ABSTRACT

HARRIS, JULIANNE ELAINE. Migration and Spawning of Anadromous Shads in the Roanoke River, North Carolina. (Under direction of Joseph E. Hightower.)

Anadromous alosines are ecologically, commercially, and recreationally valuable fishes. Some populations of alosines are at historically low levels, as a result of overfishing, pollution and habitat change, including the presence of dams, which block access to historic spawning sites upstream and alter spawning habitat downstream. To aid in the restoration of alosine stocks, I evaluated several methods for spawning habitat identification and characterization and evaluated trap and transport as a method to give American shad *Alosa sapidissima* access to additional spawning habitat above dams in the Roanoke River, North Carolina and Virginia. The Roanoke River has four anadromous alosines: American shad, hickory shad *A. mediocris*, blueback herring *A. aestivalis*, and alewife *A. pseudoharengus*. For all four alosines, spawning sites river-wide were most efficiently identified using plankton tows, which collect eggs of all species. Spawning habitat selection for hickory shad and river herring (blueback herring and alewife) could be evaluated using spawning pads, which collected their eggs in clumped distributions. American shad eggs were not successfully sampled by spawning pads and spawning habitats could be best examined by visual observations of spawning splashes. Unlike the other alosines in this study, little is known about spawning habitat for hickory shad. Hickory shad eggs were collected at water temperatures from 10 to 23 ºC, and peaked from 11 to 14 ºC. Spawning generally occurred in water velocities ≥ 0.1 m/sec, over substrates free from silt. A habitat suitability model for

hickory shad was developed using a Bayesian belief network. Bayesian belief networks are a relatively new method for modeling habitat suitability for fishes, but could prove very useful in the future, especially for species such as American shad which have been the focus of more study and are in need of restoration. I evaluated movement patterns and spawning of sonic-tagged adult American shad transported to habitats above dams on the Roanoke River. Most transported fish spent relatively little time in the riverine habitat considered suitable for spawning, and no eggs were collected by plankton sampling. American shad appeared to move more effectively through a smaller, as compared to a larger, reservoir, but fish released directly into riverine habitat spent the longest amount of time in suitable spawning habitat. Although the mortality associated with moving downstream through a dam turbine was generally low, few adults completed the passage, and many were observed just upstream from a dam late in the season, suggesting that structures to increase downstream passage may be beneficial. I used data on behavior and outmigration of American shad adults and fry released above and below dams on the Roanoke River to develop a deterministic, density-dependent, stage-based matrix model to predict possible population-level effects of transporting American shad to upper basin habitats. The American shad population in the Roanoke River appears small compared to assumed values of carrying capacity in the lower river and would appear to benefit from transport only under optimal conditions of young survival and effective fecundity. The matrix model predicted that under present conditions, improvements to survival rates of young or adults would likely lead to greater improvements in the stock size of American shad in the Roanoke River.

Migration and Spawning of Anadromous Shads in the Roanoke River, North Carolina

by
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BIOGRAPHY

I grew up in Philadelphia, Pennsylvania, and graduated from Germantown Friends School in 1997. During high school, I was inspired by my biology teacher, Gen Nelson, to pursue a career in conservation and management of natural resources, although I was not sure on what I wanted to focus. Over the summer between my junior and senior years in college, I completed a Research Experiences for Undergraduates (REU) program at the Florida Institute of Technology, working on horseshoe crabs in Sebastian Inlet on the Indian River. I really enjoyed many aspects of that project and decided that I wanted to study fisheries.

I graduated from Tufts University in the spring of 2001 and headed back to Florida to start graduate work under the insightful direction of Dr. Daryl Parkyn, where I studied estuarine habitat use and feeding of Gulf sturgeon and discovered that Gulf sturgeon are one of the coolest fish ever! I then worked for Dr. Rich McBride at the Fish and Wildlife Research Institute in St. Petersburg, Florida, where I studied anadromous alosines in the St. Johns River, Florida.

From there, I decided to go back to graduate school to work on a Ph.D., which I have been doing since 2005. I am very lucky to study under Dr. Joe Hightower, who not only works on habitat and spawning of anadromous fishes and quantitative fisheries, both of which are of interest to me, but also has a commendable work ethic, is always available, and is an outstanding professor.

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I have been very lucky to have numerous other mentors who provided me with encouragement and inspiration. Especially, I appreciate Gen Nelson, who first instilled in me an interest in becoming a scientist; Dr. Mike Allen, who has been a great role model, inspired me to love quantitative fisheries and statistics, and probably had a good deal to do with my acceptance at NC State; Dr. Rich McBride, who has given me more opportunities to grow as a fisheries scientist than I could ever have expected or deserved; and Dr. Derek Aday, who taught me a lot about what it means to be a good teacher and gave me both freedom and encouragement when I taught the laboratory section of his class.

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CHAPTER 1. INTRODUCTION

Alosines are a sub-family within Clupeidae and are found on all continents except Australia and Antarctica (Waldman 2003). On the Atlantic coast of North America there are four anadromous alosines: American shad *Alosa sapidissima,* hickory shad *A. mediocris*, blueback herring *A. aestivalis,* and alewife *A. pseudoharengus* (Waldman 2003). All four species are of economic value, since they support commercial and recreational fisheries (Smith 1894; Marshall 1977; Batsavage and Rulisfon 1998; Limburg et al. 2003; Hightower et al. 1996; Schmidt et al. 2003), but are also of ecological value, since they import marine derived nutrients to the freshwater river systems where they spawn (Garman 1992; Garman and Macko 1998).

Many anadromous species are in decline as a result of overfishing, pollution, and habitat changes, especially anthropogenic changes to river systems. Degradation of riverine habitat where anadromous fishes spawn can be attributed to a variety of sources including: water withdrawals, dredging, urbanization, pollution, and presence of dams (Pringle et al. 2000; Freeman et al. 2003; Schlit 2007). Dams provide benefits to humans in the form of water supply, flood control, recreation and hydroelectric power generation (Shuman 1995; Schilt 2007), but they can cause declines in anadromous fish populations by blocking access to upstream spawning sites and altering the quality and quantity of spawning habitat downstream (Rulifson and Manooch 1990; Rulifson 1994; Pringle et al. 2000; Trush et al. 2000; Dauble et al. 2003; Freeman et al. 2003; Schilt 2007).

Like other anadromous species, research and assessment suggest that many populations of American shad and river herring (blueback herring and alewife) are depressed compared to historic levels and are in need of restoration (Rulifson 1994; Hightower et al. 1996; Cooke and Leach 2003; Schmidt et al. 2003; ASMFC 2007). To improve stock sizes, harvest has been reduced or eliminated, fry and adults have been stocked, structures to improve access to historic spawning habitats have been constructed, and flow volumes have been altered in regulated systems (Cooke and Leach 2003; Hendricks 2003; Olney et al. 2003; St. Pierre 2003; ASMFC 2007). Some restoration efforts have been successful (Cooke and Leach 2003; Olney et al. 2003); however, many populations remain small compared to historic levels, suggesting that additional research and management may be necessary in some systems (ASMFC 2007). Specifically, further research regarding the benefits of access to historic spawning habitat would help determine when fish passage or transport might benefit these populations.

In contrast to American shad and river herring, comparatively little research attention has focused on the stock status or biology of hickory shad. Hickory shad spawn in rivers from Maryland south to Florida (Richkus and DiNardo 1984). Research on the status, spawning migration, age, growth, and reproduction of hickory shad has been completed in a few rivers (Rulifson 1994; Batsavage and Rulifson 1998; Murauskas 2006; Harris et al. 2007; McBride and Holder 2008); however, little is known about its spawning habitat use.

This dissertation examines methods to effectively and efficiently identify, characterize and model spawning habitat for anadromous shads and subsequently evaluates

results and possible population-level effects of transporting American shad to historic spawning habitats blocked by dams that lack fish passage. This research was completed on the Roanoke River, North Carolina and Virginia, a river system with a series of dams, but suitable spawning habitat both above and below the lowest dam (Rulifson and Manooch 1990; Sparks 1998; Hightower and Sparks 2003; Read 2004; Walsh et al. 2005). This study also incorporates data from other studies of American shad in North Carolina (Burdick 2005; Smith 2006; Burgess et al. 2007; North Carolina Wildlife Resources Commission, unpublished data). Results from this research could be used to better survey, manage and restore alosine populations in North Carolina and elsewhere.

This dissertation includes four main chapters and a conclusion that synthesizes the results and identifies future research needs. For chapter 2, we evaluate the effectiveness and efficiency of plankton sampling, spawning pads, visual observations of spawning, and examination of female gonads by histology, to identify spawning sites river-wide and to evaluate spawning habitat selection for alosines. Results from this chapter could help guide future research efforts to identify both used and potential spawning habitats.

For chapter 3, we examined spawning habitat selection of hickory shad from data collected in the Roanoke, Tar and Neuse rivers in North Carolina. Habitat suitability models have been developed for American shad and river herring (Pardue 1983; Stier and Crance 1985), but not for hickory shad. We developed preliminary habitat suitability models for hickory shad using a more common format and a Bayesian belief network. Bayesian belief networks can incorporate both empirical data and expert opinion, can be updated, and can

help evaluate data gaps to guide future research needs (Marcot et al. 2006; Smith et al. 2007; Uusitalo 2007), suggesting their usefulness in habitat suitability and flow modeling studies in regulated rivers.

For chapter 4, we examined the movement patterns and spawning of sonic-tagged adult American shad transported upstream of dams on the Roanoke River. We used stationary receivers and manual tracking to examine movement patterns of fish released in new reservoir and riverine habitats and to address outmigration downstream past dams. We used plankton sampling to check for spawning activity in the upper basin rivers. We evaluated when adult American shad could be best transported with low mortality to habitats upstream of dams to aid in their restoration in regulated rivers.

For chapter 5, we developed a deterministic, density-dependent matrix model to evaluate possible population-level effects of transporting American shad on the Roanoke River to upstream habitats otherwise inaccessible because of dams. American shad transported upstream of dams have access to additional spawning habitat, but experience migration delays and mortality associated with downstream passage to return to the ocean. The balance between positive and negative impacts would determine the population-level effects of transport. We also evaluated the predicted population-level impacts of different levels of improved survival of young and adults. After appropriately altering some vital rates, this model could prove useful for evaluating restoration and management options for American shad in regulated river systems coast-wide.

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CHAPTER 2. EVALUATION OF METHODS FOR IDENTIFYING SPAWNING SITES AND HABITAT SELECTION FOR ALOSINES

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Abstract

Characterization of riverine spawning habitat is important for management and restoration of anadromous alosines. We examined the relative effectiveness of oblique plankton tows and spawning pads for collecting eggs of American shad *Alosa sapidissima*, hickory shad *A. mediocris* and river herring (alewife *A. pseudoharengus* and blueback herring *A. aestivalis*) in the Roanoke River, North Carolina. Relatively non-adhesive American shad eggs were only collected by plankton tows, whereas semi-adhesive hickory shad and river herring eggs were collected by both methods. Compared to spawning pads, oblique plankton tows had higher probabilities of collecting eggs and identified longer spawning periods. In assumed spawning areas, twice-weekly plankton sampling for 15 minutes throughout the spawning season had a ≥95% probability of collecting at least one egg for all alosines; however, probabilities were lower in areas with more limited spawning. Comparisons between plankton tows, spawning pads and two other methods to identify spawning habitat, direct observation of spawning and examination of female histology, suggested differences in effectiveness and efficiency. River-wide information on spawning

sites and timing for all alosines is most efficiently obtained by plankton sampling. Spawning pads and direct observations of spawning best characterize microhabitat selectivity for appropriate species, especially when spawning sites have previously been identified. Histological examination can help determine primary spawning sites, but is most useful when information on reproductive biology and spawning periodicity are also desired. Target species, riverine habitat conditions, and research goals should be considered when selecting methods to evaluate alosine spawning habitat.

Introduction

Anadromous alosines grow in productive marine waters and ascend coastal rivers at appropriate temperatures to spawn (Mansueti 1962; Leggett and Whitney 1972; Loesh 1987; Limburg et al. 2003). These species support valuable recreational and commercial fisheries throughout their native ranges and are ecologically important because they import marine-derived nutrients into freshwater systems (Smith 1894, Garman 1992; Garman and Macko 1998; Limburg et al. 2003). As a result of overfishing and anthropogenic changes to spawning habitat in rivers, many populations are at historically low levels and some are in critical need of conservation (Rulifson 1994; Hightower et al. 1996; Cooke and Leach 2003; Schmidt et al. 2003). Identifying and characterizing riverine spawning habitat may be critical to restore depleted alosine stocks.

A variety of methods are used to identify and characterize alosine spawning in rivers. Alosines are broadcast spawners and most information on spawning has been obtained by collecting eggs and larvae using various types of plankton nets (Massman 1952; Marcy 1972;

Bilkovic et al. 2002; Overton and Rulifson 2007). Spawning habitat selection and timing can also be determined by direct observation of spawning behaviors (Leim 1924; Layzer 1974; Ross et al. 1993; Beasley and Hightower 2000), as long as spawning events are identifiable and differentiable to species and observations can be made when spawning occurs. Examination of gonads by histology can be used to identify spawning locations and timing since gravid and recently spawned fish are often still on spawning grounds (Brewer et al. 2006). Histological examination of gonads has been used to differentiate female American shad *Alosa sapidissima* and hickory shad *A. mediocris* into maturity classes (Olney et al. 2001; Olney and McBride 2003; Hyle 2004; Harris et al. 2007), and to describe spawning periodicity (Hyle 2004).

Four alosines are native to rivers on the Atlantic coast of North America: American shad, hickory shad, blueback herring *A. aestivalis*, and alewife *A. psuedoharengus*. American shad spawn large (2.5 – 4 mm) relatively non-adhesive eggs in mainstem areas primarily between dusk and midnight (Leim 1924; Layzer 1974; Jones et al. 1978; Sparks 1998). Hickory shad eggs are smaller (0.98-1.65 mm), somewhat adhesive, and semi-demersal, but can be buoyant in flowing water (Mansueti 1962). Little is known about spawning habitat of hickory shad, but they appear to use both tributaries and mainstem areas (Sparks 1998; Burdick and Hightower 2006). Blueback herring and alewife eggs are difficult to distinguish and are often grouped as river herring eggs (Sparks 1998; Walsh et al. 2005). River herring eggs are between 0.80 and 1.11 mm in diameter, initially somewhat adhesive, and have been described as demersal, semi-demersal or pelagic (Jones et al. 1978). In river

systems, alewife may prefer to spawn in lentic habitats, whereas blueback herring spawn in both lentic and lotic environments (Loesh and Lund 1977; Loesh 1987; Walsh et al. 2005).

The main purpose of this study was to compare the effectiveness of oblique plankton tows and spawning pads for characterizing alosine spawning habitat and timing. Plankton tows are commonly used to study spawning by alosines. In contrast, spawning pads have previously been used in rivers to collect eggs of Gulf sturgeon *Acipenser oxyrinchus desotoi* (Marchant and Shutters 1996; Sulak and Cluston 1998; Fox et al. 2000), white sturgeon *A. transmontanus* (Paragamian et al. 2001; Perrin et al. 2003), shortnose sturgeon *A. brevirostrum* (Duncan et al. 2004), paddlefish *Polyodon spathula* (Firehammer et al. 2006) and walleye *Sander vitreus* (Manny et al. 2007), but not alosines. Using information from our field study and published literature, we compared the effectiveness of plankton tows, spawning pads, direct observations of spawning, and examination of female histology, for identifying spawning habitat and timing for each alosine. Comparisons were made in terms of cost, flexibility of use in different habitat types, time commitment in the field, and specific information obtained.

Methods

Plankton tow and spawning pad sampling was conducted at three locations (bypass, Roanoke Rapids, and Weldon) on the Roanoke River, North Carolina (Figure 1). All sites were below the most downstream dam (Roanoke Rapids Dam) located at river kilometer (rkm) 221. The bypass is the original river channel located adjacent to the tailrace of the Roanoke Rapids Dam and was sampled as part of a study examining use of this re-watered

habitat for spawning by anadromous fishes. The bypass is braided, shallow and characterized mainly by the presence of riffle and pool habitats. Sampling also occurred in the main channel just below the Dam's tailrace at Roanoke Rapids (rkm 218) and slightly farther downstream at Weldon (rkm 209; Figure 1). In the Roanoke River, Roanoke Rapids is the predominant spawning area for American shad (Hightower and Sparks 2003) and Weldon is considered the main spawning area for hickory shad (Marshall 1977; Sparks 1998). River herring eggs have been collected at Roanoke Rapids, Weldon, and further downstream (Sparks 1998; Walsh et al. 2005). In 2005, plankton tows and spawning pads were sampled in the bypass every three days from early March to late May. In 2006, sampling was completed once per week from early March to late May in the bypass and at Weldon and from early March to late July at Roanoke Rapids. In 2007, sampling was completed at Roanoke Rapids and Weldon approximately once per week from March to early July.

