoptic weather bands during the spring. The effects of wind stress were rarely correlated with larval production; however, on occasion the seasonal transition from winter weather patterns to spring weather patterns produced strong winds that originated from the northwest. Under these conditions, wind stress caused larvae to be advected from habitats in Roanoke River. The river's orientation and course of travel through the North Carolina coastal plain probably contributed the most to this phenomenon. Juveniles were more susceptible to the effects of wind forcing during the spring. Juvenile abundances were highest when winds were from the south-southwest, the dominant wind field for spring. Given the size distribution of juveniles, we are unsure about the direct effect of wind on individuals. We suspect that south-southwest winds produced circulation patterns and conditions that were favorable for production of river herring and their food resources. In contrast, spring winds from the north-northeast structured nursery habitat with biotic and abiotic factors and produced an unfavorable environment for river herring. Under these conditions it is possible that water quality was impacted, fish were advected from nursery habitats, or prey resources were diminished in some capacity. While much research has been done to model circulation in the

Albemarle-Pamlico system (Pietrafesa and Janowitz 1985; Pietrafesa et al. 1986; Xie and Eggleston 1999; Taylor et al. 2010), this system is quite large and most research has not occurred within the area of this study, western Albemarle Sound.

The Roanoke River empties into Albemarle Sound at its western end and supplies more than half the total freshwater input to the region (Giese et al. 1985). It is a large river, with roughly the same mean flow as the Colorado River through the Grand Canyon (Manring and Pearsall 2005). The average annual discharge is about 225 m^3/s (USGS 2011). It is not surprising the river had such a significant effect on larval and juvenile river herring abundances. Flows in the Roanoke have been extensively studied to assess their impact on striped bass recruitment (Rulifson and Manooch 1990a). After monitoring striped bass in the postdam construction era, Hassler et al. (1981) and Manooch and Rulifson (1989) independently concluded best recruitment of juveniles in Albemarle Sound occurs in years with moderate river flow (141 – 311 m^3/s). We share the same conclusion with these previous authors and recommend extension of a managed flow regime for anadromous alosines earlier in the season. Following the same strategy proven effective for the past 30 years, we recommend flows approximate preimpoundment conditions in February and March. Flows should also remain within the historical Q1 – Q3 thresholds. We believe moderate river flow during this time period will directly influence: (1) seasonal timing and location of spawning; (2) daily and hourly patterns in spawning activity; (3) egg and larval transport downstream; (4) location of nursery grounds near the river mouth and estuary; (5) production of phytoplankton, zooplankton, and other food resources, and (6) water quality and nutrient enrichment (Rulifson and Manooch 1990a).

Numerous examples exist in which recruitment of anadromous fishes varies with river flow. Alosines, striped bass, and white perch *M. americana* have a positive association between river

flow and recruitment in Chesapeake Bay (Houde and Rutherford 1993; McGovern and Olney 1996; North and Houde 2001; North and Houde 2003b). River flow historically was a good predictor of striped bass and American shad abundance in San Francisco Estuary (Turner and Chadwick 1972; Stevens 1977; Kimmerer 2002); however, population declines have reduced the capacity to predict recruitment (Kimmerer et al. 2001). Not all rivers demonstrate a positive association between fish abundance and river flow. Jessop (1994) found that river herring mortality was high and abundances decreased with high flows during the summer. In the well-studied Connecticut River and Hudson River, American shad recruitment appears to be negatively correlated with freshwater flow (Crecco and Savoy 1984; Limburg 1996). Similar conclusions were made by Kosa and Mather (2001), but these authors highlight the importance that high flow serves to stimulate emigration of juveniles from the estuary.

Recent observations (2008 – 2009) in Roanoke River demonstrate that temporal variation in river flow can have a significant effect on river herring spawning (see Chapter 2). Moderate flows (236 ± 143 m^3/s) in March 2009 stimulated rigorous and widespread spawning of river herring early in the season (Figure 5.4). Detailed analysis at the species level indicated these flows had similar effects for blueback herring and alewife. In contrast, river flow in March 2008 was unusually low (71 ± 10 m3/s; below Q1). Spawning was sporadic throughout the spring extending into late June. Under these conditions, river herring experience an extended larval period, competition with other larval alosines, and intense predation from striped bass and other piscivores. Although river herring share similar life histories with striped bass, it is possible that flow management guidelines could be refined to support species-specific production goals within a given year. Kimmerer (2002) reports that while river flow management within a system is

usually generalized, the underlying flow effects on each species are different and unique to each estuarine system. This finding is especially important as fisheries management transitions to multi-species ecosystem approaches.

In summary, several important themes emerge from our work with long-term datasets on Roanoke River and Albemarle Sound. River flow shows considerable variation despite flow regulations and stakeholder cooperative agreements that are well established. This work has extended our knowledge of recruitment dynamics for anadromous alosines. Although not unexpected, synchrony was not observed between larval and juvenile river herring production. It appears that density-independent processes (climate, water quality, river flow) and density-dependent processes (predation, competition, disease) work in concert to regulate recruitment. Long-term data are essential to document and interpret variations in the timing and magnitude of recruitment. Fisheries management that supports the recovery of anadromous stocks will require continual monitoring and data collection within the many habitats these species traverse. Ichthyoplankton sampling can provide immediate insight into the duration and extent of spawning activity. Use of length-based ageing techniques coupled with catch curve analysis offered a means to estimate growth and mortality for historical datasets. These techniques proved useful in assessment of interannual variability in growth and mortality. Investigators should use caution using these techniques at more discrete scales (*i.e.*, cohort analysis). Successful recovery of the Roanoke-Albemarle striped bass stock offers great promise that revision of flow management guidelines would support recovery of river herring and other alosines in this coastal river system.

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Table 5.1. Negotiated (Q1 – Q3) water flow regime (m^3/s) for Roanoke River below Roanoke Rapids Dam for 1 April - 15 June each year. River flow during March does not follow a specific regime for anadromous fish production; however, average daily flows are maintained above 99 m^3/s.

Dates	Expected average daily flow	Lower limit (Q1)	Upper limit (Q3)
April 1 - 15	241	187	388
April 16 - 30	221	164	311
May 1 -15	184	133	269
May 16 - 31	167	125	269
June 1 - 15	150	113	269

*Q1 and Q3 are historical 25 and 75% quartiles of daily river flow, respectively.

Table 5.2. Percent composition and size distribution of river herring collected from five long-term monitoring stations within lower Roanoke River, North Carolina. Samples were collected at weekly intervals from April 15 to June 15. Despite extensive sampling in 1987, no fish were collected as a result of local flooding and high water. Values represent mean (SD).

	Yolk-sac larvae		Larvae		Juvenile	
Year	Percent composition (%)	Total length (mm)	Percent composition (%)	Total length (mm)	Percent composition (%)	Total length (mm)
1984	11.9 (20.5)	4.4 (0.6)	86.6 (21.4)	12.5 (6.1)	1.5 (5.6)	28.4 (4.5)
1985	5.2 (12.6)	5.7 (3.5)	90.8 (18.1)	1.4 (5.3)	4.0 (14.6)	28.1 (4.6)
1986	26.7 (22.3)	4.6 (0.6)	73.1 (22.7)	6.9 (3.4)	0.2 (2.0)	33.0 (1.7)
1987	0	-	0	-	0	-
1988	35.2 (25.7)	5.0 (0.6)	64.7 (27.2)	5.8 (1.4)	0	-
1989	47.7 (25.9)	4.5 (0.6)	51.3 (25.4)	6.5 (2.7)	0.9 (6.0)	25.5 (2.4)
1990	47.6 (37.3)	4.1 (0.6)	51.8 (36.6)	7.3 (3.0)	0.6 (3.2)	30.3 (4.5)
1991	33.6 (35.1)	4.6 (1.1)	66.4 (35.1)	10.0 (5.7)	0	-
2001	12.3 (27.5)	4.7 (1.3)	60.6 (45.9)	5.2 (1.3)	27.1 (45.1)	20.8 (0.1)
2002	6.2 (13.0)	4.4 (0.6)	77.4 (31.7)	6.0 (1.5)	16.4 (31.9)	25.5 (7.0)
2003	32.9 (23.5)	3.5 (0.6)	60.5 (24.4)	5.6 (1.9)	6.6 (20.9)	17.6 (7.1)
2008	62.3 (38.9)	4.2 (0.7)	11.6 (24.3)	7.8 (3.2)	26.1 (34.2)	29.5 (4.9)
2009	78.4 (28.2)	4.4 (0.5)	9.4 (17.2)	6.6 (0.6)	12.2 (23.6)	33.9 (5.3)

Table 5.3. A summary of larval river herring data used to investigate long-term recruitment trends in relation to river flow and climate. Larval abundances (number / 100 m^3) were calculated using mean catch per unit effort data from ichthyoplankton surveys in Roanoke River, North Carolina. Growth and mortality could not be determined for 1987 and 1991 because of limited catch.

	Larval abundance		Instantaneous growth				Instantaneous mortality			
Year	Mean	SE	Mean	SE	r^2	P	Mean	SE	r^2	P
1984	122	74	0.0254	0.0017	0.25	0.044	0.0262	0.0014	0.29	0.040
1985	31,448	26,836	0.0434	0.0019	0.40	0.017	0.0063	0.0012	0.21	0.048
1986	414	246	0.0047	0.0013	0.31	0.025	0.0582	0.0015	0.62	0.0001
1987	0	-	-	-	-	-	-	-	-	-
1988	115	62	0.0311	0.0014	0.37	0.019	0.0499	0.0021	0.80	0.0001
1989	186	135	0.0139	0.0010	0.28	0.035	0.0667	0.0060	0.86	0.0001
1990	6,356	6,340	0.0221	0.0006	0.58	0.008	0.0562	0.0085	0.83	0.0001
1991	391	265	-	-	-	-	-	-	-	-
2001	25	3	0.0157	0.0007	0.39	0.019	0.0480	0.0080	0.80	0.0001
2002	223	130	0.0108	0.0004	0.33	0.020	0.0349	0.0042	0.82	0.0001
2003	107	38	0.0174	0.0002	0.75	0.0001	0.0157	0.0020	0.79	0.0001
2008	16	4	0.0126	0.0003	0.64	0.002	0.0384	0.0059	0.81	0.0001
2009	55	24	0.0074	0.0009	0.67	0.002	0.0402	0.0018	0.48	0.003

Table 5.4. A summary of river herring data used to investigate long-term trends in juvenile recruitment as related to larval production, river flow, and climate. The juvenile abundance index was calculated using mean catch per unit effort data for fish caught by 18.3-m bag seine in Albemarle Sound, North Carolina. Instantaneous growth and mortality were estimated using a length-based catch curve method.

	Juvenile abundance index		Instantaneous growth				Instantaneous mortality			
Year	Mean	SE	Mean	SE	r^2	P	Mean	SE	r^2	P
1984	1.50	0.31	0.0011	0.0010	0.23	0.035	0.0034	0.0009	0.48	0.013
1985	1.91	0.46	0.0006	0.0012	0.23	0.050	0.0005	0.0007	0.22	0.048
1986	1.51	0.28	0.0046	0.0019	0.36	0.013	0.0114	0.0013	0.57	0.009
1987	1.32	0.34	0.0031	0.0012	0.63	0.001	0.0116	0.0014	0.57	0.0001
1988	0.90	0.26	0.0018	0.0011	0.39	0.010	0.0040	0.0014	0.27	0.029
1989	0.07	0.04	0.0033	0.0012	0.40	0.008	0.0214	0.0020	0.90	0.0001
1990	0.95	0.27	0.0021	0.0014	0.33	0.013	0.0044	0.0021	0.71	0.0001
1991	0.53	0.24	0.0017	0.0011	0.41	0.004	0.0113	0.0014	0.32	0.013
2001	1.32	0.32	0.0020	0.0013	0.28	0.015	0.0070	0.0016	0.67	0.0001
2002	0.40	0.17	0.0026	0.0018	0.26	0.021	0.0038	0.0012	0.30	0.027
2003	0.88	0.24	0.0019	0.0007	0.26	0.029	0.0005	0.0014	0.26	0.046
2008	0.66	0.28	0.0021	0.0014	0.28	0.016	0.0014	0.0014	0.26	0.047
2009	0.43	0.15	0.0038	0.0013	0.35	0.013	0.0016	0.0018	0.26	0.047

Table 5.5. Annual climate and weather patterns for Albemarle Sound, North Carolina. Data were acquired from National Climatic Data Center (SCONC 2009). The intensity of the El Niño Southern Oscillation Pattern was based on the Oceanic Niño Index derived from sea surface temperatures in the tropical Pacific Ocean. Data were summarized by production periods for larvae (Spring: March-June) and juveniles (Fall: July-October).