On each date, one fifteen-minute oblique plankton tow was completed from a stationary position using a bongo frame with two 0.3-m diameter plankton nets with 6:1 tail to mouth ratios and 500-um mesh. A standard General Oceanics Environmental flow meter was deployed next to the net to estimate the volume of water filtered. At Roanoke Rapids, tows were completed just after dark because American shad spawn there between dusk and midnight (Sparks 1998) and the site is just below the Roanoke Rapids Dam, so eggs cannot come from far upstream. Tows at Weldon and in the bypass were completed during the day

because hickory shad and river herring eggs were found to be successfully collected during the day in the bypass during 2005.

Polyester floor buffing pads similar to those first used by Marchant and Shutters (1996) to collect Gulf sturgeon eggs, were used as spawning pads. Spawning pads were red in color, 0.5 m in diameter and weighted to lie flat on the river bottom. The area sampled by an individual spawning pad was 0.196 m^2. Spawning pads were specifically placed to sample the variety of depths, velocities and sediment types present in the general location. The number of spawning pads examined could not be held constant over a season because some were destroyed, removed from the water, or washed out of the area by high flows. Only sampling events when five or more spawning pads were retrieved and examined for eggs from a given site were used for analyses.

All eggs collected were immediately fixed in 5-10% buffered formalin in the field and later counted, identified and staged for approximate age using guides (Mansueti 1962; Jones et al. 1978; Burdick 2005). Eggs dead prior to fixation cannot be staged and in many cases cannot be confidently identified so are often removed from samples. For this study, the number of dead eggs found in a sample with American shad, hickory shad, or river herring eggs alive at the time of fixation (termed "live eggs"), was tabulated if dead eggs had appropriate characteristics. The number of dead eggs was recorded to evaluate the percentage of unusable eggs collected by a particular method. Except for examination of the percentage of dead eggs as compared to live, all dead eggs were removed from analyses.

While completing plankton tows and examining spawning pads, the sampling location was scanned for visual evidence of spawning. Spawning behavior has been described for American shad and blueback herring (Walburg and Nichols 1967; Layzer 1974; Loesh and Lund 1977). American shad spawning behavior is described as multiple fish at the water's surface quivering and producing visible splashes (Walburg and Nichols 1967; Layzer 1974). Similarly, blueback herring spawning has been described as multiple fish swimming in a circular pattern near the surface before diving down to spawn (Loesh and Lund 1977). Sometimes, in shallow water, blueback herring can be observed darting back and forth while spawning (Loesh and Lund 1977). Spawning behaviors of hickory shad and alewife have not been described. The collection of young eggs (≤1 hour in age) might suggest that spawning occurred during the sampling period and could have been observed.

The effectiveness of each gear was examined in terms of its ability to identify spawning sites, describe the spawning period, and collect eggs that could be properly identified and staged. To evaluate differences in the apparent length of the spawning season for each species as estimated by plankton tows and spawning pads, the number of days from collection of the first egg to collection of the last egg, was calculated for each year (termed "spawning period"). The spawning period calculated by method (plankton tow or spawning pad) was compared using a paired t-test with years treated as replicates (N = 3 years). In addition, we estimated probabilities of collecting at least one egg during a season by plankton tows and spawning pads, given different amounts of sampling effort. Probabilities were based on a binomial model (Ott and Longnecker 2001) and sampling from 1 to 10 times

weekly within the average estimated spawning period for each alosine. If data from plankton tows and spawning pads produced different estimates of the spawning period, the longest average estimate was used. The probability of collecting at least one egg with either method was examined by sampling location and was set equal to the percentage of positive samples from that location during the estimated spawning periods.

The probability of collecting at least one egg from a site depends not only on the efficiency of the gear and sampling effort, but also on the species' population size and spawning periodicity, proximity of the sampler to the spawning location, river current and morphology, and other physical and environmental factors. Our samples were from presumed spawning sites, but many studies focus on locating and characterizing spawning sites throughout a river (Marcy 1972; Bilkovic et al. 2002; Smith 2006). To address efficiency under those objectives, we examined the probability of collecting American shad and hickory shad eggs from multiple sites over a large portion of a river, using published data from studies on the Neuse (Burdick 2005) and Tar (Smith 2006) rivers, both in North Carolina (Figure 1). Both studies employed the same plankton sampler as used in this study and both sampled each of their sites at least once per week for two complete spawning seasons (Burdick 2005; Smith 2006). Similar to this study, Burdick (2005) completed 15-min oblique tows, whereas Smith (2006) completed 6-min tows, with two minutes on the bottom, two in the mid water column, and two near the surface, unless water levels were very low and then 4-min tows were completed. Methods to estimate spawning periods and the probabilities of collecting at least one egg were similar to those used for our field data.

Spawning pads are suggested for use to examine spawning microhabitat selection since adhesive eggs of some species have presumably been collected in close proximity to the location where spawning occurred (Marchant and Shutters 1996; Sulak and Clugston 1998; Firehammer et al. 2006). To evaluate whether eggs were collected non-randomly with respect to spawning pads, catch per spawning pad during the spawning period at sites where eggs were collected was compared to a Poisson distribution using a Pearson's Chi-Square Goodness-of-Fit-Test. Spawning pads at sites where no eggs were collected during the season or that were sampled outside the detected spawning period were omitted from these analyses. Fits with similar values for variance and mean suggest a random distribution, whereas significantly higher values for variance compared to mean suggest a clumped distribution and significantly lower values for variance compared to mean suggest a uniform distribution (Zar 1999). All tests were considered significant at the $\alpha = 0.05$ level.

To compare plankton tows, spawning pads, direct observation of spawning and examination of female histology, we used a ranking system similar to that used by Diana et al. (2006) to evaluate sampling methods for round gobies. Data from this study and from published literature were used to evaluate each method. Diana et al. (2006) used qualitative ranks from 1 to 3 to evaluate each gear in terms of flexibility of use in different habitats, cost, and time required to sample, among other parameters. Ability to collect data on spawning location, timing, and microhabitat characteristics was included in this analysis. The method with the lowest sum (termed "score") for all categories was considered the most efficient

method for sampling spawning habitat, in that it would help obtain the most information at the lowest cost.

Results

Plankton tows collected eggs of all alosines at their predominant spawning sites, whereas spawning pads only collected hickory shad and river herring eggs (Table 2.1; Figure 2.1). American shad eggs were collected by plankton tows mainly from Roanoke Rapids, to a lesser extent from Weldon, and not at all from the bypass, although the diel time period of collection may have factored into the lack of catch in the bypass. Hickory shad eggs were collected most frequently at Weldon by both plankton tows and spawning pads, but were also collected in the bypass by both methods. Only one hickory shad egg was collected from Roanoke Rapids by plankton sampling. River herring eggs were mainly collected from the bypass and Weldon using both plankton tows and spawning pads, but were also collected in low densities at Roanoke Rapids by plankton tows (Table 2.1). Additionally, one river herring egg was collected at Roanoke Rapids on a spawning pad; however, this date was removed from analysis because of the small number of spawning pads examined (N = 3). Both plankton tows and spawning pads identified main spawning sites for hickory shad and river herring; however, plankton tows collected eggs from a greater proportion of samples and collected some eggs from sites where only a small amount of spawning presumably occurred.

Compared to spawning pads, plankton tows identified longer spawning periods in all years, suggesting that they may better document complete spawning runs. Hickory shad eggs

were collected from mid-March to mid-April with an average spawning period of 27.7 days (standard error (SE) = 4.3 days) using data from plankton tows and 18.0 days (SE = 7.8 days) using data from spawning pads. River herring spawned from mid-April to mid-May; their average spawning period was 26.0 days (SE = 8.4 days) using data from plankton tows and 14.5 days (SE = 8.6 days) using data from spawning pads. The spawning period was significantly longer using plankton tows, as compared to spawning pads, for river herring (df = 2, t = 5.71, $p = 0.029$) but not for hickory shad (df = 2, t = 2.36, $p = 0.142$). Annually, the range and peak egg collections were similarly characterized using both methods (Figure 2.2). We were not able to compare gears for identifying the American shad spawning period, since no eggs were collected using spawning pads. American shad spawned from early May to late June or early July, with an average spawning period of 54.5 days (SE = 6.5; Figure 2.2).

The probability of collecting at least one egg from a site by weekly sampling was greater using plankton tows compared to spawning pads (Figure 2.3). With the exception of hickory shad at Roanoke Rapids, the probability of collecting at least one egg of any alosine from any site was at least 0.95 if twice weekly plankton tow sampling was completed. Spawning pads did not collect eggs successfully when densities were low and generally required a greater number of samples to achieve a probability of collection above 0.95 (Figure 2.3). As an example, at Weldon, 19 spawning pads would need to be sampled weekly to identify river herring spawning with a probability of 0.95, as compared to just one plankton tow sample weekly. For alosines with eggs effectively collected by spawning pads,

considerably more field effort would be required to achieve a similar probability of detecting spawning using spawning pads compared to plankton tows.

The probability of collecting American shad and hickory shad eggs by plankton tows from randomly chosen sites in the Neuse and Tar river systems was river and site dependent (Figures 2.4 and 2.5). In the Neuse River (data from Burdick 2005), the estimated spawning period averaged 83.5 days (SE = 12.5) for American shad and 61.5 days (SE = 10.5) for hickory shad. In the Tar River (data from Smith 2006), the average spawning period was estimated at 76 days (SE = 12.0) for American shad and 64 days (SE = 4.0) for hickory shad. Plankton sampling had a higher probability of collecting at least one egg of either species for a given number of tows from more sites in the Neuse River than the Tar River (Figures 2.4 and 2.5). This trend may be due to differences in the alosine population sizes, the distribution of spawning river-wide, or simply the length of the plankton tows—Burdick (2005) sampled for 15 minutes and Smith (2006) sampled for six minutes. Similar to our field results in the Roanoke River, the probability of collecting eggs from areas of concentrated spawning was near or above 0.95 with twice weekly sampling during the spawning period for both systems. Sites with low densities of eggs or those where eggs were collected only during one year had lower probabilities and would likely require more intensive sampling to guarantee collection of at least one egg. Sites where no eggs were collected in either year received a probability of zero under any level of sampling effort (Figure 2.5).

Most collected eggs were identifiable to stage and were young, indicating that sampling occurred within the temporal and spatial limits of spawning. Most eggs were less than 1-h in age, including all American shad eggs from Roanoke Rapids, 84% of hickory shad eggs from Weldon and the bypass and 78% of river herring eggs from Weldon and the bypass. Similar age distributions were observed for hickory shad eggs collected by plankton tows and spawning pads, whereas a higher proportion of river herring eggs collected on spawning pads in the bypass were older than those collected by plankton tows in the same location (Figure 2.6). Hickory shad spawning was visually observed once in the bypass and once at Weldon, both instances during the afternoon in water less than 1 m in depth. Spawning behavior was similar to that of American shad, where fish moved rapidly and their fins could be seen near or above the water's surface. American shad spawning was observed on most evenings when their eggs were collected at Roanoke Rapids. River herring spawning was not observed on any occasion. The percentage of eggs that were dead and unidentifiable to stage appeared to vary by species and gear. A higher percentage of hickory shad and river herring eggs were dead compared to American shad eggs (Table 2.1). For both hickory shad and river herring, more dead eggs were collected by spawning pads than by plankton tows (Table 2.1).

Most spawning pads sampled during the spawning period contained no eggs (hickory shad = 81%, river herring = 93%). The number of eggs collected per spawning pad for hickory shad ranged from 0 to 2,458 and for river herring ranged from 0 to 150. The distributions of both hickory shad and river herring eggs on spawning pads were significantly

different from Poisson and both had higher variances than means (mean = 33, variance = 51984, $p < 0.001$ and mean = 2, variance = 144, $p < 0.001$, respectively) suggesting clumped distributions of eggs on spawning pads.

The most efficient method for collecting information on spawning habitat and timing differed by species. The most effective and efficient method for American shad was direct observation of spawning (Table 2.2). Plankton tows received a lower ranking than direct observation of spawning since they collect less information on diel timing and microhabitat selection for spawning, although they are less time consuming and easier to complete in the field. Examination of female histology was generally less efficient and spawning pads were completely ineffective. For hickory shad, spawning was most efficiently characterized by spawning pads (Table 2.2). Plankton tows only received a slightly lower ranking, since they collect less information on microhabitat selection, but are quicker to complete and detect spawning earlier and later in the season. Direct observation of spawning and examination of histology received the lowest rankings, because spawning was not often observed and enough gravid females may be hard to collect. Plankton tows were the most efficient method for collecting information on river herring spawning, but histology of females and spawning pads were only slightly less efficient (Table 2.2). River herring eggs were not as effectively collected by spawning pads as were hickory shad eggs, but spawning pads were the only method to collect information on spawning microhabitat. Histology has a distinct advantage over the other methods for river herring, since adult

blueback herring and alewife can be differentiated to species. Spawning by river herring was not observed.

Discussion

Our results indicate that oblique plankton sampling is highly effective for collecting eggs of all alosines, whereas spawning pads appear only successful for adhesive eggs. Twice-weekly plankton sampling using oblique plankton tows had a probability ≥95% of collecting eggs of all alosines at concentrated spawning sites and also often collected eggs in areas with only limited spawning. Spawning pads have a considerably lower probability of collecting eggs at a given level of effort than do plankton tows and thus, their use may result in the identification of fewer spawning sites river-wide and estimation of shorter seasonal spawning periods. Spawning pads did identify main spawning sites for hickory shad and river herring and, similar to Gulf and shortnose sturgeon eggs (Marchant and Shutters 1996; Duncan et al. 2004), collected eggs in clumped distributions, supporting their use to evaluate microhabitat selection for alosines and other river-spawning fishes with adhesive eggs, especially those that spawn near the bottom or have negatively buoyant eggs.

Plankton sampling would be a preferred method for collecting information on spawning site selection and the seasonal spawning period, especially if little about a particular population is known or if information about multiple alosines is desired. Plankton sampling is logistically simple and generally requires a short period of time at each field site (<30 minutes for a 15 minute tow), allowing a modest crew to collect information over a large portion of a river during a given season (Weisburg and Burton 1993; Bilkovic et al.

2002; Burdick and Hightower 2006; Smith 2006). River-wide sampling helps locate areas of concentrated spawning in a system, especially when sites with high concentrations of eggs can be identified. Plankton tows have not only been used to locate spawning sites, but also to identify spawning in newly accessible areas previously blocked by a dam (Burdick and Hightower 2006) or areas of poor water quality (Weisburg and Burton 1993). Plankton nets collect eggs even when densities are low and thus might be the most effective method in systems with small or depressed populations. In such cases, increased sampling intensity may be required. Catch of American shad eggs can vary by diel period (Layzer 1974; Burdick 2005) and net location in the water column (Massman 1952), thus these logistics should be considered before starting a project. Although often useful, some plankton nets and protocols may not be feasible in systems with high or changing water velocities or high concentrations of debris or algae, since drag from water pressure and material could clog nets (Overton and Rulifson 2007), and reduce egg collection. Also, plankton tows collect eggs that may have floated down from an undetermined spawning site upstream (Marcy 1972; Layzer 1974). This disadvantage can be partially offset by staging eggs to estimate their approximate age, so that inferences can be made about the distance to upstream spawning locations (Burdick and Hightower 2006). However, eggs float for an indeterminate amount of time in the water column and developmental rates vary by individual and with temperature (Mansueti 1962; Jones et al. 1978), making age assignments only approximate and possibly leading to imprecise estimates of specific spawning sites, especially if few young eggs are collected. In the present study, most eggs were young (≤1 hour in age), suggesting that they

were spawned nearby; however some eggs were older and suggest additional spawning upstream. Sites where only a few eggs were collected, such as Roanoke Rapids for hickory shad and Weldon for American shad, may represent areas that eggs have floated into, rather than selected spawning sites. In contrast, areas where large numbers of young eggs are collected likely represent main spawning sites. Plankton sampling is an excellent method to identify spawning areas and the annual spawning period, however, they often do not provide good information about spawning microhabitat.

In contrast, direct observations of spawning and collection of eggs by spawning pads are highly effective methods for studying microhabitats selected for spawning. Fine-scale information on spawning habitat requirements is important for, and often lacking from, flow modeling studies in regulated rivers (e.g., instream flow incremental method, Bovee 1982). Direct observations are optimal when spawning fish can be identified to species and when detectability is high and constant across time and habitat types, since there is no uncertainty about when and where spawning occurred. Additionally, when spawning is visible, no added equipment or laboratory processing is required, leading to comparatively lower costs. Spawning splashes have been used in multiple studies to identify spawning microhabitat and the diel spawning period for American shad (Leim 1924; Layzer 1974; Ross et al. 1993; Beasely and Hightower 2000), since American shad spawning behavior appears both highly visible in a variety of habitats and generally correlated with the collection of young eggs (Layzer 1974; Ross et al. 1993). A critical question, however, is whether some spawning occurs below the surface that is undetected visually. Layzer (1974)

reported the collection of eggs at one location where spawning splashes were not observed and suggested that spawning splashes may not be as evident at sites with deep water. Visual observations of spawning by hickory shad were rare and by river herring were non-existent at our sampling locations in the main channel of the Roanoke River, North Carolina, suggesting that direct observation may not be a viable option for these species in large, turbid systems where spawning is likely to be often missed. Tiffan et al. (2005) used a combination of visual observation and footage from underwater cameras during the day when spawning could be detected, and dual-frequency identification sonar (DIDSON) during the night, when spawning was not visible, to identify spawning behavior of chum salmon *Oncorhynchus keta*. For systems with adequate water clarity, underwater cameras and snorkeling could be used to validate species identifications from visual observations. For deep or turbid waters, the combination of traditional sampling gears and more recent acoustic techniques, could be effective for describing spawning behavior.

Spawning pads are an effective sampling gear for alosines with adhesive eggs. Sampling multiple spawning pads, as done in this study, would be needed to equal the effectiveness of one plankton tow sample, which would require a greater time commitment per site in the field. Examining and removing eggs from one spawning pad can take a variable amount of time depending on the number of eggs and the type and amount of sediment also deposited on the spawning pad, but was often more than the amount of time required to complete a 15-min plankton tow in the field. Another disadvantage of spawning pads is that they must be left in the river, sometimes for multiple days, and thus can be

disturbed by people, washed out by high flows and covered by fine sediments. Firehammer et al. (2006) found spawning pads difficult to use for collecting paddlefish eggs in the Yellowstone River because the samplers were constantly being covered or buried by sediment. In response, they created spawning tubes, which were made with similar material but held the sampler in the water column, so it would not become covered by shifting sediments (Firehammer et al. 2006). In this present study, spawning pads were never buried, but were sometimes coated with sand, which may have reduced their ability to sample eggs. However, despite being sometimes mixed in with sand, hickory shad and river herring eggs were still sampled by spawning pads. It is possible that sedimentation may have resulted in the higher percentage of dead eggs from spawning pads, as compared to plankton tows. Kock et al. (2006) found that when covered by silt, adhesive white sturgeon eggs had reduced survival and growth in the laboratory. Also, numerous spawning pads were lost downstream or were unable to be sampled during periods of high flows, thus reducing sample size. Spawning pads generally sampled young eggs, suggesting that they may most effectively collect eggs during the initial stages when eggs are most adhesive (Mansueti 1962; Jones et al. 1978). Thus, similar to plankton tows, if eggs are not spawned constantly during the day, the diel time period when spawning pads are examined may affect the number of eggs collected. The best use of spawning pads and direct observation of spawning may be for fine-scale studies of spawning habitat use when general information on spawning sites and periods has been obtained for the system.

To evaluate spawning habitat selection, a sampling method must either be similarly effective under different conditions or an understanding of its effectiveness in different habitat types is required. It can be difficult to determine the effectiveness of a sampling method under different field conditions, since differences in the intensity of use in habitats could be confounded with differences in gear effectiveness. Relative effectiveness can be determined through side-by-side sampling using multiple methods. For example, Duncan et al. (2004) attached plankton nets to spawning pads to collect shortnose sturgeon eggs, Layzer (1974) observed spawning splashes and set plankton nets to detect American shad spawning, and Aunins and Olney (2009) used both bongo and set plankton nets to collect American shad eggs. In general, oblique plankton tows work well in areas with adequate depth and directional flow, whereas pushnets may be more useful in lower flow areas when eggs are buoyant, and bottom set nets could work well in shallow rocky areas or those with low or tidally-influenced flow when eggs would be expected to settle out near the bottom (Williams et al. 1975; Hightower and Sparks 2003; Burdick and Hightower 2006; Walsh et al. 2005; Aunins and Olney 2009). Spawning splashes may be most visible in shallow areas with high water clarity (Layzer 1974) and spawning pads may be most effective in areas with low sediment deposition (Firehammer et al. 2006). Further research to quantify the effectiveness of sampling methods under different environmental conditions would be helpful for selecting a single sampling method or a combination of methods in future studies.

The method least affected by differences in habitat or environmental conditions may be the examination of female gonads by histology. Histology has been suggested to evaluate

spawning sites and habitats for fishes in large river systems, where spawning cannot be observed visually (Brewer et al. 2006). Full characterization of maturity classes by histology for North American alosines has only been completed for American shad (Olney et al. 2001). American shad are batch spawners (Olney et al. 2001; Olney and McBride 2003) and the proximity of a female to releasing a batch of eggs can be determined by examination of the gonads (Olney et al. 2001; Hyle 2004). Histology can be used to determine both spawning frequency and the diel time frame when spawning occurs (Hyle 2004) and has the distinct advantage of using adult spawners that can easily be differentiated to species and collected by a combination of field methods (Olney and McBride 2003). Therefore, adult spawners can be collected from a variety of habitats while completing other forms of sampling during the spawning period. Additional information about the spawning cycle and fecundity can also be determined by examination of gonads by histology (Olney et al. 2001; Hyle 2004). These studies have not been done for most alosines but would contribute greatly to the understanding of their biology. Histological preparation may be more costly than other methods and could require a large sample of adult spawners to precisely evaluate proximity of spawning sites and diel spawning periods. The sacrifice of numerous individuals could be problematic for depressed or listed populations or species, such as Alabama shad *A. alabamae* (Jelks et al. 2008). In general, examination of histology is not likely to be the most efficient method for collecting information about spawning site selection or timing, unless it otherwise fits into a sampling protocol and additional information on reproductive biology is desired.

Seasonal spawning periods for alosines on the Atlantic coast are thought to be dependent on river water temperature (Leggett and Whitney 1972; Loesh 1987; Harris et al. 2007). Spawning periods estimated for American shad and hickory shad from plankton tow data collected river-wide in the Neuse (Burdick 2005) and Tar (Smith 2006) rivers, were longer than those estimated using our plankton tow data from specific spawning sites collected over a small range of the Roanoke River (rkm 209 to rkm 221). Spawning in the Roanoke River may occur over a shorter seasonal period; however, Walsh et al. (2005) used age data from larval blueback herring and alewife collected in the Roanoke River and estimated much longer spawning periods for those species than identified in this study, which suggests that our sampling from only a few specific spawning sites may have led to shorter estimated spawning periods than what actually occurred river-wide. Longer spawning periods estimated from river-wide studies suggests that spawning may occur at slightly different seasonal periods at different sites within a river system, maybe as a result of differences in water temperature or other environmental factors. A river-wide sampling design may not only help locate sites of concentrated spawning, but also better identify the complete seasonal spawning periods, compared to only sampling in some areas.

Selection of an appropriate design for field studies depends not only on the research objectives and species of concern, but also on time commitment and financial expense. Each of the evaluated methods (collection of eggs by plankton tows or spawning pads, direct observation of spawning, and examination of female histology) would be relatively inexpensive and would require only a modest crew size of two people, but could be time

consuming, with specific costs and time requirements varying with respect to research objectives and study system. Each method may require the use of a boat to obtain samples and all but direct observations of spawning would require a dissecting microscope and considerable time spent in the laboratory, either sorting and examining eggs or preparing and reading histology slides. Regardless, differences in direct costs are unlikely to be prohibitive; thus selection of a method should be guided more by the overall research objectives of the program, the availability of field and laboratory technicians, and the specific species and research questions to be addressed.

In summary, methods and sampling protocols selected to evaluate spawning timing and habitat selectivity depend on the species in question and the overall research objectives of the program and specific study. When little is known about the species' biology or a system-wide understanding of spawning is required, plankton tows would likely be a good first step. To obtain more specific information on microhabitat use and reproduction, alternative methods such as spawning pads, direct observation of spawning, and examination of female histology could be more appropriate. Identification of spawning sites and characterization of specific spawning habitat requirements for alosines is warranted to better manage populations and understand the effects of anthropogenic changes to river systems.

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Tables

Table 2.1.—Proportion of samples with eggs and estimated egg densities, by species group and sampling site, for plankton tows and spawning pads. Density estimates were calculated as eggs/m^3 for plankton tows and eggs/m^2 for spawning pads. Also included is the proportion of live, identifiable eggs collected by each method.

Factor	American shad		Hickory shad		River herring	
	Plankton tows	Spawning pads	Plankton tows	Spawning pads	Plankton tows	Spawning pads
Proportion in bypass	0.00	0.00	0.45	0.08	0.83	0.09
Density in bypass	0.00	0.00	7.49	62.91	3.12	9.13
Proportion at Roanoke Rapids	0.94	0.00	0.13	0.00	0.33	0.00
Density at Roanoke Rapids	0.47	0.00	<0.01	0.00	0.01	0.00
Proportion at Weldon	0.30	0.00	1.00	0.31	1.00	0.04
Density at Weldon	<0.01	0.00	1.09	287.76	0.17	0.26
Proportion with live eggs	0.86		0.78	0.66	0.78	0.58

Table 2.2.—Rating of methods to sample spawning habitat for American shad, hickory shad, and river herring based on eight factors (1 = excellent, 2 = fair, and 3 = poor). A = American shad, H = hickory shad, R = river herring. NE means that the method did not appear to be effective for identifying spawning in a large river.

Factor	Plankton tows			Spawning pads			Observation of spawning			Female histology		
	A	H	R	A	H	R	A	H	R	A	H	R
Ease of use	1	1	1	NE	1	1	2	2	NE	1	1	1
Equipment cost	2	2	2	NE	2	2	1	1	NE	2	2	2
Field time commitment	1	1	1	NE	2	2	2	3	NE	2	2	2
Usability in different habitats	2	2	2	NE	1	1	2	2	NE	1	1	1
Spawning site selection	1	1	1	NE	1	2	1	1	NE	1	1	1
Spawning microhabitat	3	3	3	NE	1	2	1	1	NE	3	3	3
Seasonal timing of spawning	1	1	1	NE	2	3	1	3	NE	2	3	2
Diel timing of spawning	2	2	2	NE	2	2	1	3	NE	3	3	3
Method score	13	13	13	NE	12	15	11	16	NE	15	16	15

Figures

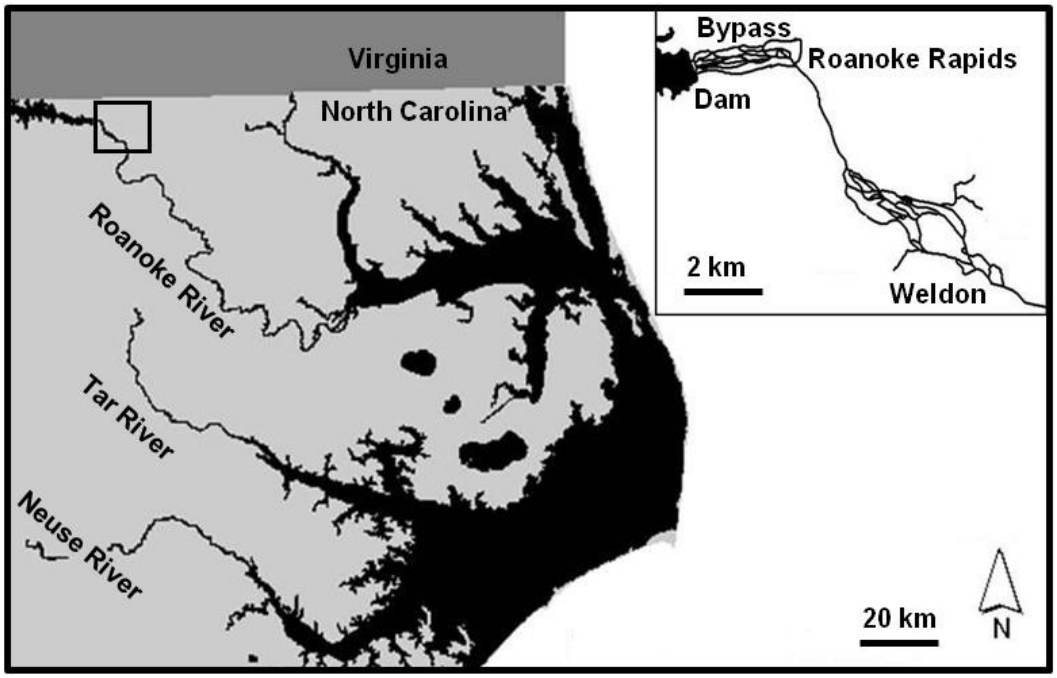


Figure 2.1.—Map of the Roanoke, Tar and Neuse rivers in North Carolina. Inset (location shown by the open rectangle on the larger map) illustrates locations of the sampling sites on the Roanoke River and the Roanoke Rapids Dam.

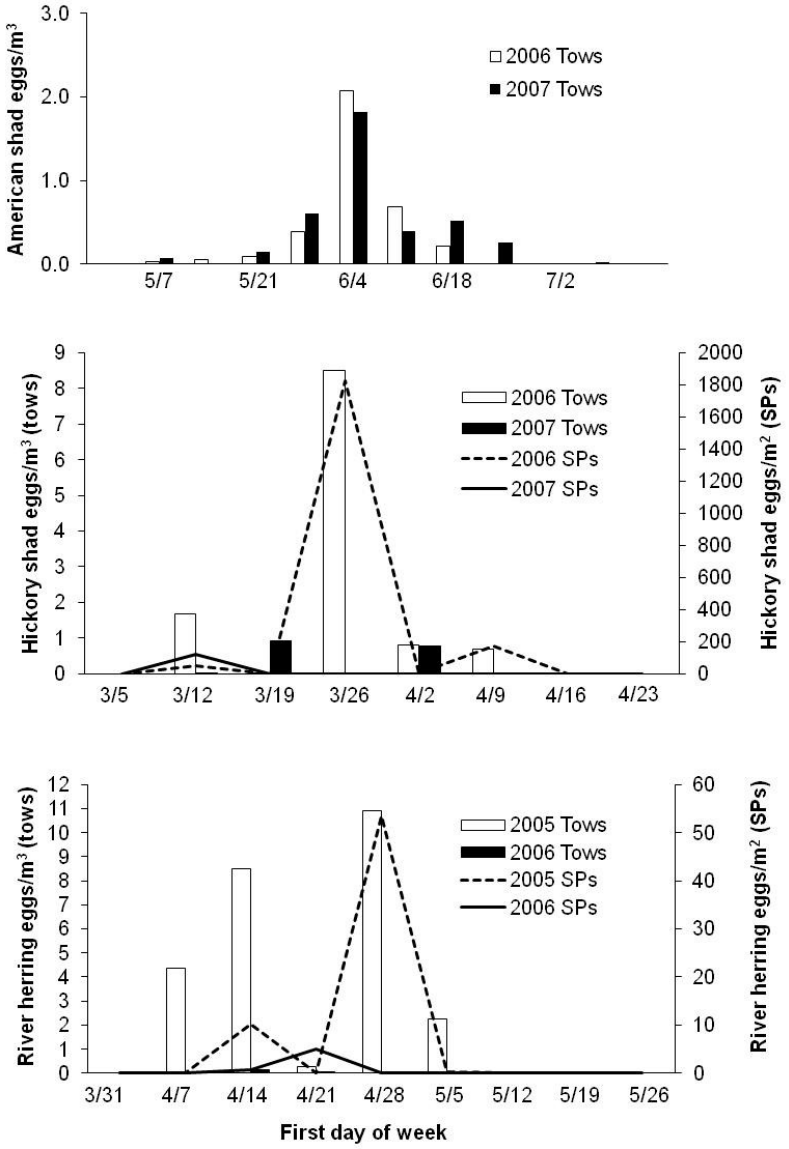


Figure 2.2.— Egg density, by weekly sampling period, for American shad (from Roanoke Rapids), hickory shad (from Weldon) and river herring (from the bypass), collected by 15-minute plankton tows and spawning pads from spawning areas in 2005-2007. The specific years shown were those when sampling was completed at the spawning location (i.e. sampling was completed at Roanoke Rapids and Weldon in 2006 and 2007, but in the bypass in 2005 and 2006). The date shown is the first date of the week when samples were collected. Tows = plankton tows and SPs = spawning pads.