				Temperature (°C)		Wind Dominant Period (% cumulative)	
Year	El Niño / La Niña	Climate intensity	Precipitation (cm)	Spring	Fall	Spring	Fall
1984	La Niña	Weak	8.0	14.3 (0.6)	22.7 (0.3)	SW (35%)	SW (33%)
1985	-	-	3.2	16.8 (0.6)	23.1 (0.3)	SW (34%)	NE (22%)
1986	El Niño	Moderate	4.1	16.0 (0.6)	23.6 (0.4)	SW (29%)	SW (25%)
1987	El Niño	Moderate	6.3	15.4 (0.7)	23.0 (0.5)	SW (32%)	SW (23%)
1988	La Niña	Strong	6.1	15.6 (0.6)	22.6 (0.5)	S (23%)	SW (27%)
1989	-	-	10.3	15.6 (0.6)	23.5 (0.4)	SW (32%)	NE (30%)
1990	-	-	8.4	17.0 (0.6)	23.6 (0.4)	SW (30%)	S (25%)
1991	El Niño	Strong	7.1	17.8 (0.6)	23.5 (0.4)	SW (23%)	SW (29%)
2001	-	-	6.2	15.8 (0.6)	22.2 (0.5)	S (27%)	SW (24%)
2002	El Niño	Moderate	6	17.0 (0.6)	23.8 (0.4)	SW (29%)	SW (27%)
2003	-	-	8.6	16.5 (0.5)	23.3 (0.4)	SW (24%)	S (28%)
2008	-	-	5.1	16.3 (0.5)	22.7 (0.4)	SW (39%)	NE (26%)
2009	El Niño	Strong	5.4	16.3 (0.7)	22.9 (0.4)	SW (32%)	S (37%)

Table 5.6. Daily mean river discharge (m^3/s) for lower Roanoke River, North Carolina. River discharge rates were acquired from Roanoke Rapids Dam water monitoring gage (USGS gage 2080500). Data were summarized by production periods for larvae (Spring: March-June) and juveniles (Fall: July-October). Ranks based on average spring discharge for the last 100 years.

		River discharge		Spring days with river discharge		Percent of time within Q1 – Q3 flow	Percent of time below Q1 flow	Percent of time above Q3 flow
Year	Rank	Spring	Fall	≤ 100	≥ 300			
1984	10	436 (17)	169 (11)	13	89	17	0	83
1985	95	112 (6)	151 (13)	75	3	33	67	0
1986	92	129 (7)	80 (4)	54	3	46	54	0
1987	2	569 (26)	181 (15)	8	94	14	4	82
1988	91	132 (8)	79 (4)	53	3	70	28	3
1989	13	403 (14)	318 (16)	2	82	42	4	54
1990	18	366 (15)	178 (14)	7	65	26	1	72
1991	34	321 (13)	92 (5)	8	48	68	0	32
2001	69	205 (11)	102 (5)	14	19	50	21	29
2002	98	63 (1)	79 (1)	122	0	0	100	0
2003	1	659 (15)	428 (16)	0	122	0	0	100
2008	77	178 (9)	90 (5)	43	19	55	13	32
2009	42	280 (12)	93 (4)	6	35	87	0	13

Table 5.7. Percent of days that Roanoke River flow was within the negotiated Q1-Q3 discharge criterion for years within each category of river herring juvenile abundance index (JAI). Values represent means (SE).

JAI category	Years	Percent of days within Q1-Q3*	JAI
< 0.50	1989, 2002, 2009	38.7 (11.4)	0.23 (0.06)
0.50 - 1.00	1988, 1990, 1991, 2003, 2008	48.5 (9.3)	0.74 (0.06)
1.01 - 1.50	1987, 2001	56.4 (8.5)	1.20 (0.07)
1.51 - 2.00	1984, 1985, 1986	41.5 (7.9)	1.64 (0.10)

*Q1 and Q3 = historical 25 and 75% quartiles of daily river flow, respectively.

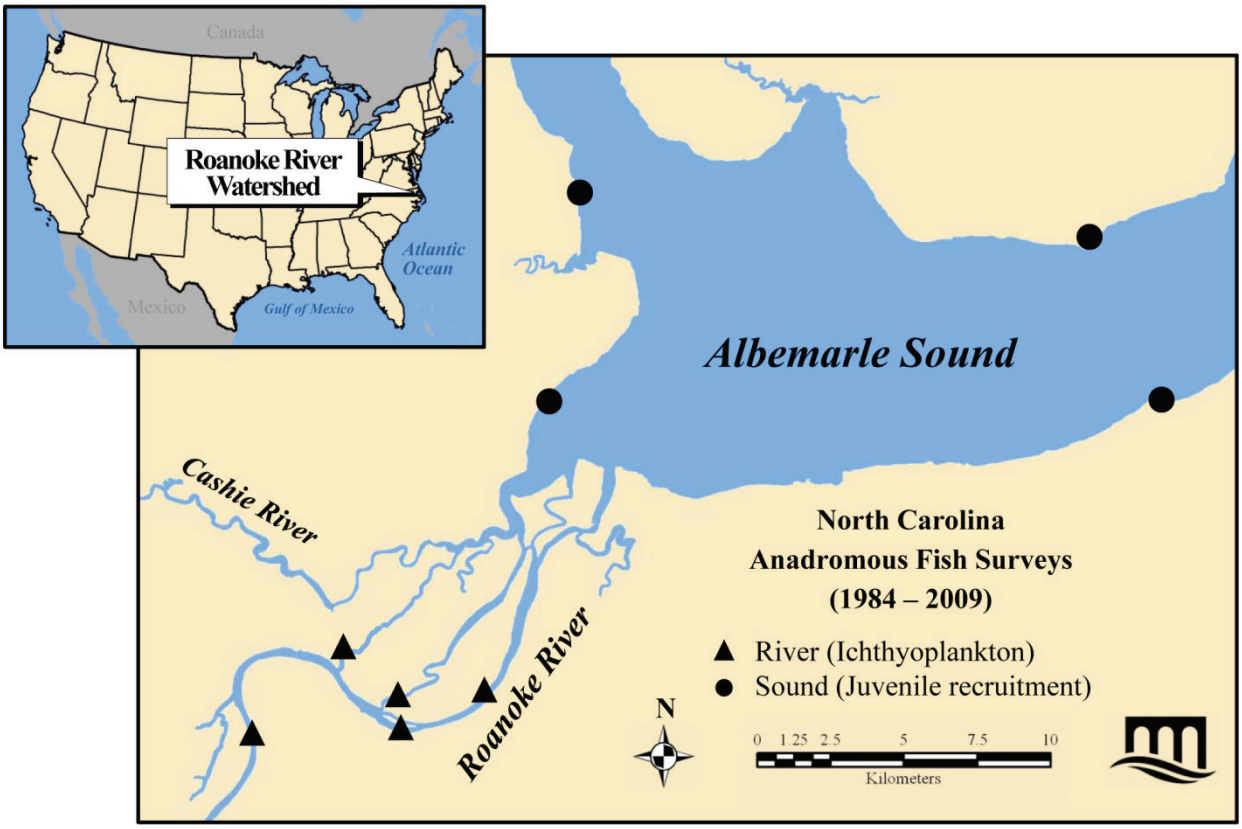

Figure 5.1. Map depicting fixed sampling locations used to investigate long-term recruitment trends for river herring (blueback herring *Alosa aestivalis* and alewife *A. pseudoharengus*) in lower Roanoke River and western Albemarle Sound, North Carolina.

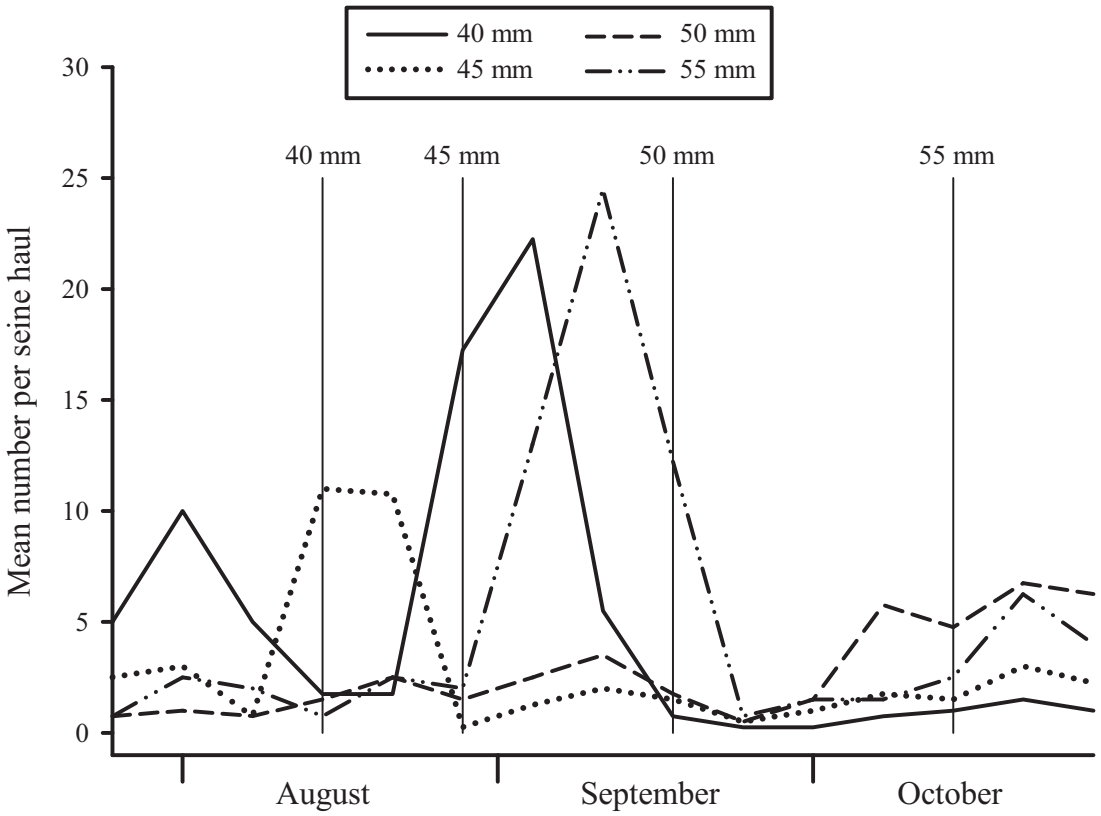

Figure 5.2. An example of the temporal changes in abundances of selected 5-mm size classes of juvenile river herring collected during 2009 through the Albemarle Sound Juvenile Anadromous Fish Survey. Vertical bars indicate the abundance-weighted mean date on which fish achieved each length. In calculating instantaneous growth and mortality using length-based aging techniques, mean dates of abundance were adjusted every year to account for changes in the population size structure.

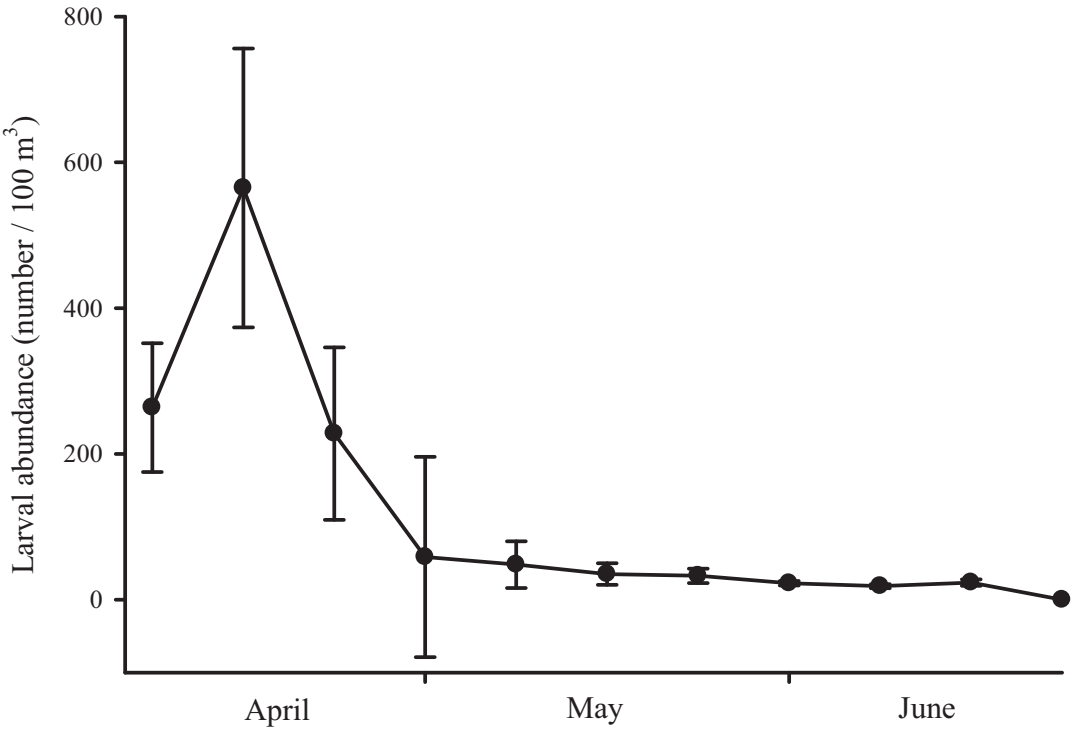

Figure 5.3. Abundance and distribution of larval river herring from lower Roanoke River, North Carolina. Abundance indices were summarized from three different studies (1984-1991; 2001-2003; 2008-2009). Values represent means (SE).

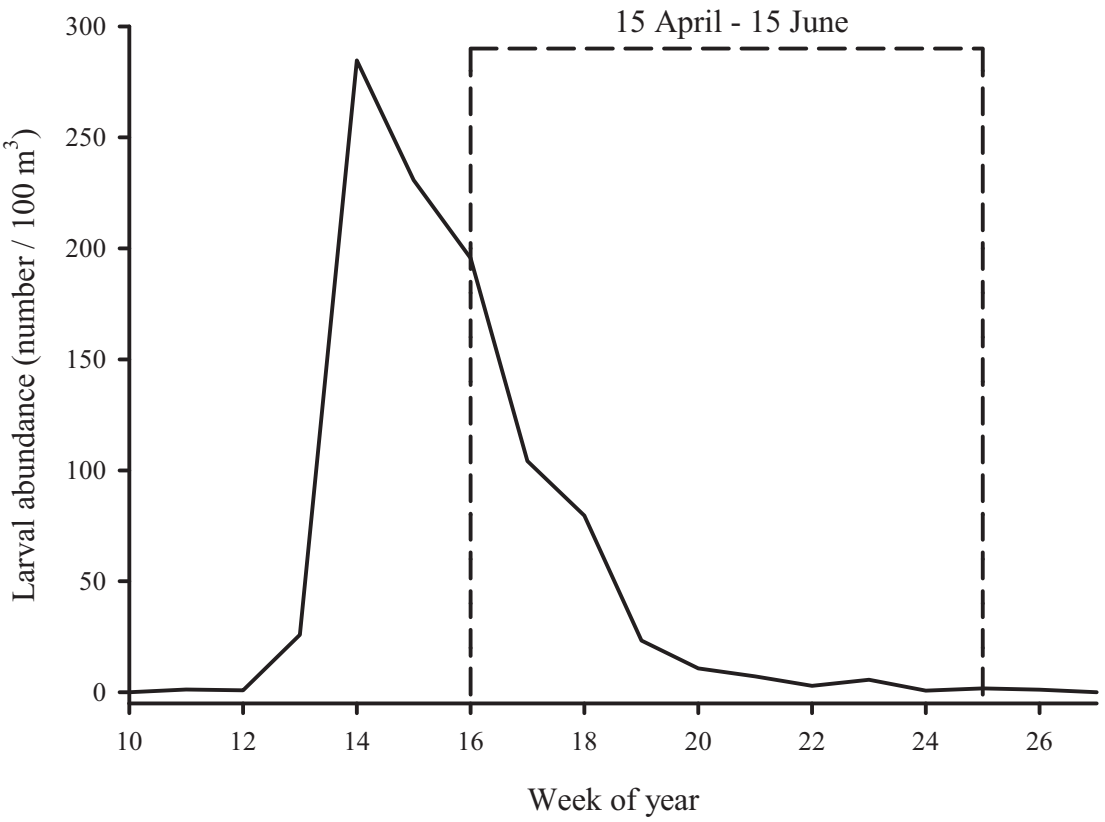

Figure 5.4. Analysis of data for some years (1985, 2002, 2003, 2009) suggests river herring abundances may have peaked before the temporal period used with the present study (15 April – 15 June). For example, retrospective analysis of recruitment of river herring in Roanoke River revealed fish were most abundant during the last week of March and first week of April in 2009. Caution should be used in comparing year-class size based on occurrence of peak larval abundance.

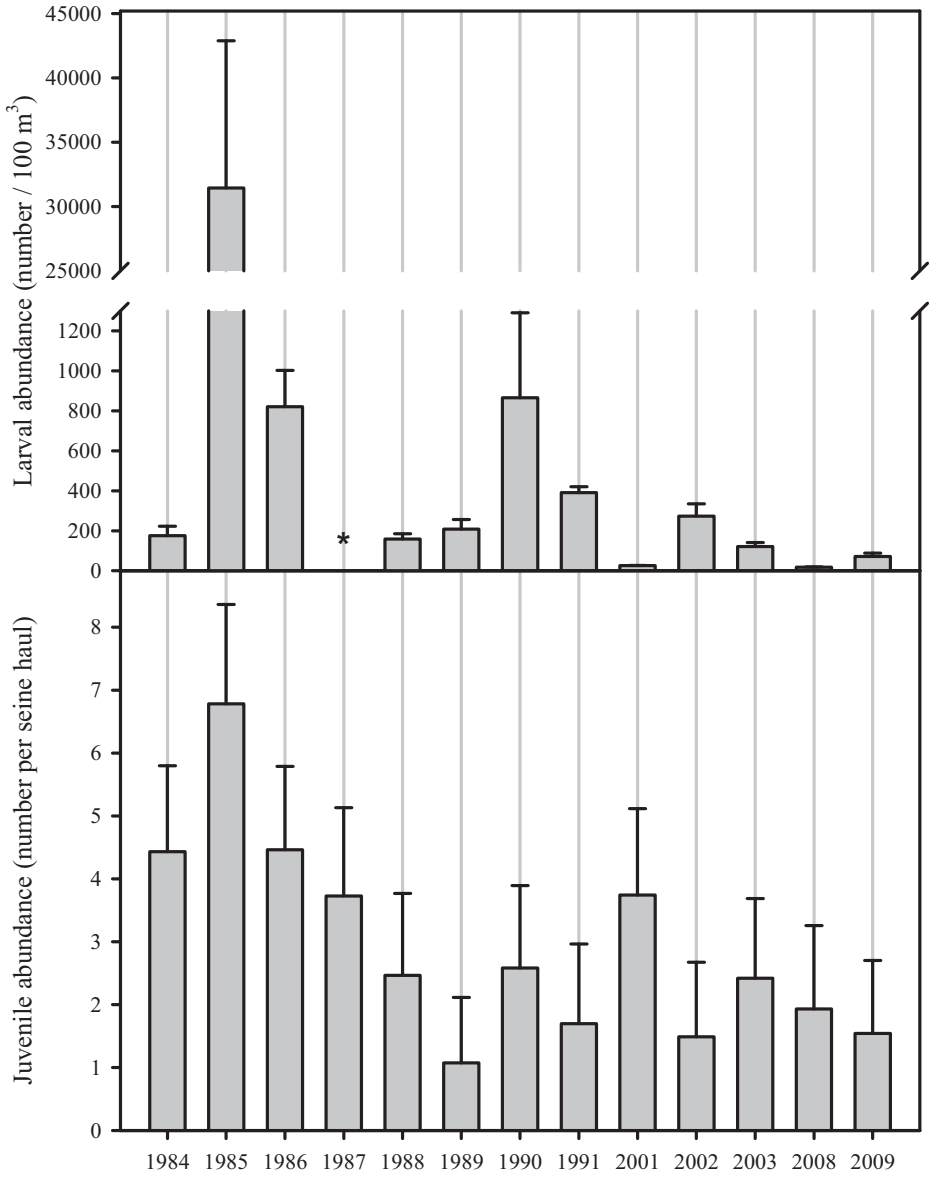

Figure 5.5. The relationship between larval river herring production in the lower Roanoke River was compared to the abundance of juveniles in Albemarle Sound, North Carolina. Larval abundance in 1985 was the highest on record and corresponded with production of a strong year class; however, the strength of this relationship was not easily observed for most years. Despite an intensive sampling effort, no larvae were caught in 1987 as a result of flooding within the watershed.

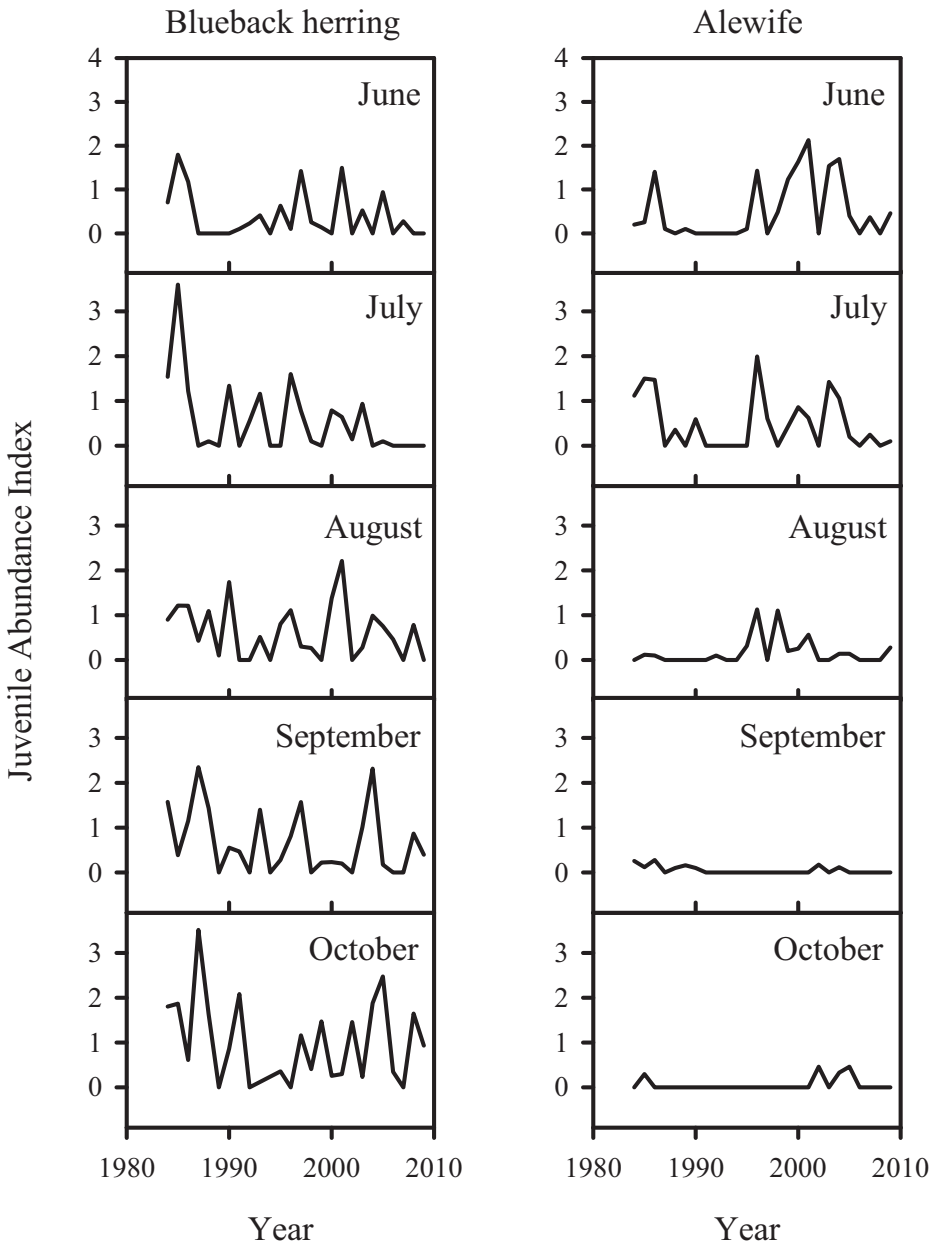

Figure 5.6. Recruitment of juvenile blueback herring and alewife to Albemarle Sound was similar for June, July, and August. Declines in alewife abundance in September and October were probably related to seaward emigration.