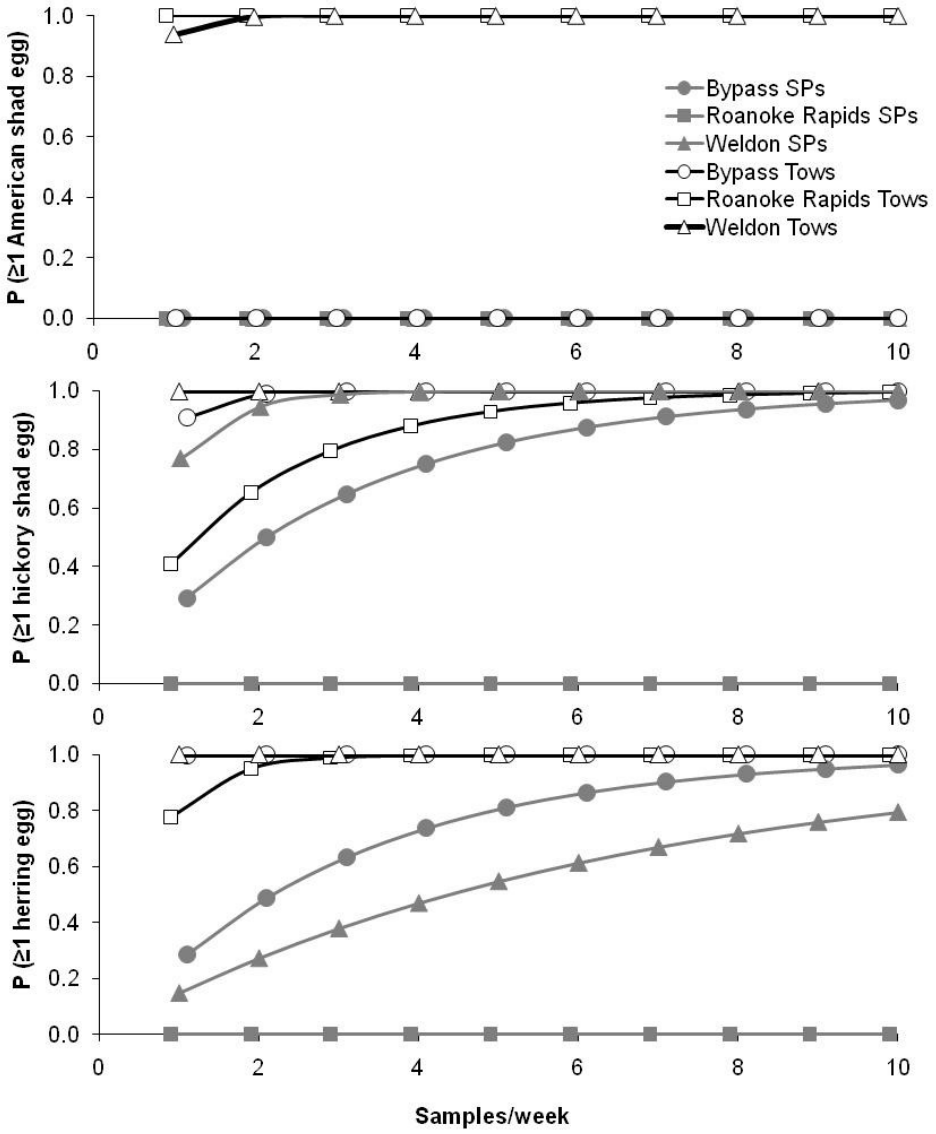


Figure 2.3.— Probability of collecting at least one egg during the spawning season of American shad, hickory shad, and river herring using 15-minute oblique plankton tows and spawning pads under different amounts of weekly sampling effort. One sample/week is either one plankton tow or one spawning pad sampled each week. Probabilities were based on a binomial model and p was estimated as the proportion of samples that contained at least one egg in the sampling area (bypass, Roanoke Rapids or Weldon). Tows = plankton tows and SPs = spawning pads. A probability line on the x-axis illustrates that no eggs were collected by the method in the indicated sampling area.

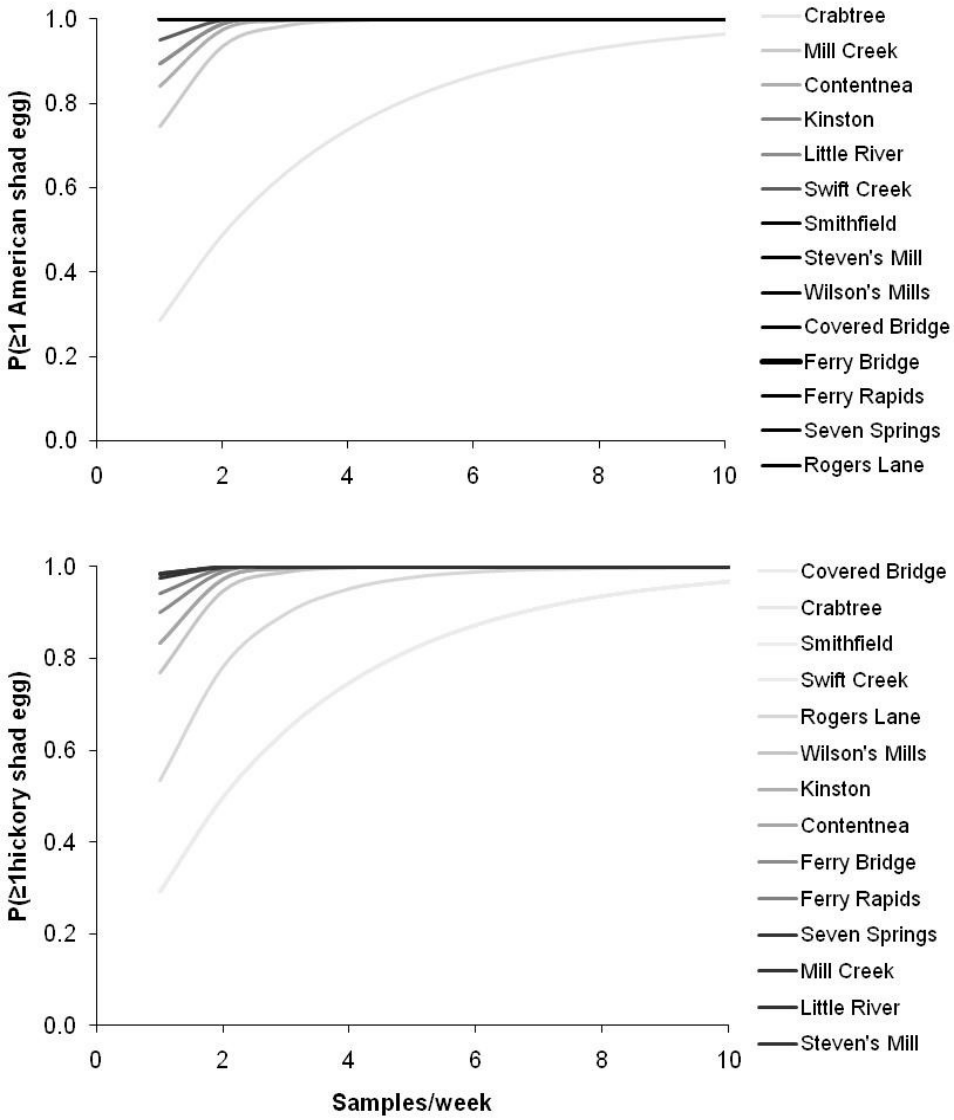


Figure 2.4.— Probability of collecting at least one egg during the spawning season of American shad and hickory shad using 15-minute oblique plankton tows from sites in the Neuse River, North Carolina (data from Burdick 2005), under different amounts of weekly sampling effort. One sample/week indicates one plankton sample completed each week. Sites are ordered in the legend from lowest to highest probability of collecting at least one egg with a given amount of effort (top to bottom). For information on the specific named sites, see Burdick (2005). Probabilities were based on a binomial model and p was estimated by the proportion of samples that contained at least one egg in the sampling area.

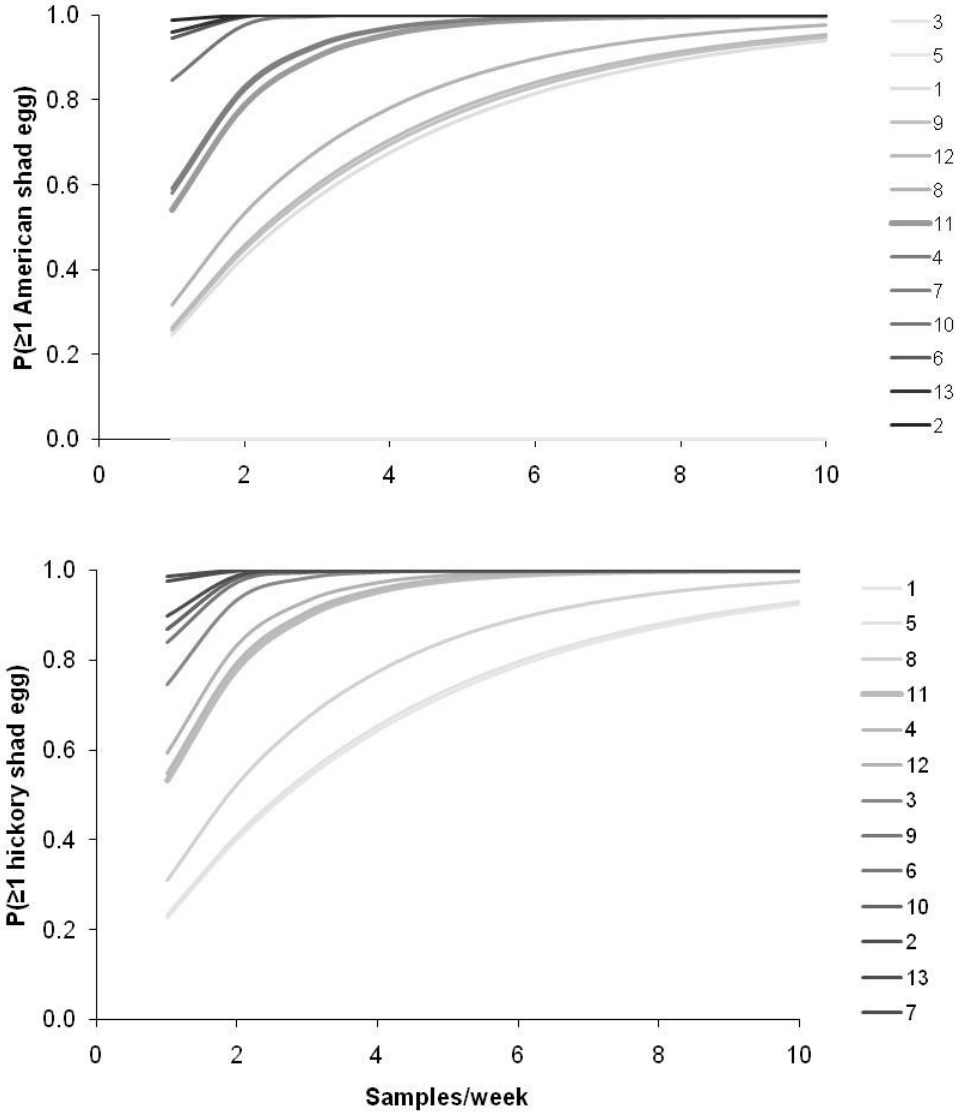


Figure 2.5.— Probability of collecting at least one egg during the spawning season of American shad and hickory shad using 6-minute plankton tows from sites in the Tar River, North Carolina (data from Smith 2006), under different amounts of weekly sampling effort. One sample/week indicates one plankton sample completed each week. Sites are ordered in the legend from lowest to highest probability of collecting at least one egg with a given amount of effort (top to bottom). For information on the specific numbered sites, see Smith (2006). Probabilities were based on a binomial model and p was estimated by the proportion of samples that contained at least one egg in the sampling area. No American shad eggs were collected at sites 3 and 5; thus probability lines for those two sites are on the x-axis.

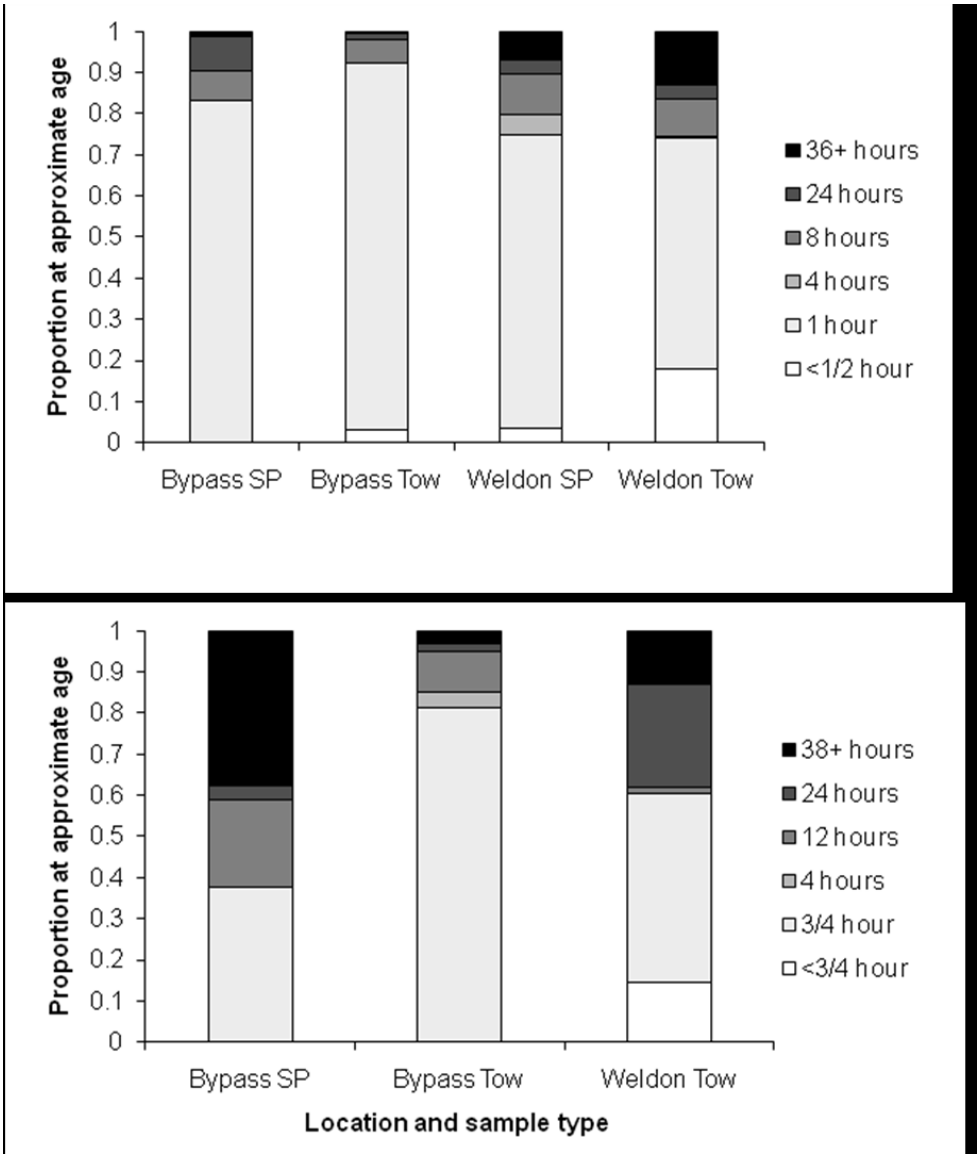


Figure 2.6.— Proportion of eggs, by age class, for hickory shad and river herring collected by spawning pads and plankton tows from sampling sites in the Roanoke River, North Carolina. Egg ages were assigned from stages using Jones et al. (1978) and Mansueti (1962). Egg ages for river herring were based on those for alewife (Jones et al. 1978) since more information was available for alewife than for blueback herring. Sites or methods where less than 20 eggs were collected were not included. Tows = plankton tows and SPs = spawning pads.

CHAPTER 3. SPAWNING HABITAT SELECTION OF HICKORY SHAD

Abstract

Little is known about spawning habitat requirements for hickory shad *Alosa mediocris*, although they are seasonally common in some rivers on the Atlantic coast of North America. Plankton tows and artificial substrates (spawning pads) were used during 2005-2007 to collect hickory shad eggs in the Roanoke River, North Carolina, to identify spawning timing, temperature, and microhabitat use. Results from this study and three additional studies in North Carolina indicate that ~90% of spawning occurs in water temperatures between 11.0 and 18.9 °C. Eggs were collected in run and riffle habitats, sometimes immediately downstream of changes in gradient. Spawning behaviors were infrequently observed, but were similar to those of American shad and occurred during the afternoon in shallow riffle habitats. Water velocity and substrate were significantly different at spawning pads with eggs compared to those without eggs suggesting that they are important microhabitat parameters for spawning. Hickory shad eggs were usually collected in velocities ≥ 0.1 m/s and on all substrates except those dominated by silt. Eggs were most abundant on gravel, cobble, and boulder substrates. Hickory shad spawned farther upstream in years with higher flow, as compared to a drought year, suggesting that flows may affect spawning site selection and the quantity and quality of spawning habitat available at a macrohabitat scale. Preliminary habitat suitability models were developed using a common format and a Bayesian belief network. Additional data from other river systems along the

species' range, information on spawning at a macrohabitat scale, and verification would help finalize a habitat suitability model for hickory shad.

Introduction

Hickory shad *Alosa mediocris* are anadromous fish that spawn in coastal rivers from Maryland to Florida, USA (Richkus and DiNardo 1984). Within river systems, hickory shad appear to spawn in both tributary and main channel habitats (Sparks 1998; Hawkins 1980; Burdick and Hightower 2006; Smith 2006). Like other anadromous alosines, water temperature may regulate the annual timing of the spawning run for hickory shad (Leggett and Whitney 1972; Loesh 1987; Aprahamian et al. 2003; Bagliniere et al. 2003; Harris et al. 2007). Diel periodicity in spawning has also been suggested, with most spawning speculated to occur between dusk and dawn (Mansueti 1962). Hickory shad eggs are initially semi-adhesive and semi-demersal, but can be buoyant in moving water (Mansueti 1962). Hatching generally occurs approximately 48-76 h after fertilization, depending on water temperature (Mansueti 1962). Although hickory shad eggs have been collected from multiple rivers (Godwin and Adams 1969; Sholar 1977; Hawkins 1980; Burdick and Hightower 2006), and egg development has been studied (Mansueti 1962), little on the specific macro- and micro-habitats required for spawning is known. Understanding critical spawning habitat in rivers is important to facilitate conservation and management of anadromous fish populations.

One approach for characterizing spawning habitat is the development of a habitat suitability model. The U.S. Fish and Wildlife Service (USFWS) began using habitat suitability models in the early 1980s to facilitate habitat management, impact assessment, and

project planning (USFWS 1981). These models can be developed in a variety of ways, often including information gathered from field data and surveys of knowledgeable scientists, but generally produce an estimate of relative habitat suitability between 0 (unsuitable) and 1 (optimally suitable) based on criteria considered important to the species at a particular life stage (USFWS 1981; Steir and Crance 1985). Habitat suitability models focused mainly on riverine habitat requirements have been developed for American shad *A. sapidissima* and river herring *A. aestivalis* and *A. pseudoharengus* (Pardue 1983; Stier and Crance 1985), but not for hickory shad. Limited information on the life history and habitat requirements of hickory shad may have prevented development of a habitat suitability model for this species.

Quantifying important relationships between a species and habitat can also be completed through construction of a Bayesian belief network (Rieman et al. 2001; Marcot et al. 2006; McCann et al. 2006; Smith et al. 2007). Bayesian belief networks (BBNs) are also called probability networks and they can be used to illustrate the hypothesized influence of environmental parameters on the probability of a specific ecological response, such as the probability of occurrence or abundance, response to habitat alteration, or probability of population viability under certain environmental conditions (Marcot et al. 2006; Smith et al. 2007). To create a BBN, experts first construct an influence diagram illustrating how selected variables affect the response (conceptual model), then develop defendable probabilities for responses under different conditions (predictive model; Marcot et al. 2006; Smith et al. 2007). Bayesian belief networks can combine various forms of data, collected at multiple spatial scales, with expert opinion, to identify species-habitat relationships (Marcot

et al. 2006; Smith et al. 2007; Uusitalo 2007). Like other modeling tools, BBNs can and should be updated as additional empirical information is collected to improve and validate the relationships (Marcot et al. 2006; Smith et al. 2007). Bayesian belief networks can be simple or complex and can be used to guide management decisions and future research (McCann et al. 2006; Uusitalo 2007).

The primary objective of this research was to examine the seasonal timing and habitats selected for spawning by hickory shad. We used oblique plankton tows to identify the seasonal period and temperature range at spawning. We integrated our plankton tow data with those from previous studies on three North Carolina rivers to more completely describe the regional temperature range at spawning. We also collected hickory shad eggs by placing spawning pads in a variety of habitats within presumed spawning areas to identify spawning microhabitat use. Using both types of data, we developed a preliminary habitat suitability model for spawning hickory shad. We incorporated these data into a preliminary BBN model to predict the probability of detecting spawning by hickory shad.

Methods

Study area.—The Roanoke River runs over 600 river kilometers (rkm) from western Virginia to the Albemarle Sound, North Carolina. Anadromous fish migration is limited to the lower 221 rkm by a dam in the town of Roanoke Rapids (Rulifson and Manooch 1990; Walsh et al. 2005; Figure 3.1). The tailrace of the Roanoke Rapids Dam was constructed adjacent to the original river channel, which is referred to as the bypass. Regular flows were reintroduced into the bypass in 2004 as part of the Federal Energy Regulatory Commission

license for the Roanoke Rapids Dam. To assess anadromous fish use of this restored habitat, sampling in 2005 and 2006 was done at the lower end of the bypass (Figure 3.1), which is shallow (usually < 2 m in depth) and mainly characterized by riffle and pool habitats. Sampling in 2006 and 2007 was completed in the main channel of the Roanoke River near Weldon, North Carolina, at rkm 209 (Figure 3.1). At Weldon, the river is deeper and characterized mostly by run habitat with some eddies and riffles during low water. A sharp elevation drop occurs at Weldon and boulders are visible and water is swift during periods of drought or low water releases from the Roanoke Rapids Dam, as was the case in 2006.

Field sampling.—We collected hickory shad eggs using plankton tows and spawning pads during 2005-2007 from the start of March to the end of May. We sampled in the bypass every three days in 2005 and once per week in 2006. We sampled once per week at Weldon in 2006 and 2007 (Figure 3.1). Weldon is historically considered a primary spawning area for hickory shad (Marshall 1977; Sparks 1998). We also conducted plankton tows at least weekly in 2005-2007 at Roanoke Rapids, an area that is 1-3 km below the Roanoke Rapids Dam (Figure 3.1). We sampled at Roanoke Rapids because it is the primary spawning site for American shad in this river (Hightower and Sparks 2003) and we were interested in examining spawning by that species for inclusion in Chapter 2. Although these plankton tow samples were not collected specifically for this study of hickory shad, we used the information on eggs at Roanoke Rapids and average daily water discharge (m^3/s) from the United States Geological Survey (USGS) gauging station there (Roanoke Rapids: 02080500), to examine the effects of water level on the upstream spawning extent of hickory shad.

We used oblique plankton tows to evaluate the seasonal spawning period and temperature range during spawning. Plankton tows have collected hickory shad eggs in numerous past studies (Hawkins 1980; Sparks 1998; Burdick and Hightower 2006; Smith 2006). Fifteen-minute oblique plankton tows were conducted using a bongo frame with two 0.3-m diameter plankton nets with 6:1 tail to mouth ratios, 500-um mesh, and solid sampling cups. Water temperature was recorded from 60% of the water depth. A standard General Oceanics Environmental flow meter was deployed adjacent to the net to estimate the volume of water filtered during each tow. At the bypass site, the plankton tow was completed immediately downstream of an elevation change where flows were high enough to maintain the plankton tow in the water column. At Weldon, the plankton tow was completed near the sharp elevation change, which was the most upstream area passable by boat during 2006. All eggs collected were fixed in 5-10% buffered formalin in the field. In the laboratory, hickory shad eggs were identified, counted, and staged for approximate age (Mansueti 1962; Jones et al. 1978). Dead eggs were removed because they often cannot be identified reliably.

Water temperature likely affects the timing of the spawning run for hickory shad, but not the exact location of spawning within a river, as flowing waters are often well mixed. Three previous studies in North Carolina collected hickory shad eggs using similar plankton tow methods and also recorded temperature: Hightower and Sparks (2003) from the Roanoke River (Data in Sparks 1998), Burdick and Hightower (2006) from the Neuse River (Data in Burdick 2005), and Smith (2006) from the Tar River (Figure 3.1). Results from all four studies were used to examine the relationship between water temperature and presence or

absence of hickory shad eggs. For all studies, only sites where eggs were collected on at least one date during the sampled year were used, as other areas might have had appropriate temperature, but were not used for spawning as a result of other environmental or physical factors. Plankton tow and spawning pad samples had highly skewed distributions, with most samples containing no hickory shad eggs. For this reason, analyses were completed using presence or absence, rather than abundance, of eggs.

Polyester floor buffing pads used in this study as spawning pads were similar to those used by Marchant and Shutters (1996) to collect Gulf sturgeon *Acipenser oxyrinchus desotoi* eggs. Spawning pads are considered useful for collecting information on spawning habitat requirements for fish with adhesive eggs (Marchant and Shutters 1996; Sulak and Clugston 1998; Firehammer et al. 2006). Spawning pads were observed to collect hickory shad eggs in clumped distributions within spawning sites, mostly when eggs were young (usually ≤ 1hr in age) and most adhesive, suggesting that they collect eggs in close proximity to the location where the fish actually spawned (Chapter 2). Spawning pads were red in color, 0.5 m in diameter and weighted with plate weights to lie flat on the river bottom. During 2005, we placed seven spawning pads on 5 March, an additional one on 24 March, and two others on 2 April in the bypass. During 2006, we placed eight spawning pads on 8 March in the bypass, as well as eight spawning pads on 9 March and one additional spawning pad on 23 March at Weldon. During 2007, we placed seven spawning pads on 7 March at Weldon. On each sampling date, we removed all eggs from the spawning pad; thus, each spawning pad was considered an independent sample on each date. The specific locations where spawning pads

were placed were selected to represent the range of available substrates, velocities, and depths in the area. In 2007, we specifically selected locations for placement of spawning pads to fill gaps in combinations of substrate type, water velocity, and depth. On each sampling date, we recorded depth, as well as dissolved oxygen and velocity from the water column at 60% of the depth, at each spawning pad. We recorded the primary substrate at each spawning pad as an ordered categorical variable (silt, sand, gravel, cobble, boulder, or bedrock). We also recorded a secondary type, if it represented ≥ 30% of the overall substrate at the site.

Statistical tests were used to examine the importance of environmental parameters other than temperature (dissolved oxygen, depth, velocity, and substrate) on the microhabitat selected for spawning. To examine for differences in the distributions of microhabitat parameters between spawning pads with and without eggs, a Kolmogorov-Smirnov test was completed for each continuous parameter separately (dissolved oxygen, depth, and velocity) and a Fisher exact test was used for substrate (Hollander and Wolfe 1999). All eggs more than 24-h old were removed, as water velocity and depth sometimes changed dramatically between the time when eggs were spawned and sampling was completed due to changes in releases from the Roanoke Rapids Dam. For these analyses, data from an area (bypass or Weldon) where spawning was not detected that year were excluded because the area may have been avoided due to unmeasured macrohabitat features or may have been unreachable due to low flows.

Correlations between environmental parameters are inherent in nature and by examining correlations between environmental parameters at all spawning pads and only those with eggs, a more specific understanding of habitat selection could be possible. To test for interactions between environmental parameters that significantly differed in the above Kolmogorov-Smirnov or Fisher exact tests, we completed Spearman rank correlations (Hollander and Wolfe 1999). To examine whether environmental correlations on spawning pads with eggs differed from overall correlations between environmental parameters, we also completed Spearman rank correlations including only measurements associated with spawning pads with eggs.

Habitat suitability model.—We included temperature and all environmental parameters found significant in the univariate tests in the habitat suitability model for spawning hickory shad. Suitability scores were calculated by dividing the number of spawning pads with eggs by the total number of spawning pads sampled, for a given range or category (bin) of the environmental variable. For each continuous variable included, evenly spaced bin widths were chosen based on data availability and the range of the parameter that was sampled. To standardize suitability scores between 0 and 1, the proportion value (proportion of sampled spawning pads with eggs) for each bin was divided by the highest proportion observed; thus, the bin with the highest proportion of spawning pads that contained at least one egg was divided by itself and given a suitability of 1 (optimal suitability). All bins for which no eggs were collected were given suitability scores of 0

(unsuitable) and all other bins were given suitability scores between 0 and 1 according to the proportion of spawning pad samples within that bin that contained eggs.

Bayesian belief network model.—We also constructed a BBN model to predict the probability of collecting at least one hickory shad egg in a sample, given environmental characteristics at the sampling site. Our model was constructed in the BBN modeling program, Netica^{R} (Norsys Systems Corporation, Vancouver, British Columbia, Canada). We included temperature as the seasonal cue for spawning and other tested environmental parameters as microhabitat cues for spawning. We again included all environmental parameters found significant in univariate tests, but also incorporated additional variables considered important for other alosines. Generally, we chose discrete levels for each parameter based on breaks observed in our data (i.e., where eggs were and were not collected and bin suitability scores), but we also used information in the literature, when needed, and combined bins with similar suitability scores when sample sizes were small or a high number of breaks would likely not be biologically meaningful or defensible. Because bin selection and the associated probabilities were from various data sources (i.e., four data sets, two different collection methods, literature), none of which provided information on detection probability by gear or habitat type, the probability of collecting hickory shad eggs should be considered approximate for any gear.

We consider both habitat suitability models to be preliminary because they include some environmental variables examined only in our study in the Roanoke River and have not been verified for other hickory shad populations. These models should be reviewed, verified

in other systems, and improved through examination by experts and further data collection range-wide. Our BBN is intended to illustrate how this modeling technique could be used to describe and predict spawning site selection by anadromous fishes.

Results

Field sampling

Hickory shad eggs were collected by plankton sampling in the Roanoke River from mid-March to mid-April in 2005-2007 (Figure 3.2). The extent of spawning at sites upstream from Weldon varies annually, possibly in response to water discharge. Hickory shad eggs were collected from the main channel at Roanoke Rapids in both years of higher flows (2005, 2007) but not in 2006, a drought year. Similarly, eggs were collected in the bypass in 2005 and 2007 (Gunter 2009), but not in 2006.

Hickory shad eggs collected by plankton tows from Weldon and the bypass ranged in approximate age from 0.5 h to > 36 h, with 84% estimated to be ≤ 1-h old. All plankton tows with eggs were completed between 1000 and 1800 hours Eastern Standard Time (EST), so diel spawning periodicity could not be described. Behavior suggestive of spawning was observed opportunistically on two occasions, once in the bypass during 2005 and once at Weldon in 2006. Similar to spawning American shad (Walburg and Nichols 1967), these hickory shad grouped close together and moved rapidly near the water surface producing splashes. Eggs were collected by plankton tows on the trips when spawning behavior was observed. On both occasions, fish engaged in these behaviors were observed in shallow (≤ 1 m) water with at least moderate water velocity (≥ 0.2 m/s), and were highly visible and

identifiable. Both observations were made from 1400-1800 hours (EST) on clear days in rocky riffle or run macro-habitats.

Hickory shad eggs were collected from our plankton tow samples in the Roanoke River at temperatures ranging from 10.7 to 17.8 °C. The temperature range for the four studies combined (Hightower and Sparks 2003; Burdick and Hightower 2006; Smith 2006; present study) was 10.2 to 22.5 °C (Figure 3.3A). Over 90% of the plankton tows with eggs were completed when temperatures ranged from 11.0 to 18.9 °C and over 50% were completed when temperatures ranged from 12.0 to 14.9 °C. The peak spawning temperature for all systems combined was 14.0 to 14.9 °C, when 52.6% of the tows contained hickory shad eggs. While the temperature ranges when eggs were collected overlapped, higher proportions of eggs were collected at colder temperatures in the Neuse River compared to the Roanoke and the Tar rivers (Figure 3.3B). Peak spawning in the Roanoke and Tar rivers was 14.0 to 14.9 °C, whereas peak spawning in the Neuse River was 11.0 to 11.9 °C (Figure 3.3B). Compared to the other systems, higher proportions of tows in the Roanoke River contained hickory shad eggs. This pattern was likely observed because sampling in the Roanoke River targeted proposed spawning sites, whereas the other studies sampled for eggs river-wide.

Hickory shad eggs were collected from spawning pads in the bypass and at Weldon. The number of eggs ≤ 24-h in age per spawning pad ranged from one to 2,450. Approximate egg ages ranged from 0.5 to 24 hrs, but > 86% of all eggs used for analyses were staged to be ≤ 1-hr in age. Kolmogorov - Smirnov tests indicated that water velocity over spawning pads

with eggs was significantly different than over those without eggs, but tests for differences in other environmental parameters were not significant (Table 3.1). Hickory shad eggs were collected in velocities ranging from 0.02 to 1.26 m/s, with a median of 0.29 m/s (Table 3.1). Although habitats with low water velocities were frequently sampled, spawning pads placed in velocities < 0.1 m/s rarely contained eggs (Figure 3.4A). A Fisher exact test found a significant difference in substrate type where eggs were collected as compared to where eggs were not collected (Table 3.1). Eggs were found on all substrates except silt, but were more frequently collected on spawning pads as substrate size increased (Table 3.1; Figure 3.4B). When both velocity and substrate were examined in relation to abundance of hickory shad eggs per spawning pad, high numbers of eggs were collected in velocities from 0.10 to 1.26 m/s and on substrates dominated by gravel, cobble, and boulder, but especially cobble (Figure 3.4C).

Velocity and substrate were significantly correlated with each other in both the complete data set (n = 124) and in the data set only including spawning pads with eggs (n = 23). In the complete data set, velocity was positively correlated with substrate (R = 0.305, p < 0.001), but in the data set including only spawning pads with at least one hickory shad egg, velocity was negatively correlated with substrate (R = -0.467, p = 0.025). When substrate sizes were smaller (sand and gravel), eggs were less frequently collected overall and were only found when velocities were ≥ 0.19 m/s, whereas when substrates were larger, eggs were collected on spawning pads over a wider range of velocity (Figure 3.4C).

Habitat suitability model.

In North Carolina rivers, water temperatures from 10.2 to 22.5 °C are suitable and those from 11.0 to 14.9 °C appear optimal for spawning hickory shad (Figure 3.5A). Hickory shad eggs were collected from spawning pads in velocities between 0.02 and 1.26 m/s, but were most frequently collected at velocities between 0.40 and 0.49 m/s. To construct the habitat suitability model graph, velocities ≥ 0.40 m/s were considered optimal and those from 0.10 to 0.35 m/s were given a similar suitability score equal to their standard average suitability score (Figure 3.5B). Although hickory shad eggs were collected on spawning pads in velocities as high as 1.26 m/s, the suitability scores of velocities ≥ 0.5 m/s should be evaluated with caution due to low sample sizes. Silt was not used by spawning hickory shad and the proportion of spawning pads with eggs increased with increasing substrate size (Figure 3.5C). Boulder and bedrock were comparatively rare and spawning pads with the highest abundance of hickory shad eggs were often on cobble substrates; thus, sand and gravel were considered suitable and cobble, boulder, and bedrock were considered optimal for purpose of the habitat suitability graph (Figure 3.5C).