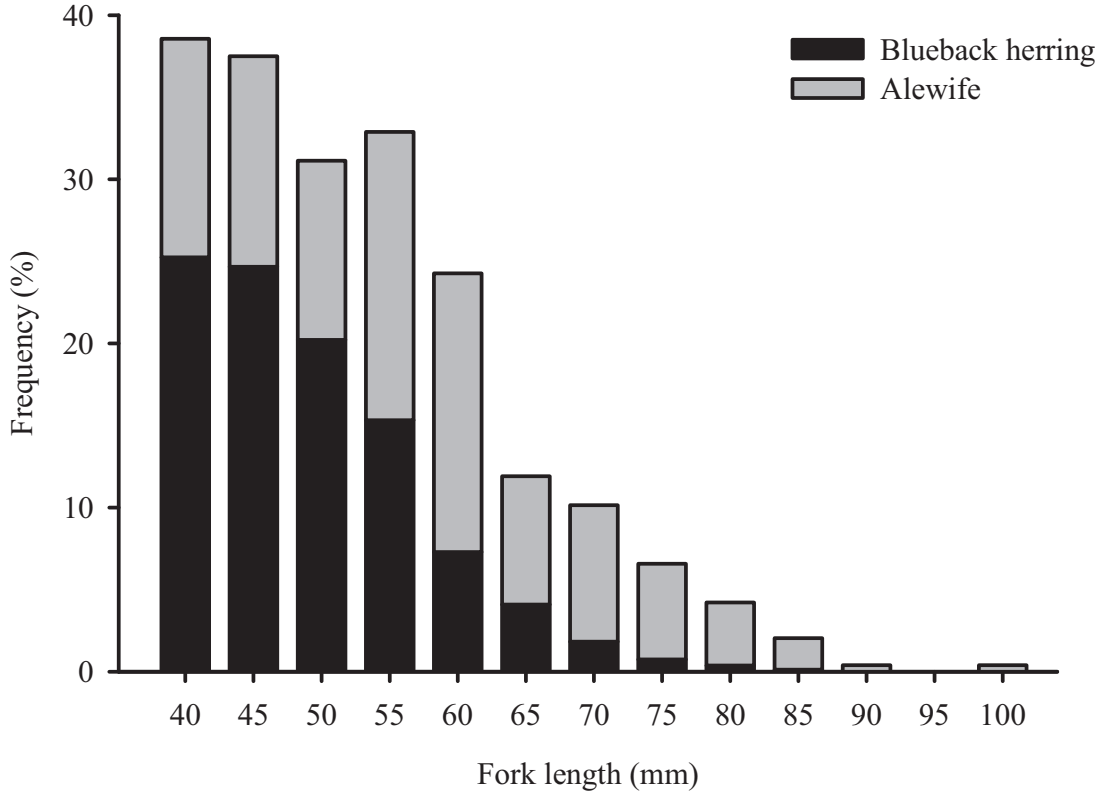

Figure 5.7. Length frequency distribution of juvenile blueback herring and alewife collected by seine in Albemarle Sound, North Carolina (1984-2009).

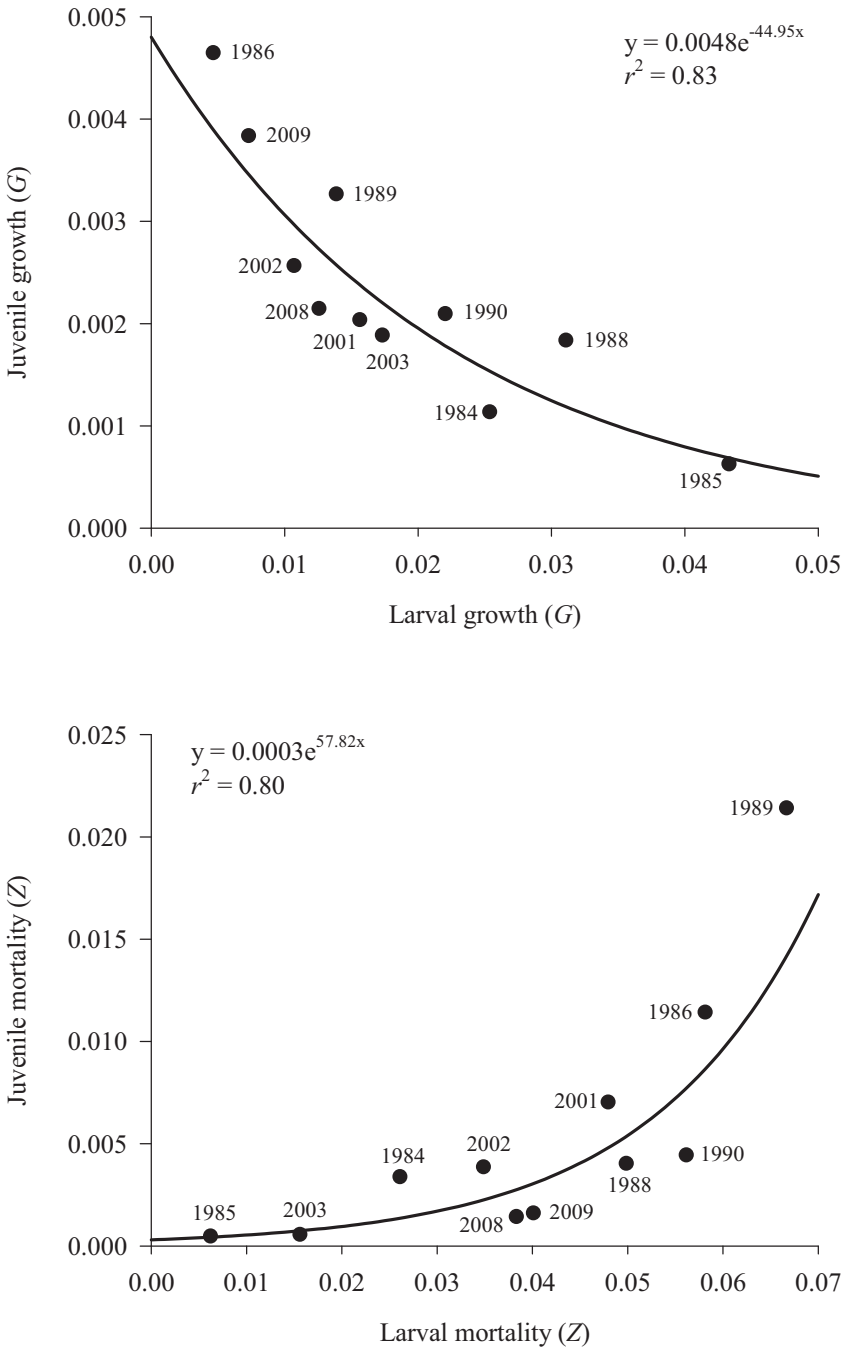

Figure 5.8. Instantaneous growth (*G*) and mortality (*Z*) was evaluated to determine if a relationship existed between river herring early life stages. Data for growth and mortality fit equally well to an exponential model.

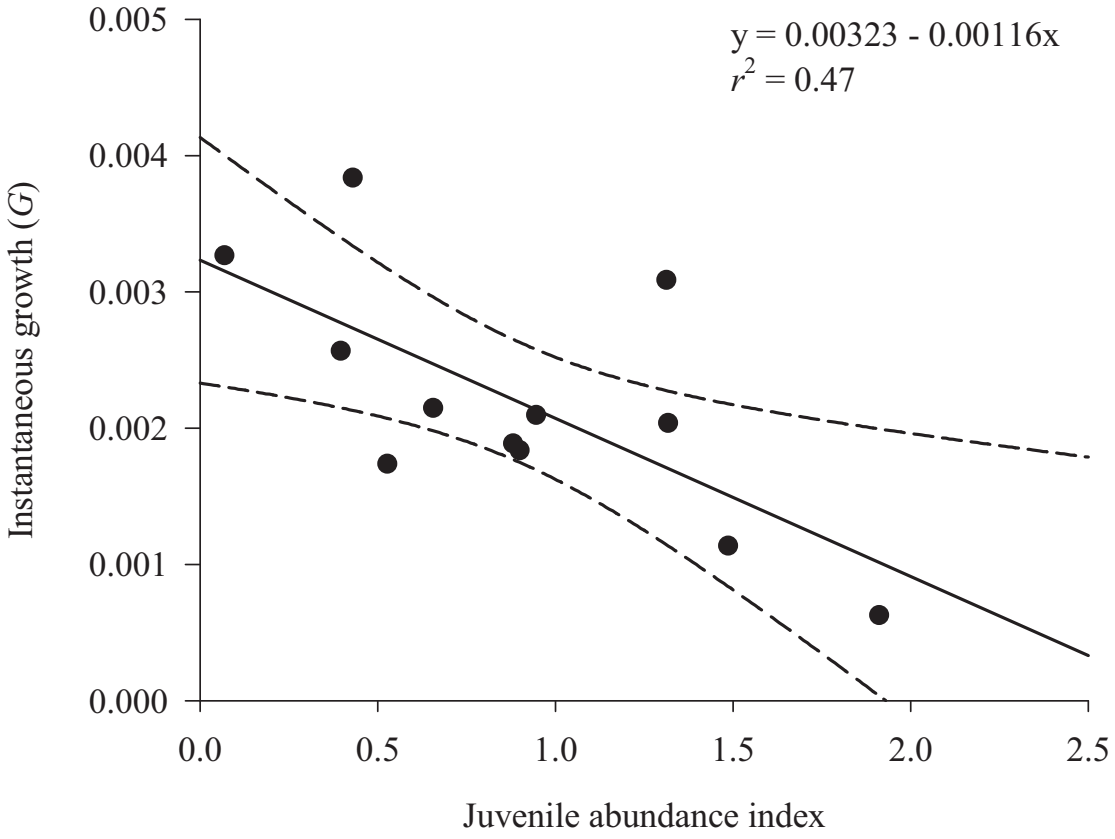

Figure 5.9. Linear regression analysis was used to assess the relationship between juvenile river herring abundance and instantaneous growth rate (*G*). During years or periods with high abundance, growth rates declined. Dashed lines represent the 95% confidence interval.

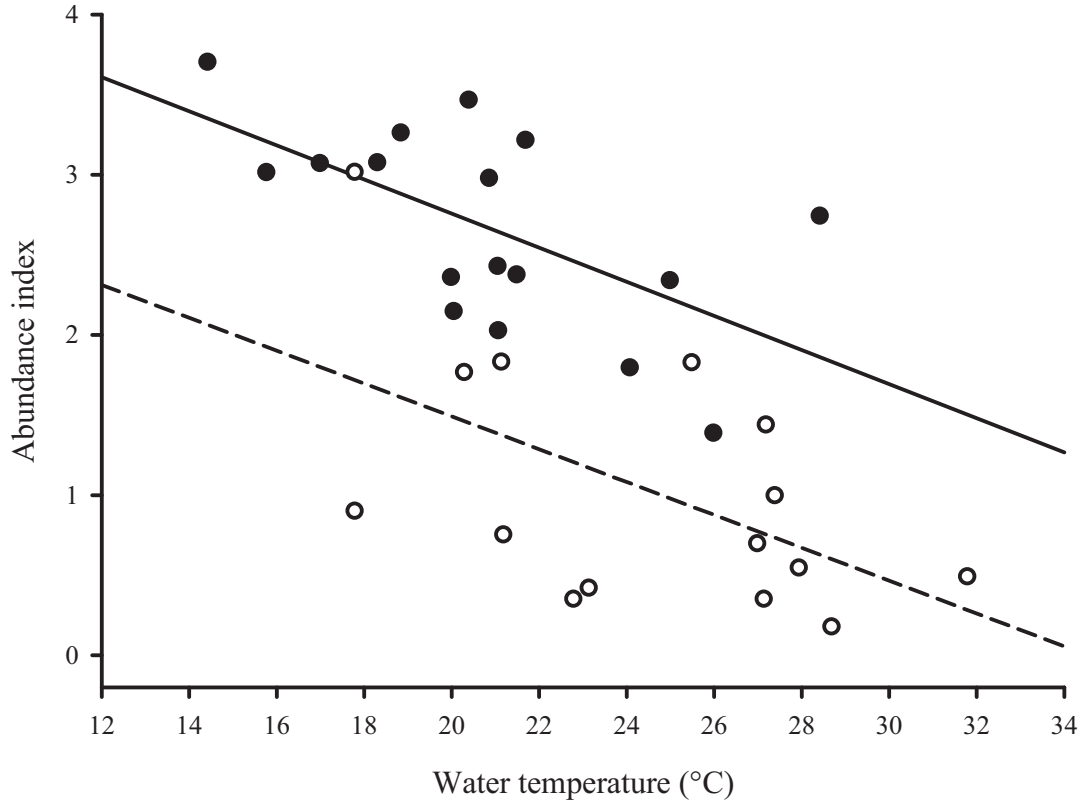

Figure 5.10. The relationship between water temperature and fish abundance was similar for both larval and juvenile river herring. The relative abundance of larvae (filled circle, solid line) and juveniles (empty circle, dashed line) declined as water temperatures increased. The relationship was similar for most years; however, for this example data represent fish collected in 2009.

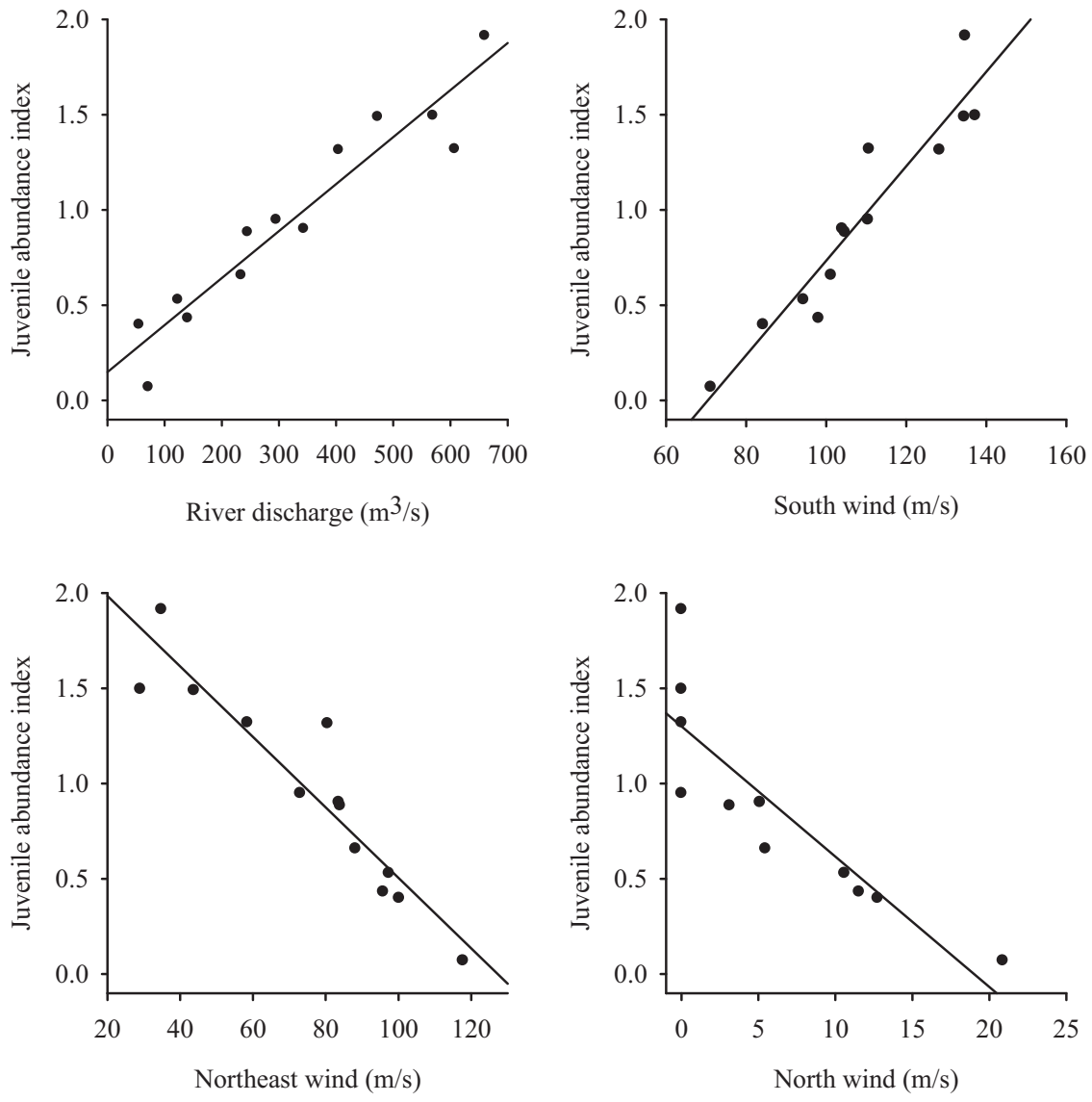

Figure 5.11. Juvenile abundance increased with river discharge ($r^2 = 0.90$, $P < 0.001$) and winds from the south ($r^2 = 0.89$, $P < 0.001$). In contrast, juvenile abundance declined with winds from the northeast ($r^2 = 0.87$, $P < 0.001$) and north ($r^2 = 0.76$, $P < 0.001$). Winds from other directions did not result in a significant amount of variation in juvenile abundance.

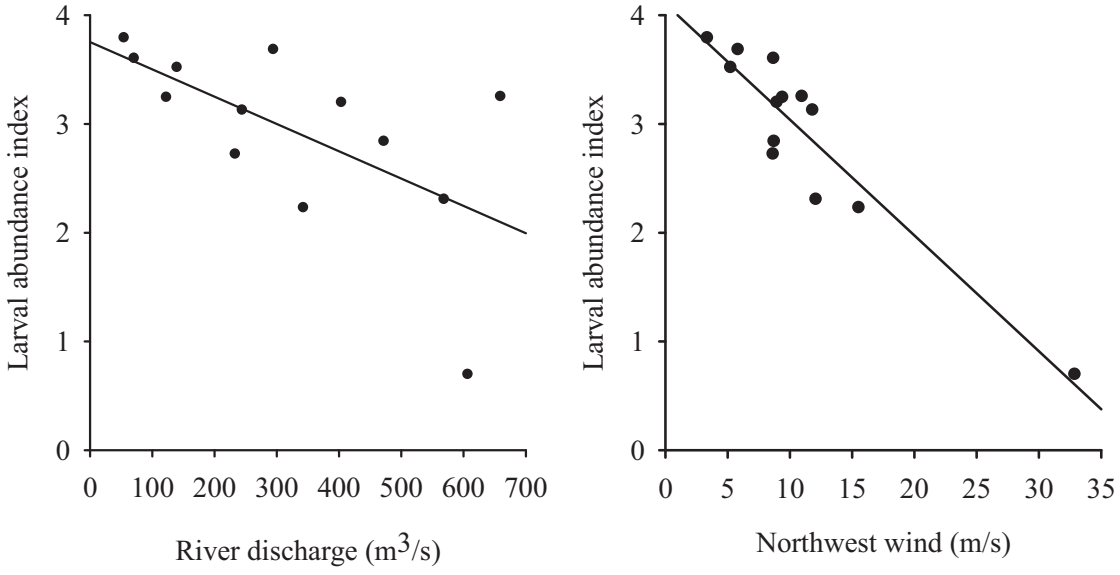

Figure 5.12. Larval abundance declined with increasing river discharge ($r^2 = 0.62$, $P = 0.02$) and light winds from the northwest ($r^2 = 0.86$, $P < 0.001$). Winds from other directions did not result in a significant amount of variation in larval abundance.

CHAPTER 6: SUMMARY AND CONCLUSIONS

From both economic and ecological standpoints, anadromous alosines are among the most important species in Albemarle Sound, North Carolina. American shad *Alosa sapidissima* and river herring (blueback herring *A. aestivalis* and alewife *A. pseudoharengus*) once supported large commercial fisheries in the region and were a major export of colonial settlements (Hightower et al. 1996). They continue to provide recreational and cultural benefits to those who value them for food and bait. Alosines are important forage for many species of fish, birds, and other animals. They serve as an important link between freshwater and marine food webs. During spawning migrations, alosines supply an influx of marine-derived nutrients to coastal rivers and estuaries (Garman and Macko 1998; MacAvoy et al. 2000). Unfortunately, most populations of shads and river herring are in decline as evidenced by decreased commercial and recreational harvests and widespread fishing regulations and closures (Schmidt et al. 2003). Understanding factors related to declining populations are complex, extending beyond overfishing. Declines are largely influenced by human activities in the coastal zone resulting in pollution, habitat alteration, and degraded ecological conditions (Waldman and Limburg 2003; Limburg and Waldman 2009).

The completion of a river herring stock assessment in 2005 as part of Amendment 1 to North Carolina's River Herring Fishery Management Plan (FMP) provided the impetus for this dissertation (NCDMF 2007). The stock assessment revealed that river herring were overfished and stocks were severely depleted. Records of landings and juvenile abundance indices showed river herring stocks were near collapse. The amendment of the FMP enacted strong conservation measures with specific provisions that called for research programs to survey spawning and

nursery areas. The amendment also recommended protection or restoration of spawning and nursery habitats to ensure the long-term health and sustainability of alosine stocks.

The goal of this project was to investigate the ecological processes that influence recruitment of anadromous alosines to nursery habitats in lower Roanoke River and Albemarle Sound. The specific objectives were: (1) to determine the spatiotemporal distribution of alewife and blueback herring during peak periods of larval production; (2) to examine how physical properties and prevailing environmental conditions, especially river flow, influence larval abundance, growth, and mortality; (3) to compare feeding ecology and dietary overlap among alosines at various habitat types, and (4) to use long-term datasets to assess fluctuations in recruitment dynamics. Throughout this dissertation, I identified nursery habitats and environmental conditions that support fast growth and low mortality. Protection of these habitats should bolster recruitment and confer a survival advantage to individuals by decreasing the time spent in vulnerable larval stages.

Evidence from this study provides some support for a review of reservoir operation and dam discharge guidelines to optimize river flow regimes for production of anadromous alosines in Roanoke River (Chapter 2). As observed in March 2009, high river flow (300 – 600 m^3/s) served as distinct migratory and spawning cue for river herring. Moderate to high flows (186 – 387 m^3/s) in April and May supported widespread spawning of blueback herring and alewife. Analysis of river flow during these months suggests a large proportion of larvae drift downstream in narrow, channelized river reaches until they are entrained in low-velocity habitats at the mouth of the river or dispersed into Albemarle Sound. The collection of a large

proportion of yolk-sac larvae indicates primary nursery habitat is located near the mouth of Roanoke River. This habitat is especially important for first-feeding larvae transitioning to zooplankton.

Spatiotemporal overlap between larval fish and their prey is thought to have important effects on growth, survival, and recruitment success. Prior to this work, feeding ecology and dietary overlap had not been studied for first-feeding blueback herring and alewife (Chapter 3). The results demonstrate river herring production in Roanoke River coincides with a significant reduction in zooplankton abundance. The composition of river herring diets changed little with larval ontogeny and small prey ($\leq$ 200 μm) were always an important component of diets. Prey selectivity was highly variable by habitat. Larval river herring showed preference for bosminids and rotifers in Roanoke River and copepods, especially naupliar stages, in Albemarle Sound. The results suggest nursery habitats near the mouth of Roanoke River offer river herring an abundant, diverse forage base with zooplankton characteristic of habitats in the River and Sound. Data from long-term field observations (Chapter 3) and short-term laboratory experiments (Chapter 4) confirm that anadromous alosines do not appear to be food limited in Roanoke River or Albemarle Sound. Because of a high-level of dietary overlap, intraspecific and interspecific competition is substantial for anadromous alosines.

It is perplexing that late-stage larvae near transformation (14 – 20 mm total length) were not caught within any of the areas sampled. Similar observations have been recorded with previous ichthyoplankton surveys on Roanoke River (Rulifson et al. 1992; Rulifson and Overton 2005; Walsh et al. 2005). In this study, sampling was conducted from March through June and through day and night in an attempt to capture larvae representing all stages of development. Collections of similar-sized schooling clupeids, Atlantic menhaden *Brevortia tyrannus* and bay anchovy

Anchoa mitchilli, would suggest that the absence of late-stage alosine larvae was not related to gear efficiency. Identification of habitats used by late-stage larvae could be beneficial for restoration or protection of nursery habitats. It would also help further elucidate transport processes for larvae and juveniles.