Bayesian belief network model

For the BBN, temperature was stratified into six levels: below (0-9.9 ºC), cool (10-10.9), medium (11.0-14.9 ºC), warm (15.0-18.9 ºC), hot (19.0-22.9 ºC), and above (23.0-30.9 ºC); substrate was stratified into four categories: silt, sand/gravel, cobble, and boulder/bedrock; and velocity was stratified into five categories: none (0-0.01), low (0.02-0.09 m/sec), medium (0.10-0.19 m/sec), and high (0.20-1.26; Figure 3.6). Dissolved oxygen was also included in the BBN, despite not being significantly different on spawning pads

with eggs as compared to those without eggs. Dissolved oxygen levels of ≥ 5 mg/L are considered important for American shad (Stier and Crance 1985). Dissolved oxygen was > 5mg/L in all of our samples, possibly suggesting that all spawning pads were placed in areas with optimal dissolved oxygen for hickory shad. Since dissolved oxygen may be important for hickory shad, but our range of samples could not adequately evaluate suitability at possibly sub-optimal levels, we included ranges similar to those used for American shad. Dissolved oxygen was considered unsuitable below 3 mg/L (low) and was given a probability of zero, considered moderately suitable between 3 and 5 mg/L (medium) and given a probability of 0.5, and considered optimally suitable at or over 5 mg/L (high) and given a probability of 1. Raw probabilities for collecting eggs on substrate and velocity combinations obtained from spawning pad data were scaled up in direct proportion to the percentage of samples collected during non-optimal temperature conditions (i.e. outside the medium range of 11.0-14.9 ºC), to reduce possible bias associated with the seasonal timing when certain habitat types were sampled. To scale up each probability value, the standardized suitability score associated with the temperature at collection was used. As an example, assume that we collected eight samples for a specific combination of velocity and substrate, four at 12 ºC and four at 16 ºC. The standardized suitability score for 12 ºC is 1.0 and that for 16 ºC is 0.55, so the probability of collecting at least one egg at this velocity-substrate combination would be scaled up to account for the four samples completed at 16 ºC. If three of the eight samples contained eggs, the probability would be estimated as: 3/[(4 * 1) + (4 * 0.55)] or 0.48, rather than 3/8 or 0.38. Standardized values above 1.0 were

entered as 1.0. When any habitat parameter was unsuitable, the probability of collecting an egg was always zero; whereas, the probability of collecting eggs during periods when all parameters were within suitable levels depended on the combined suite of values measured at the site (Figure 3.6).

Discussion

Temperature is an important factor in the timing of the hickory shad spawning period, as it is for other alosines (Leggett and Whitney 1972; Loesh 1987; Aprahamian et al. 2003; Bagliniere et al. 2003; Harris et al. 2007). In North Carolina, hickory shad are the first of the alosines to enter rivers in the winter and early spring and spawn at colder average water temperatures (Burdick and Hightower 2006; Smith 2006; Chapter 2). In this study, spawning was observed in waters ranging from 10 to 23 °C. Even at the southern limit of their range (Georgia-Florida), where hickory shad spawning may peak at slightly higher temperatures, spawning ends when temperatures reach 23 °C (Street and Adams 1969; Street 1970; Harris et al. 2007). Possibly, hickory shad eggs spawned at temperatures > 23 °C have higher mortality rates. Laboratory studies completed by Leim (1924) suggest that higher rates of mortality and developmental abnormalities occurred when American shad eggs were maintained at 22 and 26 °C, as compared to 12 or 17 °C. High water temperatures also result in increased metabolic demands for adult American shad (Leonard et al. 1999). Hickory shad are thought to be iteroparous throughout their range (Street and Adams 1969; Sholar 1977; Batsavage and Rullifson 1998; Harris et al. 2007) and spawning earlier when

temperatures are lower may reduce energetic expenditures during the spawning run and thus increase survival to spawn during another year.

Hickory shad most often spawn at water temperatures from 11 to 14 °C in North Carolina, although it is not known if this narrower range offers any advantages for development or survival of young. Mansueti (1962) examined development of hickory shad eggs and larvae at both 18 °C and 21 °C and found that young generally developed faster at the warmer water temperature. Possibly, hickory shad spawn earlier in the season when development times are longer because mortality of young is lower at cooler temperatures or there are a reduced number of predators or competing young earlier in the season. Trippel et al. (2007) found that hickory shad juveniles in the St. Johns River, Florida, were larger during outmigration, as compared to American shad and blueback herring juveniles collected during the same time period. In the Altamaha River, Georgia, hickory shad young were not prevalent in riverine nursery habitats and authors suggested that outmigration to the ocean may be rapid (Godwin and Adams 1969). Similarly, juvenile hickory shad are generally larger and less prevalent in juvenile surveys in the lower Roanoke River, than are juvenile American shad (Kevin Dockendorf, North Carolina Wildlife Resources Commission, personal communication). Limburg (2001) found that large, late-outmigrating, American shad and small, early-outmigrating, juveniles were more represented in the future adult population, as compared to those migrating in the middle of the season at moderate sizes. Although temperature may not be optimal for quick development of eggs and larvae, spawning earlier in the season may be advantageous for hickory shad by allowing the young

to start growing earlier, attain larger sizes at outmigration, or outmigrate earlier in the year, possibly leading to higher survival to adulthood.

Annual water flow volumes and the presence of dams may affect the upstream extent of the hickory shad migration and the total amount of available spawning habitat in the Roanoke River. Hickory shad migrate as far upstream as Roanoke Rapids and, in some years, spawn just below the lowermost dam in the system. In higher water years, hickory shad migrated and spawned farther upstream than in a lower flow year, as has been observed for this species in the Neuse River, North Carolina (Burdick and Hightower 2006). In a drought year, hickory shad spawning occurred only as far upstream as Weldon, the suggested primary spawning grounds in the Roanoke River (Marshall 1977; Sparks 1998). Water releases from dams in regulated rivers may affect the total amount of spawning habitat available to hickory shad annually and years with low releases could make potential spawning habitat inaccessible. However, even during higher flow years, hickory shad in the Roanoke River spawned just below a rocky area at Weldon, suggesting that they chose this type of habitat even during years when other upstream areas were accessible.

Hickory shad eggs were most often collected in riffle areas, dominated by larger substrates, often just below areas of gradient change. Hickory shad avoided spawning in locations dominated by silt or any mix of silt and sand. Adhesive eggs of white sturgeon *Acipenser transmontanus* had lower survival and slower growth rates in the laboratory when covered by fine sediments (Kock et al. 2006). Authors suggested that eggs covered by fine sediments had higher mortality as a result of reduced exchange rates of oxygen and carbon

dioxide. Similarly, decreased survival has been observed for salmonid eggs when silt is mixed with the gravel selected for spawning, even when silt represents only a very small fraction of the total substrate (Julien and Bergeron 2006). Larger substrates free of silt appear important for a variety of anadromous species that spawn demersal eggs. Larger substrates may allow for increased exchange of oxygen and carbon dioxide and are often found in areas of high gradient.

Hickory shad also appeared to avoid spawning in areas with very low or no water velocity, especially when substrates were small. When water velocities were very low, spawning only occurred on bedrock substrates. In contrast, when water velocities were higher, spawning occurred on a variety of substrate types, including gravel and occasionally sand. Hickory shad eggs are only somewhat negatively buoyant and some likely remain in the water column longer during periods of high velocity (Mansueti 1962). Perhaps, eggs are distributed over a wider variety of substrates during high flow events, when water velocities are generally higher throughout the river channel, and are more concentrated in riffle areas with larger substrates, during periods of low flow. While we collected eggs over a range of values, it appears that hickory shad mainly spawn in water velocities that are ≥ 0.1 m/s.

No pattern was observed for the distribution of eggs in relation to dissolved oxygen or water depth, but this does not suggest a lack of relationship. American shad are suggested to spawn in areas with at least 5 mg/L of dissolved oxygen and increased egg and larval mortality may result below 3 mg/L (Stier and Crance 1985). Chittenden (1976) suggested that pollution leading to low dissolved oxygen levels affected the distribution and spawning

activity of American shad in the Delaware River. On any given date in the present study, dissolved oxygen levels were similar on all spawning pads within a general sampling area (bypass or Weldon) because water in these shallow riverine areas is generally well mixed. Since concentrations did not differ between spawning pads and they all were within the range considered suitable for and often used by American shad (Stier and Crance 1985; Ross et al. 1993), we suspect that no relationship was observed because dissolved oxygen was always adequate or optimal and did not limit spawning activity at any location sampled. Thus, while dissolved oxygen likely is an important component for spawning habitat, the areas of the Roanoke River that we studied appear to have optimal levels of dissolved oxygen, which did not allow us to evaluate suitability as it related to dissolved oxygen. In this study, hickory shad eggs were collected in depths ranging from 0.2 to 4.0 m. Greater depths are common in river systems with spawning populations of hickory shad and whether depths over 4.0 m would be used cannot presently be determined.

The range of riverine microhabitat used for spawning by hickory shad in this study was similar to spawning habitat characterized as suitable for American shad. Hickory shad and American shad generally spawn in areas with overlapping ranges of depth, substrate, and velocity (Stier and Crance 1985; Ross et al. 1993; Beasley and Hightower 2000; Hightower and Sparks 2003). However, eggs of the two species are morphologically different—American shad eggs are larger and non-adhesive—and while their spawning ranges within a river system generally overlap, the specific sites selected for spawning are often different (Williams et al. 1975; Jones et al. 1978; Sparks 1998; Burdick and Hightower 2006). In the

Roanoke River, American shad appear to primarily spawn in the main channel at Roanoke Rapids, whereas hickory shad spawn little at Roanoke Rapids, despite apparently adequate habitat. In the St. Johns River, Florida, adult hickory shad have been collected along with American shad, but spawning sites have not be indentified from main channel surveys of either gravid females or eggs, suggesting that hickory shad in that system may spawn primarily in tributaries (Williams et al. 1975; Harris et al. 2007; McBride and Holder 2008). While sampling for river herring in the Cashie River, North Carolina, biologists sometimes observed hickory shad in high abundance in small tributaries (Kevin Dockendorf, North Carolina Wildlife Resources Commission, personal communication). Burdick and Hightower (2006) also suggested that hickory shad may use tributaries for spawning in the Neuse River, North Carolina, with greater frequency than do other anadromous species. Different spawning locations may be selected to reduce competition, although generally hickory shad spawn earlier than American shad, which limits temporal overlap to some degree. We did not sample river-wide, but it appears that macrohabitat parameters affect the distribution of spawning for both species.

Although, young hickory shad eggs were successfully collected on spawning pads, it is not known if spawning pads have different levels of effectiveness in different habitat types. Spawning pads have mainly been used to study spawning habitat selection for sturgeons *Acipenser* sp. (Marchant and Shutters 1996; Sulak and Cluston 1998; Fox et al. 2000; Paragamian et al. 2001; Perrin et al. 2003; Duncan et al. 2004). Like sturgeon eggs, hickory shad eggs are initially adhesive and likely adhere to spawning pads soon after spawning in

close proximity to the location of the spawning fish. Exactly how far eggs traveled before settling out is not known, but since eggs were collected on spawning pads very close to locations where spawning behavior was observed, eggs were generally young in age (most staged ≤ 1-hr in age), and eggs were collected in clumped distributions (Chapter 2), it appears that they likely give a reasonable assessment of spawning habitat use. However, like other gears, spawning pads may be more effective at collecting eggs in certain habitat types compared to others. The fact that eggs were not collected in areas with no water velocity might suggest that these habitats were not used, since eggs would likely settle in lower velocity areas, if they were spawned or drifted there. In addition, spawning pads with large abundances of eggs, such as those at sites with substrates dominated by cobble, were likely very close to a spawning fish. Research examining the ability of spawning pads to collect adhesive eggs in different habitats would help identify and correct any bias associated with their use to describe spawning habitat selection and construct habitat suitability models.

Bayesian belief networks can be implemented like more common habitat suitability model formats to examine the effects of different management scenarios on the quantity and quality of spawning habitat for anadromous species. Like more commonly used formats, BBNs can include various forms of information including expert opinion, literature, and empirical data (Marcot et al. 2006; McCann et al. 2006; Smith et al. 2007; Uusitalo 2007) and could theoretically be incorporated into flow modeling studies such as the instream flow incremental method (Bovee 1982) to assess management options in regulated rivers. Unlike many habitat suitability model formats, however, BBNs can more easily include interactions

between environmental variables with regard to habitat use, which may give a better estimate of true suitability in a habitat type. Also, BBNs can predict the actual probability of use, rather than just give a suitability score. Actual probabilities would likely be somewhat river-specific, and would result from the total amount of suitable habitat, population density of the species, as well as any predators and competitors in system. Since BBNs include a measure of uncertainty, they can also help guide future research (Uusitalo 2007). Our BBN illustrates how this type of model could be incorporated into the habitat suitability modeling process for anadromous alosines in regulated rivers.

Our habitat suitability models for hickory shad greatly improve our understanding of their spawning habitat selectivity; however, they were parameterized mostly from three years of data on one river in North Carolina and should thus be viewed as preliminary. Validation of the relationships between species and habitats is warranted for proper species and ecosystem management, but is often not completed (Marcot et al. 2006; Haxton et al. 2008). Verification (i.e., are the included environmental variables found to be similarly related to spawning in other river systems), and validation (i.e., do the models accurately describe the effects of habitat on survival, growth, or reproduction), would help strengthen our understanding of hickory shad spawning habitat requirements and our confidence in our habitat suitability models.

Our research presents new information on habitat use of spawning hickory shad. Broadcast spawning fishes, like hickory shad, presumably spawn in locations where their offspring will have high survival and fast growth; thus, spawning habitat is critical habitat.

Hickory shad appear to spawn primarily in habitats dominated by cobble and boulder substrates and adequate velocity. Hickory shad are a relatively unstudied alosine and future research in other rivers along the species range would improve our understanding of their habitat requirements and improve these habitat suitability models.

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Tables

Table 3.1.—Range and median values of examined habitat parameters for spawning pads with eggs (n = 23) compared to those without eggs (n = 101). Kolmogorov-Smirnov tests (K-S) were completed for continuous variables (dissolved oxygen, depth and water velocity) and a Fisher exact test (*) was completed for substrate type.

Parameter	Range with eggs	Median with eggs	Range without eggs	Median without eggs	K-S test value (*D*)	P-value
Dissolved Oxygen (mg/L)	6.76-11.27	9.33	6.99-16.27	9.69	0.508	0.959
Depth (m)	0.20-3.96	1.00	0.20-3.38	1.05	0.897	0.397
Water Velocity (m/s)	0.02-1.26	0.29	0.00-0.72	0.01	2.824	<0.001
Substrate (categorical)	Sand – Bedrock	Cobble	Silt-Bedrock	Gravel	*	0.003

Figures

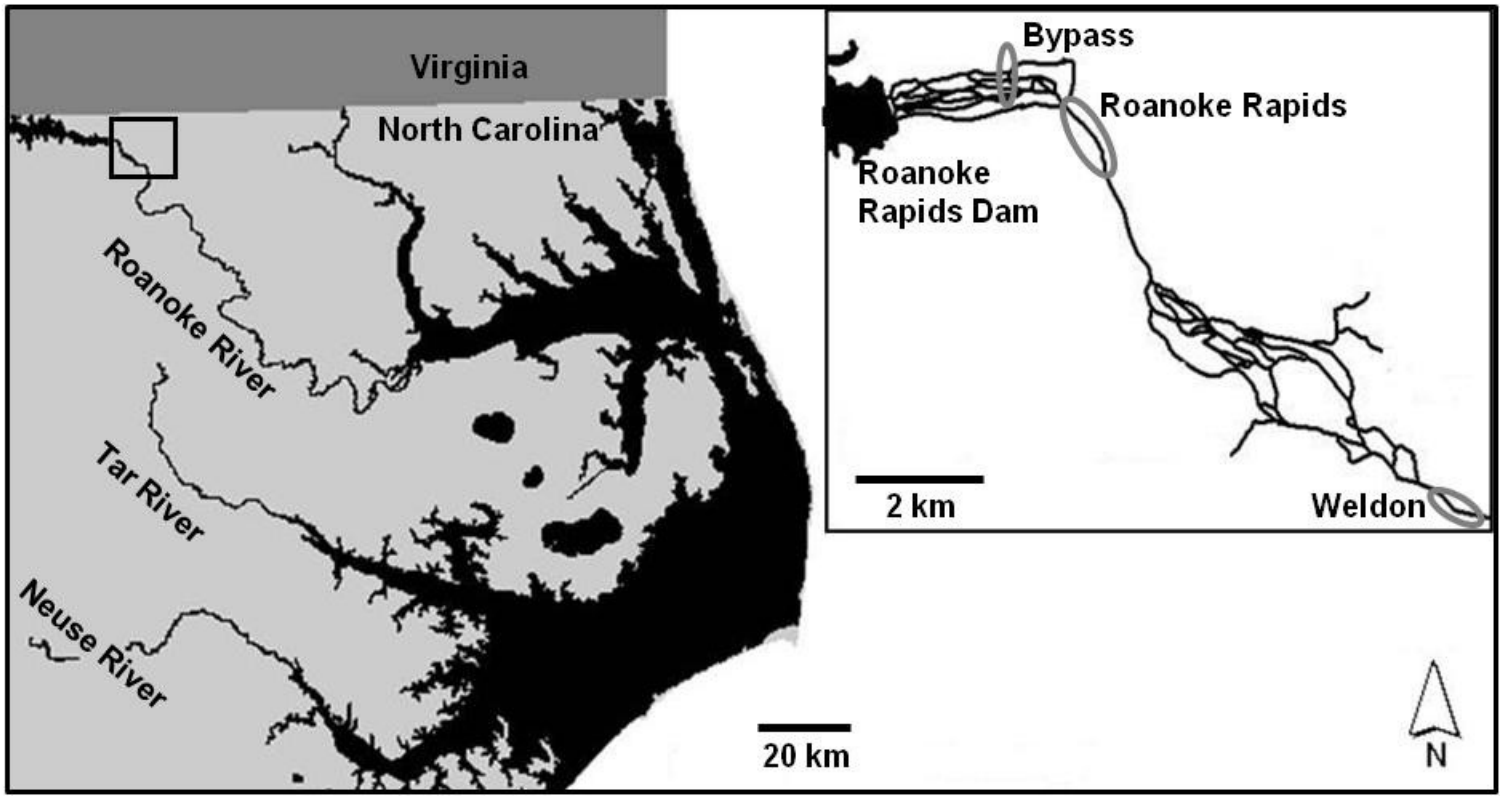


Figure 3.1.—Map of the eastern side of North Carolina, including sampling sites on the Roanoke River and other rivers cited in the study. Inset, shown by the open rectangle on the larger map, illustrates the location of the three sampling areas (Bypass, Roanoke Rapids, and Weldon) in the Roanoke River and the Roanoke Rapids Dam. All plankton tows and spawning pads were sampled within the delineated grey regions shown on the inset.