The results of long-term data analysis for larval and juvenile river herring (Chapter 5) suggests Roanoke-Albemarle stocks are in decline as previously observed with fishery-dependent data and estimates of spawning stock biomass (Carmichael 1999; Schmidt et al. 2003). Persistent declines in abundance could be attributed to increased natural mortality occurring during the early life stages when year-class strength was established. It appears that density-independent processes (climate, water quality, river flow) and density-dependent processes (predation, competition, disease) work in concert to regulate recruitment. My research on Roanoke River confirms that fluctuations in hydrography, precipitation and weather, and river flow can cause appreciable changes in fish abundance, growth, and mortality. Temperature was a critically important determinant of growth and abundance. River flow and to a lesser extent, wind was correlated with juvenile recruitment in Albemarle Sound. Multiple regression analysis with environmental factors yielded a significant model for estimating juvenile abundance (Chapter 5). The model indicates that juvenile abundance is positively related to river flow. Wind can have a variable effect on juvenile abundance depending on wind direction and intensity.

Analyses of long-term data confirm that in years with moderate spring river flow (141 – 311 m^3/s) recruitment of juveniles in Albemarle Sound is high. Although not unexpected, synchrony was not observed between larval and juvenile river herring production. It is plausible that contributions of Roanoke River alosines in Albemarle Sound were masked by large contributions

of alosines from other river systems (*e.g.*, Chowan River). Regardless of river origin, production of anadromous alosines in Albemarle Sound is affected by high outflow from Roanoke River. Management and revision of flow regimes prescribed through this dissertation could have effects that are important for the ecology and biodiversity of the region. A comprehensive monitoring program is needed to measure river health and restoration effectiveness if recommendations are implemented.

Recommendations for Fisheries Management and Future Research

- Model river flow and conduct time of travel studies to reflect changes in hydrology within the lower Roanoke River.
- Develop methods to estimate spawning stock biomass for Roanoke River stocks of American shad, blueback herring, and alewife.
- Sample juvenile alosines and use otolith chemistry to determine source and relative contributions of different rivers on juvenile recruitment.
- Evaluate predatory impact of striped bass and other high-trophic level species (*e.g.*, birds). Predatory impacts might affect the success of stock enhancement for anadromous alosines because of their small size and significance as a forage base.
- Determine Albemarle Sound's carrying capacity for anadromous fish production.

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APPENDIX A: DESCRIPTIONS OF FIXED SAMPLING LOCATIONS USED TO STUDY RECRUITMENT OF LARVAL ALOSINES TO LOWER ROANOKE RIVER AND ALBEMARLE SOUND (2008-2009)

Table A.1. Descriptions of fixed sampling locations used to study recruitment of larval alosines to lower Roanoke River and Albemarle Sound, North Carolina. Station numbers correspond to sites in Figure A1. Latitude and longitude estimates were derived using a global positioning system. Values represent means (SD).

Station	Area	Latitude, Longitude	Distance from river mouth (rkm)	Physical description	Sediment	Channel width (m)	Depth (m)	Surface flow (m/s)
1	River	35° 52.099' N, 76° 50.102' W	22.8	Roanoke River mainstem; steep banks; large wood deposition	Medium sand	119 (10)	5.7 (0.2)	0.18 (0.13)
2	River	35° 53.269' N, 76° 48.917' W	19.0	Roanoke River mainstem outside mouth of Thoroughfare distributary; steep banks; large wood deposition	Very fine sand	225 (9)	5.4 (0.2)	0.21 (0.12)
3	River	35° 53.455' N, 76° 48.937' W	18.5	In the uppermost Thoroughfare River distributary about 0.8 rkm downstream of its exit from Roanoke River; steep banks	Medium sand	46 (6)	5.2 (0.2)	0.16 (0.16)
4	River	35° 52.053' N, 76° 47.522' W	15.0	In lower Warren Neck Creek about 0.8 rkm upstream of its entrance into Roanoke River; flooded hardwood swamp; low water flow; hypoxia was frequently observed	Very fine sand	34 (2)	3.0 (0.1)	0.07 (0.06)
5	River	35° 52.390' N, 76° 46.866' W	14.6	In the uppermost Middle River distributary about 0.8 rkm downstream of its exit from Roanoke River; large wood deposition	Medium sand	66 (11)	5.2 (0.2)	0.14 (0.10)
6	River	35° 51.831' N, 76° 46.588' W	15.1	Roanoke River mainstem adjacent to Weyerhaeuser Plant; deep along bulkhead and hardened shoreline; large wood deposition; high river flow	Coarse sand	166 (30)	4.1 (0.1)	0.19 (0.09)

Table A1 continued

Station	Area	Latitude, Longitude	Distance from river mouth (rkm)	Physical description	Sediment	Channel width (m)	Depth (m)	Surface flow (m/s)
7	River	35° 52.705' N, 76° 44.275' W	9.5	Roanoke River mainstem; shallow banks; large wood deposition	Fine sand	156 (13)	4.8 (0.2)	0.12 (0.08)
8	Delta	35° 54.874' N, 76° 43.389' W	5.5	Roanoke River mainstem; shallow banks; large wood deposition	Fine sand	289 (16)	3.5 (0.2)	0.18 (0.14)
9	Delta	35° 55.406' N, 76° 42.346' W	3.3	Roanoke River mainstem; outside mouth of Conaby Creek; seasonal emergent vegetation	Very fine sand	132 (7)	3.0 (0.2)	0.10 (0.06)
10	Delta	35° 55.124' N, 76° 43.511' W	4.5	Eastmost River distributary; 0.5 rkm downstream of NC Hwy 45 bridge; large wood deposition; seasonal emergent vegetation	Very fine sand	77 (6)	2.8 (0.1)	0.13 (0.06)
11	Delta	35° 56.022' N, 76° 42.667' W	1.4	Eastmost River distributary; 3.5 rkm downstream of NC Hwy 45 bridge; seasonal emergent vegetation	Very fine sand	86 (6)	3.5 (0.1)	0.12 (0.10)
12	Delta	35° 55.433' N, 76° 43.942' W	2.3	Cashie River and Thoroughfare; 0.25 rkm downstream of NC Hwy 45 bridge; shallow banks; seasonal emergent vegetation	Coarse sand	224 (34)	3.3 (0.2)	0.17 (0.17)
13	Delta	35° 56.279' N, 76° 44.060' W	0.5	Lower Cashie River and Thoroughfare; 1.5 rkm downstream of NC Hwy 45 bridge; shallow banks and mudflat	Medium sand	327 (3)	3.4 (0.1)	0.14 (0.09)

Table A1 continued

Station	Area	Latitude, Longitude	Distance from river mouth (rkm)	Physical description	Sediment	Channel width (m)	Depth (m)	Surface flow (m/s)
14	Sound	35° 57.093' N, 76° 42.158' W	-2.0	Batchelor Bay; 2-km seaward of Middle River and Cashie River; unprotected water	Very fine sand	---	2.9 (0.1)	0.21 (0.19)
15	Sound	35° 57.430' N, 76° 41.649' W	-3.0	Batchelor Bay; 3-km seaward of Middle River and Cashie River; unprotected water	Very fine sand	---	3.2 (0.1)	0.19 (0.17)
16	Sound	35° 57.785' N, 76° 41.116' W	-4.0	Batchelor Bay; 4-km seaward of Middle River and Cashie River; unprotected water	Medium sand	---	3.2 (0.1)	0.19 (0.19)
17	Sound	35° 56.894' N, 76° 40.801' W	-2.0	Southwest Albemarle Sound; 2-km seward of Roanoke River; unprotected water	Silt	---	3.3 (0.1)	0.14 (0.12)
18	Sound	35° 57.257' N, 76° 40.294' W	-3.0	Southwest Albemarle Sound; 3-km seward of Roanoke River; unprotected water	Very fine sand	---	3.5 (0.1)	0.18 (0.15)
19	Sound	35° 57.632' N, 76° 39.857' W	-4.0	Southwest Albemarle Sound; 4-km seward of Roanoke River; unprotected water	Medium sand	---	3.8 (0.1)	0.25 (0.27)

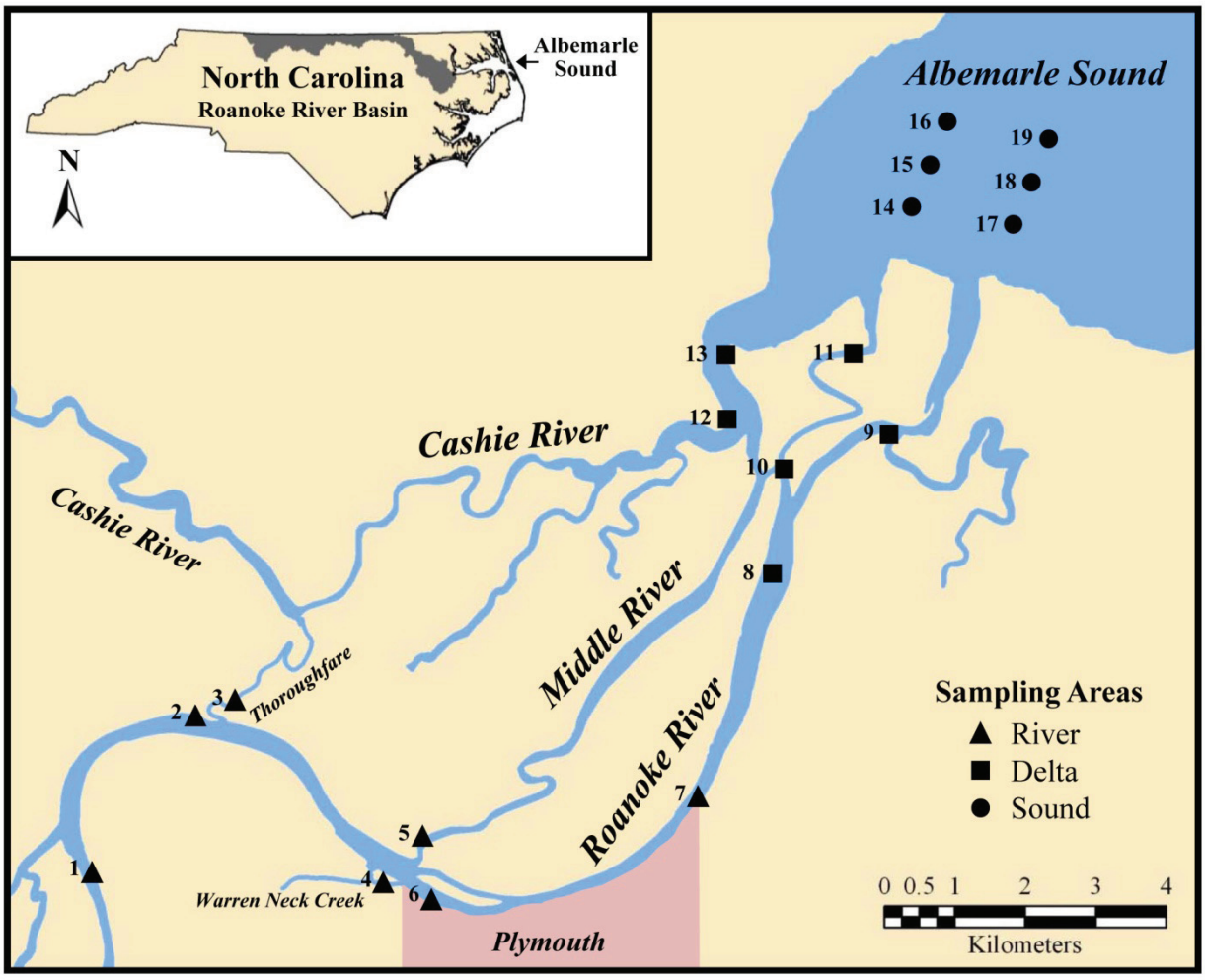

Figure A.1. Map of study sites for sampling water quality, ichthyoplankton, and zooplankton in lower Roanoke River and western Albemarle Sound, North Carolina.

APPENDIX B: SYNOPSIS OF CHARACTERS FOR DISTINGUISHING LARVAE AND JUVENILES OF CLUPEIDAE IN ALBEMARLE SOUND, NORTH CAROLINA.