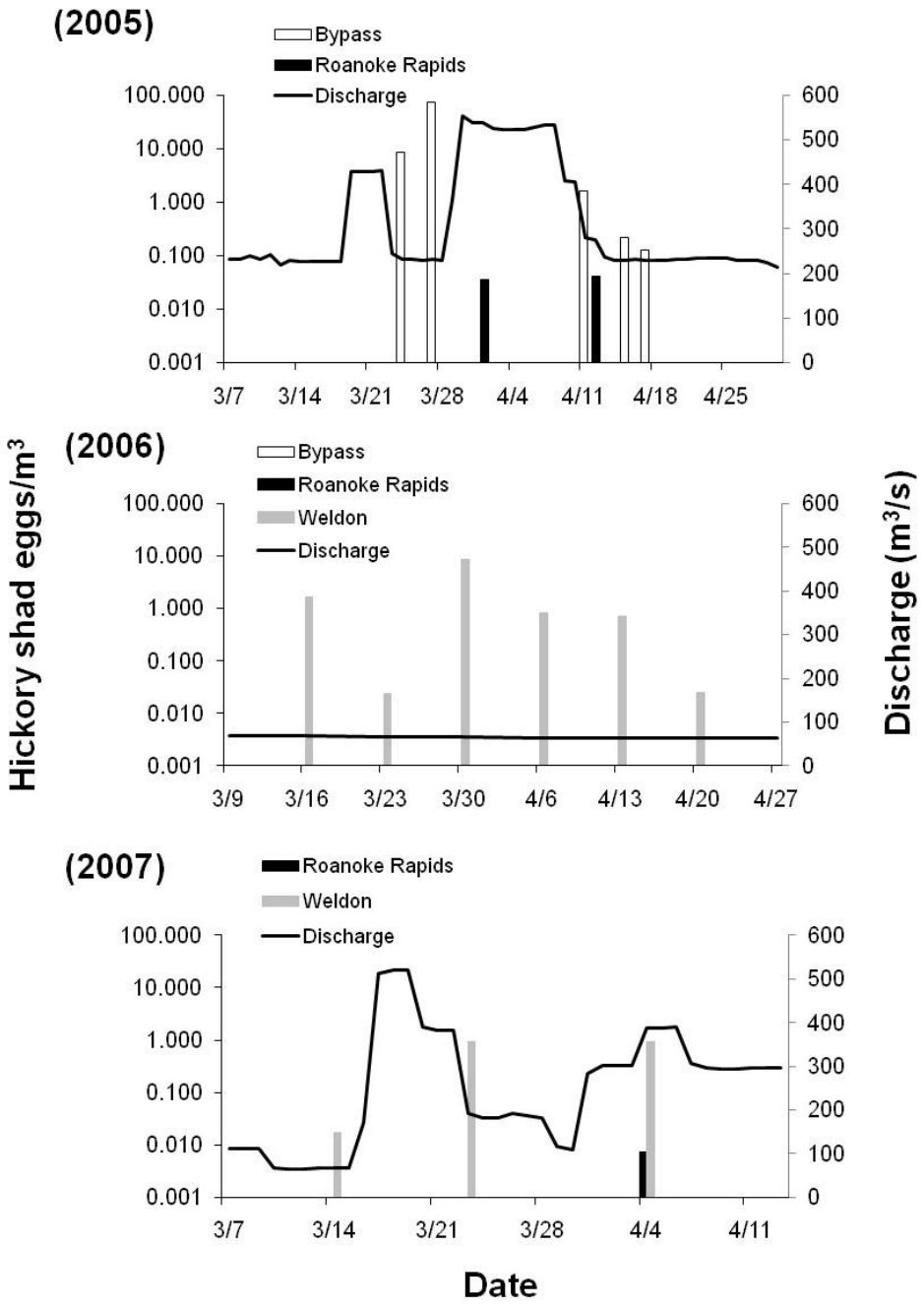


Figure 3.2.—Hickory shad eggs/m^3 collected by plankton tows (on $\log_{10}$ scale) and average daily discharge (m^3/s) at the United State Geological Survey (USGS) gauging station at Roanoke Rapids, North Carolina for 2005, 2006, and 2007. Legend includes all sites where plankton tows were completed during the year.

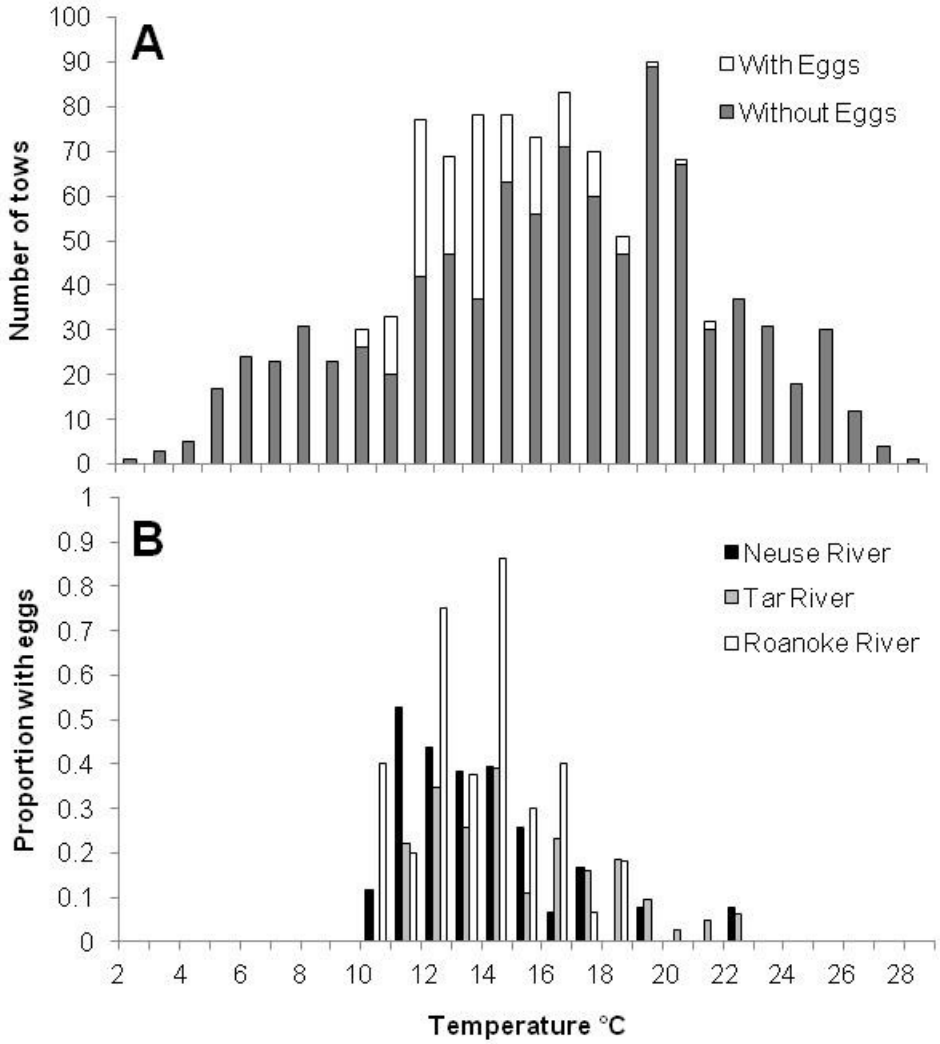


Figure 3.3.—(**A**) Number of plankton tows with and without hickory shad eggs in relation to water temperature (°C) from four studies in three North Carolina rivers: present study in the Roanoke River, Sparks (1998) in the Roanoke River, Burdick (2005) in the Neuse River, and Smith (2006) in the Tar River and (**B**) the proportion of plankton tows with hickory shad eggs, by river system, in relation to water temperature (°C).

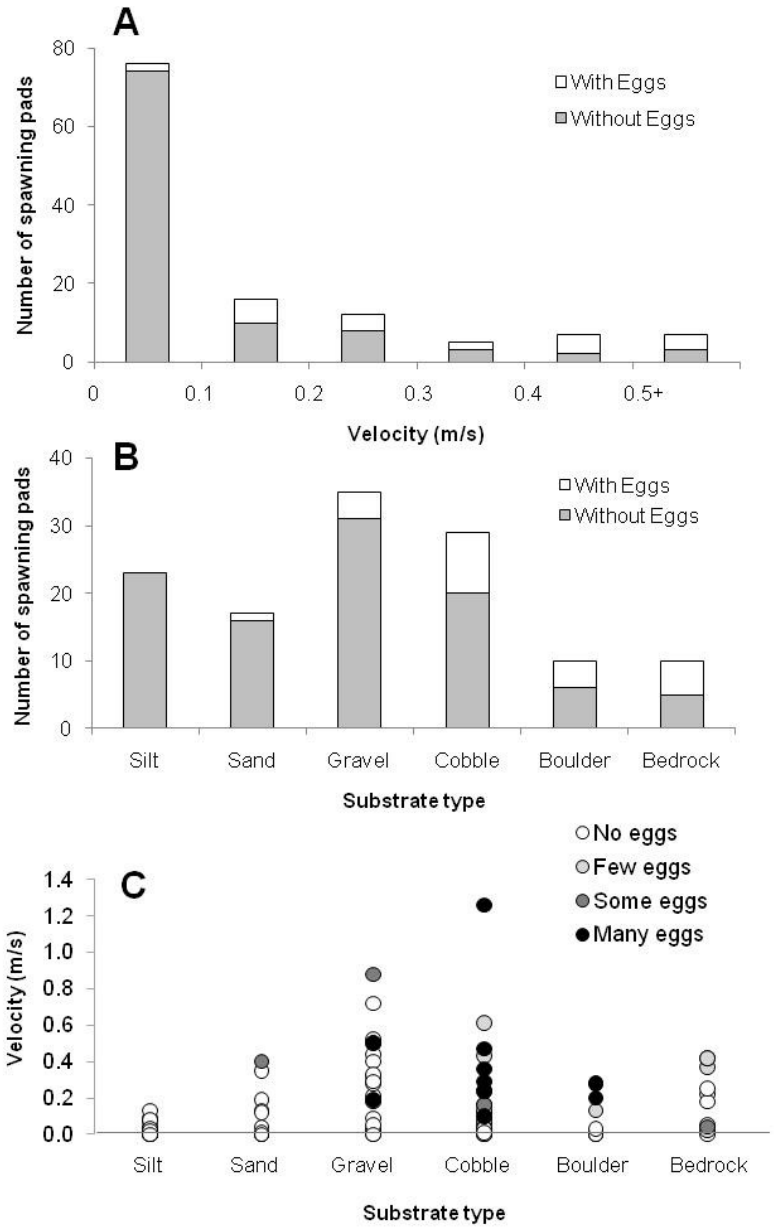


Figure 3.4.—Number of spawning pads with and without hickory shad eggs collected by (**A**) water velocity (m/s), and (**B**) substrate type, and (**C**) the velocity and substrate type at spawning pads where different numbers of hickory shad eggs were collected. For (**C**), open circles depict spawning pads where no eggs where collected, light grey circles represent spawning pads where only a few eggs where collected (1-11 total eggs), dark grey circles depict spawning pads where some eggs were collected (20-31 total eggs) and black circles depict spawning pads where many eggs were collected (55-2,450 total eggs).

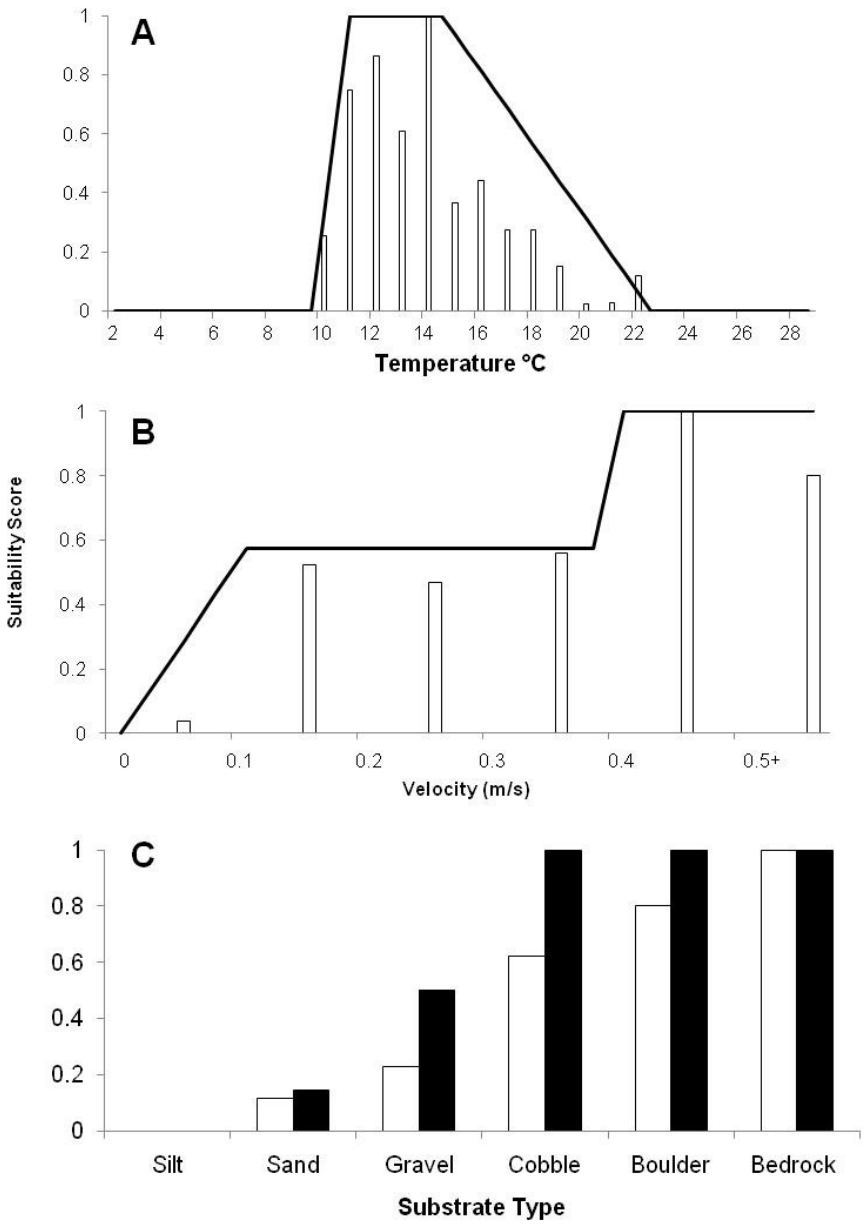


Figure 3.5.—Standardized suitability scores (open bars) and graph (line or filled bars) for the standard habitat suitability model for spawning hickory shad including values for (**A**) temperature (°C), (**B**) velocity (m/s) and (**C**) substrate type.