	Blueback herring *A. aestivalis*	**Alewife** *A. pseudoharengus*	**American Shad** *A. sapidissima*	**Hickory shad** *A. mediocris*	**Gizzard Shad** *D. cepedianum*	**Atlantic Menhaden** *B. tyrannus*
Spawning	April - May	Late March - April	April - May	Late April - June	May - June	Winter - Spring
Eggs (mm)	0.87 - 1.11	0.95 - 1.25	2.3 - 3.5	1.1 - 1.65	0.75	1.3 - 2.0
Yolk	granular	granular	granular	granular	highly granular	clear transparent
Oil globule	tiny, scattered	absent	absent	few, small	single large, posterior yolk	single small
Hatch length (mm)	3.1 - 4.2	3.5	7.0 - 10.0	5.2 - 6.6	3.25	2.4 - 4.5
Yolk absorbtion length (mm)	6.0	6.0	9.0 - 12.0	7.0	8.0	5.0
Larvae (*Myomere counts in larvae from 6 - 14 mm*)						
Myomeres						
preanal	42 - 45	40 - 41	41 -47	36 - 40	43 - 44	37 - 40
postanal	1 - 5	5 - 9	10 -16	4 - 9	3 -8	8 - 10
dorso-anal	11 - 13	7 - 9	-	7 - 8	-	-
cleithrum-anal	40 - 45	38 - 43	45 - 50	-	-	-
total	45 - 49	45 - 50	51 -63	53 - 55	46 -52	45 - 50
Notochord pigment dorsal tip	No	Yes	No	small larvae only	No	small larvae only
Notochord pigment ventral tip	Yes	Yes	Yes	Yes	No	Yes
Juveniles	48 - 66 mm	30 - 76 mm	42 - 68 mm	43 - 77 mm	65 - 80 mm	33 - 48 mm
Vertebrae	47 - 53	46 - 50	55 - 57	53 - 55	47 - 51	45 - 50
Dorsal fin rays	15 - 20	12 - 18	18 - 19	15 - 20	10 - 15	18 - 24
Anal fin rays	15 - 21	15 -20	21 - 22	19 - 23	25 - 37	18 - 24
Pectoral fin rays	14 - 18	14 - 16	13 - 18	15 - 16	14 - 17	13 - 19
Pelvic fin rays	9 - 11	10	8 - 10	9	7 - 10	7
Gill raker count	29 - 41	25 - 33	23 - 31	18 - 21	300	40 - 67
Peritoneum	black	pale with spots	pale silvery	pale with spots	-	black
Jaw formation	lower jaw with slight angle	lower jaw with steep angle	lower jaw with slight angle	lower jaw larger than upper jaw	-	-
Tongue teeth	16 - 42	7 - 27	5 - 20	13 - 19	-	0 - 4
Tongue pigmentation	along edges	along edges	heavy, 4-6 rows cover tongue	along edges	-	Few at tip

*Adapted from *Fishes of the Delaware Estuaries: A Guide to the Early Life Histories* by J. C. Wang and R. J. Kernehan (1979).

APPENDIX C: STATISTICAL COMPARISON OF SEDIMENTS AND BENTHIC HABITATS ALONG THE LOWER ROANOKE RIVER AND WESTERN ALBEMARLE SOUND (2008-2009)

Understanding the flow dynamics and geomorphology of a coastal river system is important when characterizing habitats that support healthy populations of fish and their food resources. Sediment samples were collected from 19-stations and three distinct areas (River, Delta, Sound) within lower Roanoke River and western Albemarle Sound, North Carolina (Figure A.1). To determine the substrate type at each station and within each area, sediment samples were collected once during the study using a Ponar benthic grab (sample area: 229 mm x 229 mm; volume: 8.2 L). After collection, samples were stored in plastic bags and transported on ice to the laboratory. Samples were frozen until analyzed in the laboratory to prevent any biologic growth that could alter the sediment structure. Samples were thawed and split in half vertically. Visible features were noted such as consolidation of the sediment, sorting of the sediment, color and texture, and any layering or sediment structure present.

Standard methods for sediment grain size analysis were used (Wentworth 1922; Folk and Ward 1957). Large biologic material was removed from samples by gently washing sediment through a coarse sieve (0.7-mm mesh) with distilled water. Biologic material that passed through the course sieve was not quantified or distinguished from sediments. Sediments and biologics were dried in aluminum pans at 60 °C for 48 h. Each hard, dried sample was broken up into its constituent parts using a mortar and pestle. After weighing, sediments were dry-sieved through a series of decreasing sized mesh sieves to characterize sediment composition. The series of sieves used was: - 3ϕ, -1ϕ, 0ϕ, 1ϕ, 2ϕ, 3ϕ, 4ϕ, which corresponds to the

Wentworth Scale and grain sizes of 8 mm, 2 mm, 1 mm, 0.5 mm, 0.25 mm, 0.125 mm, and 0.0625 mm. A catch pan was placed at the bottom of the sieves to collect any material finer than 4ϕ (< 0.0625 mm). Samples were mechanically sieved for 15 minutes using a Ro-Tap machine at a medium intensity setting. Sediments were collected from each sieve and weighed. Throughout the process, efforts were undertaken to reduce the amount of sediment lost. The weight of the sediment from each sieve was divided by the total weight of the sample to calculate the percentage of sediment that represented each respective grain size. The percentage of substrate categories (silt/mud, fine sand, medium sand, coarse sand, gravel, organic) was determined and sediment statistics were obtained through graphical and moment measures (Blott and Pye 2001). The final cumulative percentages of each sample were averaged to determine the amount of sediment recovered per sample.

The average sediment recovered for each sample processed was ≥ 99%. Sediment grain size analysis revealed that all stations were unconsolidated, similar in composition, and consisted of silt and sand with fine- and medium-sized grains (Figure C.1). Mean grain size was not significantly different for River (286 ± 71 μm), Delta (307 ± 140 μm), or Sound (174 ± 63 μm). Sediment grain size was not correlated with river discharge or surface currents. The accumulation of fine silts and clay in Albemarle Sound was an indicator of sedimentation resulting from decreased river flow and energy for sediment transport. Large biologic material collected in River and Delta samples consisted of coarse wood debris, humus, and leaf litter. Large unioid mussels, *Corbicula* sp. and *Rangia* sp. (≥ 40 mm shell length), were collected from benthic samples in the Sound. The mean grain size and dry-sieve percentages for each grain size for all samples are presented in Table C.1.

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Table C.1. Comparison of sediments and physiographic characteristics for stations sampled in the lower Roanoke River and Albemarle Sound, North Carolina. Station numbers correspond to sites in Figure A.1. Values represent means (SD).

Station	Habitat	Channel width (m)	Depth (m)	Surface flow (m/s)	Mean grain-size (μ)	Organic (%)	Gravel (%)	Coarse sand (%)	Medium sand (%)	Fine sand (%)	Silt (%)
1	River	119 (10)	5.7 (0.2)	0.18 (0.13)	357 (8)	23.8	1.9	6.8	23.7	22.6	21.3
2	River	225 (9)	5.4 (0.2)	0.21 (0.12)	108 (6)	0.9	2.6	6.3	22.3	36.2	31.7
3	River	46 (6)	5.2 (0.2)	0.16 (0.16)	327 (9)	15.2	2.9	7.1	23.0	29.6	22.3
4	River	34 (2)	3.0 (0.1)	0.07 (0.06)	111 (7)	0.2	3.2	10.7	26.3	21.1	38.5
5	River	66 (11)	5.2 (0.2)	0.14 (0.10)	353 (9)	20.7	3.1	8.9	22.6	20.5	24.2
6	River	166 (30)	4.1 (0.1)	0.19 (0.09)	624 (4)	20.5	1.4	4.0	39.4	30.1	4.6
7	River	156 (13)	4.8 (0.2)	0.12 (0.08)	126 (8)	4.7	1.5	8.1	29.0	20.9	35.7
8	Delta	289 (16)	3.5 (0.2)	0.18 (0.14)	241 (6)	11.5	1.1	8.2	29.6	30.8	18.8
9	Delta	132 (7)	3.0 (0.2)	0.10 (0.06)	117 (6)	0.0	1.2	7.7	31.7	26.0	33.4
10	Delta	77 (6)	2.8 (0.1)	0.13 (0.06)	109 (6)	0.9	1.4	7.0	23.9	34.0	32.7
11	Delta	86 (6)	3.5 (0.1)	0.12 (0.10)	119 (7)	3.5	1.4	7.8	28.9	23.4	35.0
12	Delta	224 (34)	3.3 (0.2)	0.17 (0.17)	991 (5)	50.7	0.7	3.5	13.0	16.4	15.7
13	Delta	327 (3)	3.4 (0.1)	0.14 (0.09)	263 (8)	25.3	2.6	4.8	14.6	27.7	24.9
14	Sound	-	2.9 (0.1)	0.21 (0.19)	63 (6)	6.2	0.2	1.0	8.5	45.2	38.8
15	Sound	-	3.2 (0.1)	0.19 (0.17)	69 (8)	5.8	1.2	3.7	16.0	21.7	51.6
16	Sound	-	3.2 (0.1)	0.19 (0.19)	377 (7)	31.5	1.5	8.1	24.5	12.2	22.2
17	Sound	-	3.3 (0.1)	0.14 (0.12)	57 (7)	8.2	0.3	1.7	11.7	21.5	56.6
18	Sound	-	3.5 (0.1)	0.18 (0.15)	115 (9)	8.7	2.1	8.5	21.3	17.2	42.3
19	Sound	-	3.8 (0.1)	0.25 (0.27)	365 (7)	34.9	0.8	5.5	22.7	14.6	21.5

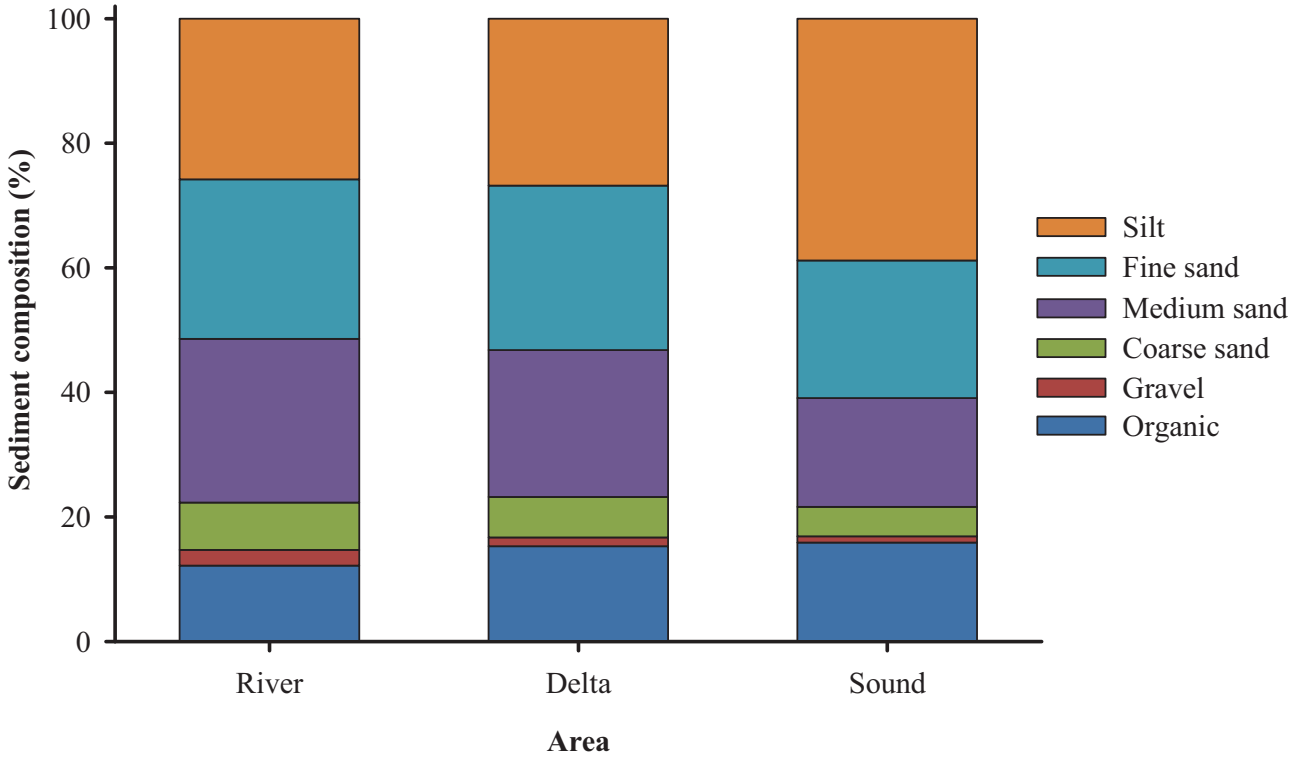

Figure C.1. Physical characteristics of sediment collected from select areas within lower Roanoke River and western Albemarle Sound, North Carolina. Sediments were unconsolidated, similar in composition, and primarily consisted of silt and sand with fine- and medium-sized grains.

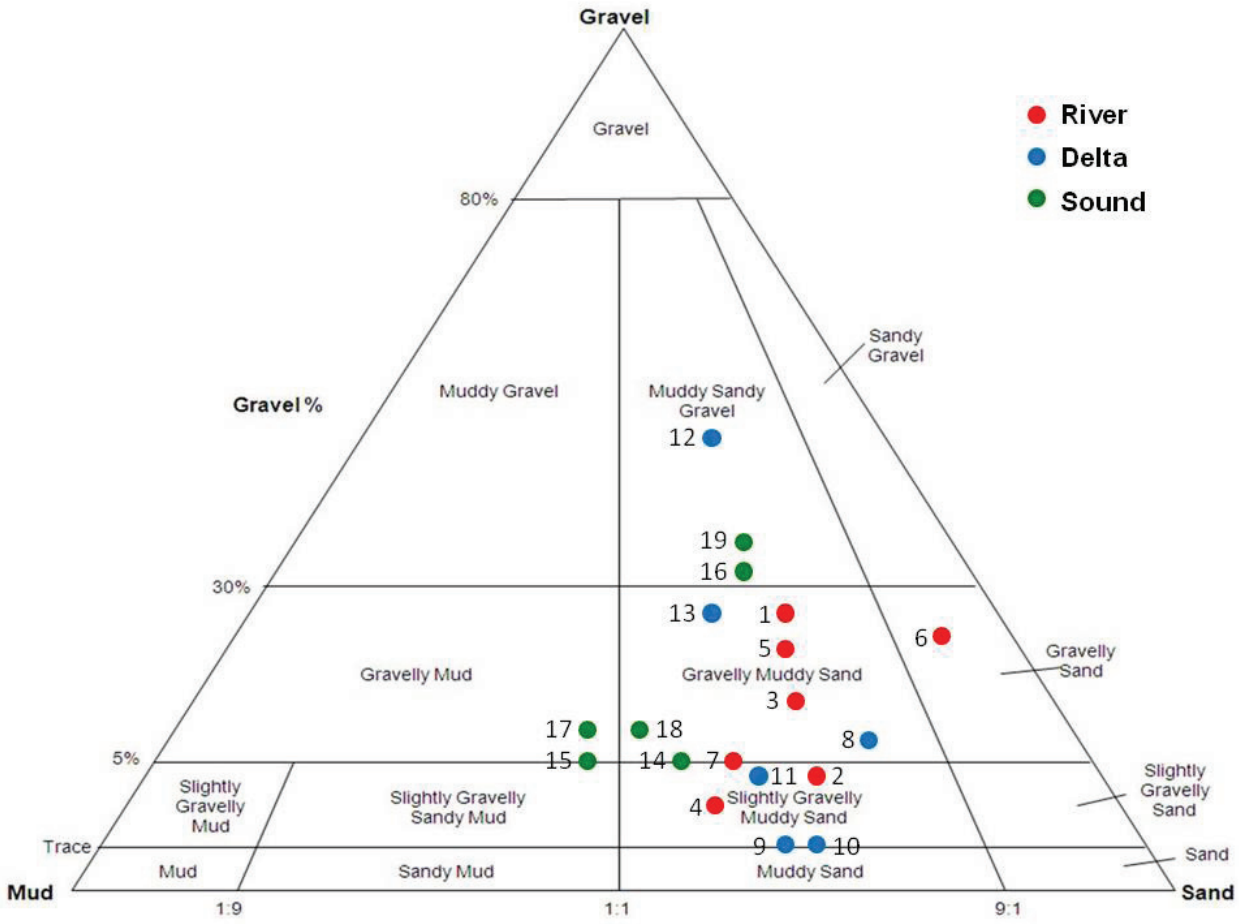

Figure C.2. Ternary diagram for textural classification of sediments in a large alluvial river system. Sediments were collected from select areas within lower Roanoke River and western Albemarle Sound, North Carolina. Numbers correspond to station locations referenced in Figure A.1 and Table C.1.

APPENDIX D: ANIMAL USE PROTOCOL APPROVALS AND PERMITS

Animal Care and Use Committee
East Carolina University
212 Ed Warren Life Sciences Building
Greenville, NC 27834
252-744-2436 office • 252-744-2355 fax

May 4, 2007

Anthony Overton, Ph.D.
Department of Biology
Howell Science Complex
East Carolina University

Dear Dr. Overton:

Your Animal Use Protocol entitled, "Defining Essential Fish Habitat in Estuaries and Coastal River Systems: A Model-Based Approach," (AUP #D214) was reviewed by this institution's Animal Care and Use Committee on May 4, 2007. The following action was taken by the Committee:

"Approved as submitted"

A copy is enclosed for your laboratory files. Please be reminded that all animal procedures must be conducted as described in the approved Animal Use Protocol. Modifications of these procedures cannot be performed without prior approval of the ACUC. The Animal Welfare Act and Public Health Service Guidelines require the ACUC to suspend activities not in accordance with approved procedures and report such activities to the responsible University Official (Vice Chancellor for Health Sciences or Vice Chancellor for Academic Affairs) and appropriate federal Agencies.

Sincerely yours,

Robert G. Carroll, Ph.D.
Chairman, Animal Care and Use Committee

RGC/jd

enclosure

EAST CAROLINA UNIVERSITY

Animal Care and Use Committee
East Carolina University
212 Ed Warren Life Sciences Building
Greenville, NC 27834
252-744-2436 office • 252-744-2355 fax

MEMORANDUM

TO: Kenneth Riley
Department of Biology

FROM: Dorcas O'Rourke, D.V.M.
University Veterinarian

SUBJECT: Certificate of Training
Training Date 9/5/06

DATE: September 7, 2006

This letter is provided to certify that you have received 2.5 hours of training in humane methods of animal experimentation, proper handling of selected species of laboratory animal, and methods for reporting deficiencies in animal care and treatment. The training was provided in accordance with the provisions of regulations of the U.S. Department of Agriculture (9 CFR 2.32) and the Policy and guidelines of the National Institutes of Health. This training and instruction was provided by Robert G. Carroll, Ph.D., Chairman of the ECU Animal Care and Use Committee, Lamar Blankenship, Ph.D., Chief of the Division of Laboratory Animal Science, and myself. Technicians of this department participated in providing training in handling of animals. We suggest that you retain this letter in your training file for future reference.

Instruction in animal handling and injection techniques included the following procedures:

1. Pick up and carry-mouse and rat
2. Restraint-mouse and rat
3. Intraperitoneal injection-mouse and rat
4. Subcutaneous injection-mouse and rat
5. Intramuscular injection-rat only

COPY

North Carolina Division of Marine Fisheries

Proof of Purchase

RENEW : Scientific or Educational Collection Permit : Permit Number 706671

Permit Number : 706671 **NC Residency :** **Sales Outlet :** DMF Morehead City Office
Permit Year : 2009 **Qualifying Product :** **Terminal Number :** N1MO153

Effective Date/Time : 01/01/2009 00:00 **Fee :** 0.00
Expiration Date/Time : 12/31/2009 23:59 **Status :** Active
Issue Date/Time : 12/05/2008 13:33 **Status Date :** 12/05/2008

Permit Holder : 660357 EAST CAROLINA UNIVERSITY (CROSIER) **Business Type:**

Physical Address : 2104 HWY 13 N FARMVILLE NC,
GREENVILLE, NC, 27858-4353
United States
County : Pitt

Mailing Address : DEPARTMENT OF BIOLOGY,
EAST CAROLINA UNIVERSITY,
GREENVILLE, NC, 27858-4353
United States
County : Pitt

Race :
Gender :
Date of Birth :
Eyes :
Hair :
Weight :
Height : ft. Inches

Home Phone :
Business Phone : (252) 348-6355
Fax : (252) 328-4178
Ids :
Primary Residence : NC
Secondary Residence :
Prior Names :
E-Mail :

Business Agent : 660340 CROSIER, JAMES THOMAS

Physical Address : 2013 PINECREST DRIVE,
GREENVILLE, NC, 27858-4353
United States
County : Pitt

Mailing Address :
County :

Race : Caucasian
Gender : Male
Date of Birth 09/17/1955
Eyes : Blue
Hair : Brown
Weight : 245
Height : 6 ft. 2 Inches

Home Phone : (252) 756-8344
Business Phone : (252) 328-6355
Fax : (252) 328-4178
ds :
Primary Residence : NC
Secondary Residence :
Prior Names :
E-Mail : CrosierJ@.ecu.edu

Contact Information

Contact Person	Contact Person DOB	Contact Person Telephone #
JAMES THOMAS CROSIER	09/17/1955	(252) 756-8344

Purpose of Collection

- [X] Research
- [X] Teaching Specimens
- [X] Educational Display (Aquariums)
- [ ] Other (specify)

Collectors

articipantId	Name	DOB	Contact Phone
	DR. ROGER RULIFSON	11/13/1951	(252) 328-6718
	DR. JOSEPH J. LUCZKOVICH	07/06/1956	(252) 328-9402
	DR. ANTHONY OVERTON	04/11/1972	(252) 328-6718
	DR. REBECCA COOPER	08/26/1977	(252) 328-6718
	DR. MARY A. FARWELL	07/08/1960	(252) 328-6718
	JASON CLEMONT	12/22/1974	(252) 328-6718
	DAVID GENTRY	10/25/1981	(252) 328-6718
	ERIC DIADDORIO	12/05/1968	(252) 328-6718
	KATHARINE KLEBER	09/22/1969	(252) 916-1191
	DR. TERRI WOODS	12/10/1953	(252) 328-3474
	ANDREW GROSS	04/22/1980	(910) 232-6304
	GARY WRIGHT	04/27/1982	(252) 328-9400
	GREGORY F. MEYER	08/01/1964	(252) 367-4934
	JOHN CONOLEY	10/19/1978	(252) 328-9988
	KENNETH LEE PICKRELL RILEY	10/11/1972	(252) 328-4121
	KEVIN HART	07/06/1982	(732) 735-0737
	REBECCA A. DEEHR	07/08/1973	(252) 321-6328

State of North Carolina
Wildlife Resources Commission
Scientific Fish Collecting License No. 1090
G.S. 113-261, 262,272.4

Issued To: **Dr. Anthony S. Overton**
East Carolina University
Department of Biology
Howell Science Complex Rm S215-A
Greenville, NC 27858-4353

Expires December 31, 2009
Collecting License Category: C
Special Conditions:
Statewide - Aquatic invertebrates and fishes

Date: 02/09/2009
DUPLICATE

By: Robert L. Curry

Assistants

Samatha Binion
Eric Diadorrio
James Edwards
Jocelyn Kim
Kenneth Riley

VITA

Kenneth Lee Pickrell Riley was born on October 11, 1972, in Durham, North Carolina. He attended the University of North Carolina at Wilmington where he received in 1996 his Bachelor of Science degree in marine biology and secondary science education. While an undergraduate, Ken developed a real interest in marine ecology and worked for four years as a research assistant in UNC-Wilmington's Benthic Ecology Laboratory. After graduation, he moved to Cocodrie, Louisiana, to work as a marine educator for Louisiana Universities Marine Consortium. For three years, he taught thousands of K-12 and college students, teachers, and the public about the functions and values of Louisiana's coastal wetlands and marine resources. In the fall of 1999, Ken and his wife, Kelly, moved to Baton Rouge to enroll in Graduate School at Louisiana State University. Ken's research focused on spawning, larval rearing, and propagation of marine fishes for aquaculture. After graduation, Ken accepted a leadership position with Harbor Branch Oceanographic Institution in Fort Pierce, Florida. During his tenure at Harbor Branch, Ken actively participated in aquaculture research, teaching, and technology transfer. Ken's research focused on the reproductive biology and early life history of marine fish. He coordinated and developed a wide variety of training manuals, industry workshops, and aquaculture degree programs. Unfortunately, the disastrous hurricanes of 2005 disrupted operations and destroyed many of the laboratories at Harbor Branch. While Ken remained at Harbor Branch during the rebuilding process, the storms provided the impetus for him to further his graduate studies. Ken returned to North Carolina in 2006 to pursue his doctorate at East Carolina University. His research has focused on mechanisms governing survival and recruitment of American shad and river herring in Roanoke River and Albemarle Sound. Ken is currently a candidate for the degree of Doctor of Philosophy in Interdisciplinary Biology, which will be awarded through the Department of Biology on May 4, 2012.