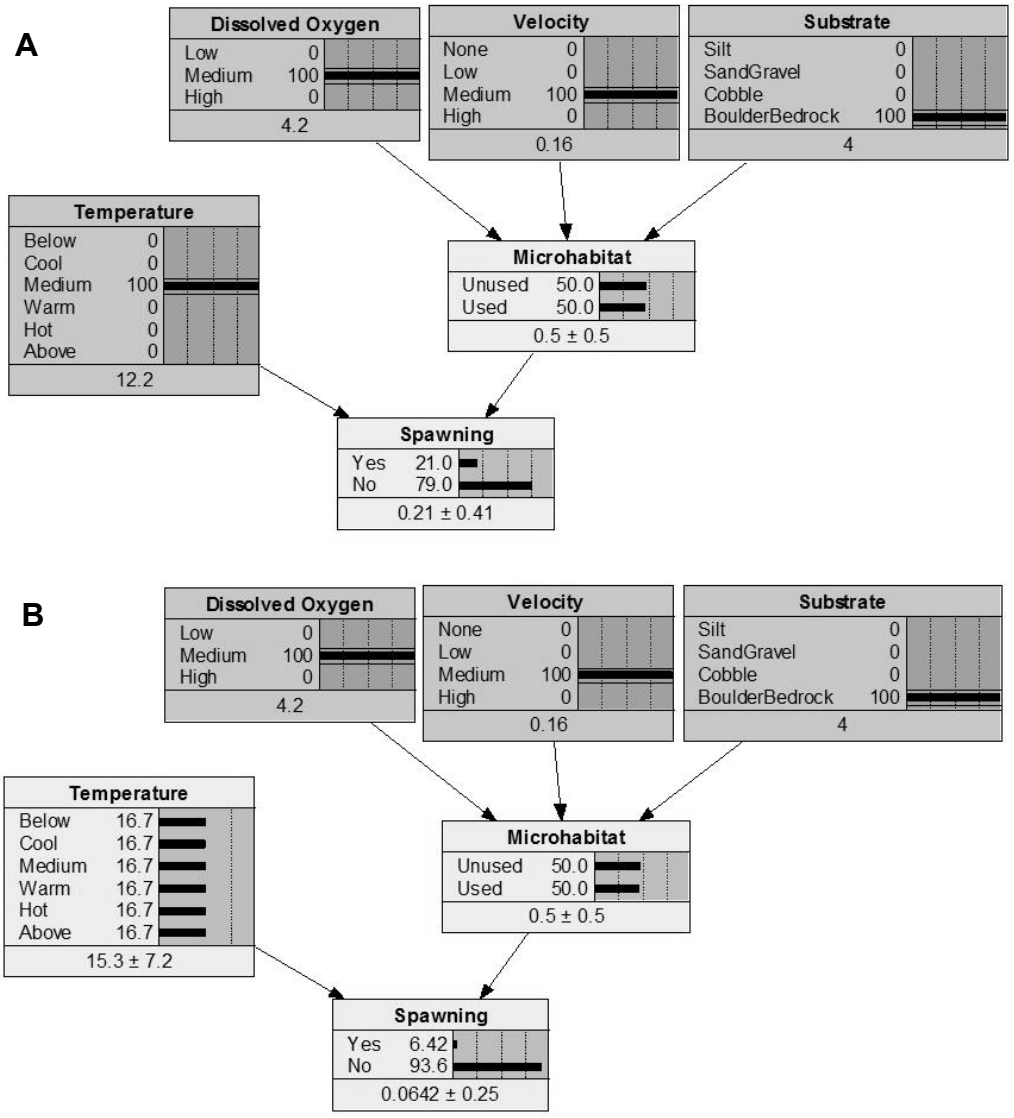


Figure 3.6.—Bayesian belief network for predicting the probability of detecting hickory shad spawning in an area. This figure illustrates the structure of the model which includes both a microhabitat (dissolved oxygen, water velocity and substrate) and a seasonal component (temperature). Each panel (**A** and **B**) illustrates the expected probability (and standard error) of observing spawning at a hypothetical site based on measured environmental parameters: (**A**) illustrates the probability of collecting hickory shad eggs under specific microhabitat conditions, when temperature is known and (**B**) illustrates the same scenario, when temperature is unknown. Dark grey boxes indicate values measured in the field (value at the bottom of the box) and light grey boxes indicate values estimated by the model (value and standard error at the bottom of the box).

CHAPTER 4. MIGRATORY PATTERNS OF AMERICAN SHAD UPSTREAM OF DAMS ON THE ROANOKE RIVER, NORTH CAROLINA AND VIRGINIA

Abstract

American shad *Alosa sapidissima* are in decline along most of their native range as a result of overfishing, pollution, and habitat alteration in the coastal rivers where they spawn. In regulated rivers, dams can limit American shad access to historic spawning sites. One approach to population restoration is to provide access to habitat above dams through a trap-and-transport program. We examined initial survival, movement patterns, spawning, and downstream passage of adult sonic-tagged American shad transported to reservoir and riverine habitats upstream of three hydroelectric dams on the Roanoke River, North Carolina and Virginia. The average survival to release was 85%, but survival decreased with increasing water temperature. Some tagged American shad released in reservoirs migrated upstream to rivers; however, most meandered back and forth within the reservoir. A higher percentage of fish migrated through a smaller (8,215 ha) compared to a larger (20,234 ha) reservoir, suggesting that population level effects of transport may depend on upper basin characteristics. Transported American shad spent little time in upper basin rivers, but were there when temperatures were appropriate for spawning and flows were at their highest seasonally. No American shad eggs were collected by weekly plankton tow sampling in upper basin rivers. Estimated initial survival of tagged adults after downstream passage through each dam was 71-100%; however, many individuals did not pass and were found just upstream of a dam late in the season. Under present conditions, transported American shad

in the Roanoke River may have reduced effective fecundity and post-spawning survival, than non-transported individuals. Research on development of young American shad in upstream habitats and the efficacy of structures to increase downstream passage for adults and young would help to better evaluate the potential benefits of transporting American shad to upstream habitats in the Roanoke River.

Introduction

American shad *Alosa sapidissima* is a recreationally, commercially, and ecologically valuable anadromous species native to coastal river systems on the Atlantic coast from the St. Lawrence River, Canada, to the St. Johns River, Florida (Limburg et al. 2003). Historically, American shad supported one of the most important fisheries on the eastern seaboard (Smith 1894; Walburg and Nichols 1967). They continue to support both recreational and commercial fisheries although many populations have declined dramatically during the past century as a result of overfishing, dams, land use changes and poor water quality (Walburg and Nichols 1967; Hightower et al. 1996; Cooke and Leach 2003; Limburg et al. 2003).

Dams provide numerous benefits to humans (Shuman 1995), but have contributed to the decline of anadromous species by blocking migration routes to historical spawning locations and altering downstream habitat (Rulifson and Manooch 1990; Rulifson 1994; Pringle et al. 2000; Trush et al. 2000; Dauble et al. 2003; Freeman et al. 2003; Schilt 2007). To mitigate the effects of dams in some rivers, fishways have been installed to help adults pass upstream, and eggs, larvae, and adults have been collected or cultured and released in upstream habitats (Hendricks 2003; St. Pierre 2003; ASMFC 2007). Stocking programs,

flow regulations, and the installation of fishways appear to have improved American shad populations in some systems (Cooke and Leach 2003; St. Pierre 2003; Weaver et al. 2003). There are concerns, however, that access to upstream habitats could negatively affect populations by causing increased mortality due to downstream passage through dams, higher energetic demands associated with a longer migration, and increased predation in impounded areas (Leggett et al. 2004; Skalski et al. 2009).

This study was completed to evaluate movement patterns and habitat use of American shad transported upstream of dams on the Roanoke River, North Carolina and Virginia. The most downstream dam is located in Roanoke Rapids at river kilometer (rkm) 221 (Rulifson and Manooch 1990). This dam was completed in 1955 for hydroelectric power generation and replaced a smaller dam present in the same location since about 1900 (Rulifson and Manooch 1990; Hightower et al. 1996; Hightower and Sparks 2003). The next two upstream dams are Gaston Dam at rkm 233 and Kerr Dam at rkm 288 (Figure 4.1). None of these dams provide fish passage. American shad in the Roanoke River historically migrated as far upstream as Salem, Virginia; presently, most spawning occurs in the main river channel just below the Roanoke Rapids Dam (Hightower and Sparks 2003).

Above Kerr Lake in the Roanoke River basin, there are approximately 400 rkm of potential spawning habitat for American shad (Read 2004). Read (2004) examined habitat features and environmental parameters in five main channel and tributary rivers above Kerr Lake to evaluate their suitability for spawning by American shad. Read (2004) used three models to estimate suitability and found that even with the most conservative model, at least

62 rkm and 39 rkm of suitable habitat for spawning American shad would be present in May and June, respectively. Read (2004) also found that American shad eggs in incubators in riverine locations above Kerr Lake successfully hatched, further demonstrating that access to these upstream areas could increase the spawning and nursery habitat available to American shad in the Roanoke River.

The primary purpose of this research was to examine whether American shad collected on the spawning run in the lower Roanoke River and transported to upstream habitats would successfully migrate and spawn in suitable riverine habitat. Another purpose was to examine movements of tagged fish released in the Staunton River, Kerr Lake, and Lake Gaston in terms of absolute distance, direction, and diel patterns. The lower Staunton River has detectable flow, whereas Kerr Lake is a 20,234-ha reservoir and Lake Gaston is an 8,215-ha reservoir, so any differences in the ability of American shad to migrate through these three areas could help identify the conditions under which transport to upstream waters could be most successful. A final purpose of this project was to evaluate how and when trap and transport could be used most effectively to help restore American shad populations.

Methods

Preliminary assessment of collection and tag mortality.—To evaluate short term mortality associated with our procedures before initiation of the transport experiment, we collected and tagged American shad and monitored their survival in holding tanks. On 4 April 2007, we collected 22 adult American shad by boat electrofishing at Roanoke Rapids, in the area between one and two kilometers below the Roanoke Rapids Dam (Figure 4.1),

and held them in a tank with flow through water on board the boat during processing. All fish were measured for total length to the closest mm, identified to sex, and tagged with an ultrasonic transmitter. Tags were coated in glycerin and inserted carefully through the esophagus into the stomach using the eraser end of a pencil. Transmitters were 9 mm in diameter, 24 mm in length, 3.6 g in air, had a battery life of 70 days, a delay period of 10 to 30 seconds, and used a single frequency of 69 kHz (V9-1L, Vemco Division/AMIRIX systems, Halifax, Nova Scotia, Canada). These transmitters were smaller in size and weight than those used in previous American shad telemetry studies (Beasley and Hightower 2000; Moser et al. 2000; Hightower and Sparks 2003, Sprankle 2005; Olney et al. 2006; Aunins and Olney 2009). We quickly placed fish by dip nets into a 2,271-L circular hauling tank with circulating current and added oxygen. Water from the river was used to fill the hauling tank and salt was added to help reduce osmotic stress to the fish (Hendricks 2003). Typical hauling densities for American shad are 2 to 3 fish per 100 L (Hendricks 2003), so a hauling tank of this size should successfully transport 45 to 68 adult American shad per trip with low mortality. The hauling tank was driven for over an hour to simulate transport to the upper basin and then brought to the North Carolina Power/Dominion (Dominion) powerhouse at Roanoke Rapids. Once at the powerhouse, we randomly placed 11 fish into each of two circular holding tanks with flow through water from Roanoke Rapids Lake, the reservoir impounded by the Roanoke Rapids Dam (Figure 4.1). Each afternoon for four days, we recorded dissolved oxygen (DO) and temperature using a Yellow Springs Instrument (YSI85), and examined each tank for any dead individuals. On 9 April 2007, we sacrificed

all fish to collect the tags. Only one fish died during this experiment. For this one female, the tag was slightly posterior in the stomach than it was for other fish, although no harm was apparent and the fish showed no obvious reasons for its death. Overall, our collecting, transporting, and tagging procedures appeared to result in a low level of mortality.

Trap and transport.—We collected adult American shad in April and early May of 2007 and 2008, tagged some individuals with sonic transmitters, and transported all fish for release in reservoir and riverine habitats upstream of dams on the Roanoke River (Figure 4.1). On sampling each date, we collected approximately 50-60 American shad by boat electrofishing at Roanoke Rapids. During 2007, we released approximately half of the collected American shad from each of two locations per sampling date within one reservoir, either Lake Gaston or Kerr Lake. Generally, movement patterns for fish released at different sites within a reservoir were similar; thus in 2008, we released all collected fish from only one location per day in either Lake Gaston, Kerr Lake, or the lower Staunton River (Figure 4.1). On each release date, 8-12 American shad were implanted with sonic tags. In 2007, most American shad were tagged at the release site, since all fish were transported in the same tank and it was otherwise not possible to ensure that equal numbers of tagged fish would be released at each of the two locations within the reservoir. In 2008, all fish were tagged on the electrofishing boat, before being placed in the haul tank, since there was only one release site in each reservoir. All American shad selected for tagging appeared healthy and were moving vigorously. We did not tag either all females or all males on a given date,

but no other factors were considered in choosing individuals for tagging. We transported fish in the hauling tank to the release site, as described above.

Once at the release site, we placed all American shad into a net pen attached to a dock until the morning following transport. Penning overnight was done to decrease the likelihood of losing transmitters due to immediate mortality associated with capture, handling, and transport, and to facilitate fish moving together as a school. Net pens were rectangular and had frames made of polyvinyl chloride (PVC) pipe 3.0 m in length and 1.8 m in both width and depth. The top frame was sealed and therefore floated on the water surface and the bottom frame filled with water and sank. All sides, the top, and the bottom were covered by 0.63-cm ace knotless netting (Midlakes Corporation, Knoxville, Tennessee), so fish could not exit prior to release. On the morning after transport, we opened a flap of net facing outward so fish could swim out. We lifted the closed side of the pen to encourage outward movement, but fish were generally not handled. All fish that died in transit or in the pen were measured for total length, identified to sex, and examined for the presence of a sonic tag. To evaluate conditions under which trap and transport could be best used to move American shad for restoration or aquaculture purposes, we used logistic regression to examine the relationship between mortality during transport (yes or no) and different environmental and physical conditions (river temperature, total time spent in the tank, fish length and fish sex). Logistic models were blocked by collection date, since fish collected on a given date were subjected to the same conditions. The most parsimonious model was selected using Akaike's Information Criterion (AIC; Burnham and Anderson 2002).

Telemetry.— Movement patterns of tagged American shad were examined in Kerr and Gaston lakes and the Staunton and Dan rivers, mainly using stationary receivers (VR2s; Vemco, Halifax, Nova Scotia, Canada). Each receiver monitored continuously and recorded the time, date, and unique transmitter code for any detected tags. We placed three stationary receivers in Kerr Lake and two in Lake Gaston to assess movement patterns in these reservoirs during both 2007 and 2008 (Figure 4.1). Another receiver was placed in Roanoke Rapids Lake to assess fallback or out-migration through Gaston Dam (Figure 4.1). We put one receiver at the entrance to the Dan River, another at the entrance of the Staunton River, and others (2 in 2007 and 4 in 2008) farther upstream in the Dan and Staunton rivers (Figure 4.1). In 2008, we placed two receivers at Roanoke Rapids to obtain information about downstream movements of transported American shad (Figure 4.1). We checked stationary receivers (VR2s) for detections of tagged American shad approximately every two weeks from mid-April to late June or July. We also manually tracked tagged American shad, when possible, using a VEMCO model VR100 manual receiver, to examine specific movement patterns in reservoir and riverine habitats. In 2007, we tracked tagged fish for up to four hours after each release, to examine their behavior immediately after release from the pens.

To estimate the proportion of time that tagged American shad spent in habitat suitable for spawning, we calculated the amount of time spent in all upper basin habitats and the amount to time spent in riverine habitat. The apparent total amount of time (total duration) spent in upstream habitats was estimated for each fish as the time from release to either the last detection in the system (by VR2 or manual relocation) or the time when the fish was first

picked up on a receiver in the next lower reservoir. Duration in riverine habitat (riverine duration) was calculated as the sum of the amount of time between events of river entry (either from release or when the fish passed VR2 9 or 10 to enter a river) and river exit (when the fish passed VR2 9 or 10 on the way back to Kerr Lake). American shad are batch spawners, so they mature and spawn eggs over time during the spawning season (Olney et al. 2001; Olney and McBride 2003; Hyle 2004); therefore, both the amount and proportion of time spent in riverine habitat could influence the number of batches that they could release in suitable habitat and their overall annual fecundity. The proportion of time in riverine habitat was calculated as riverine duration divided by total duration. Duration in riverine habitat was compared between males and females and between fish released on different dates in the lower Staunton River using Analyses of Variance (ANOVA). Such tests were not done for fish released in Kerr Lake, since only a few fish released there entered riverine habitat.

In addition, we estimated the distances moved by tagged American shad to evaluate differences in movement patterns between fish released in different habitats and the general consequences of transporting fish upstream of dams. The minimum total distance moved was calculated as the total linear distance between VR2s and manual tracking locations for a fish over the entire season. Minimum upstream distance, calculated from the release point to the most upstream location where the fish was recorded, was also calculated. Minimum total and minimum upstream distances were both calculated to evaluate the relative amount of movement that was directed upstream toward or within riverine habitat. We compared total migration distances and upstream migration distances for fish released at different sites

(Gaston, Kerr, Staunton) using ANOVAs. We estimated the linear distances between release locations and VR2s in ArcMap (ESRI) from the United States Geological Survey's National Hydrography Dataset (http://nhd.usgs.gov/) maps for the upper Roanoke River basin, using a conical equidistant projection. We tested data for deviations from normality using Shapiro-Wilk tests and $\log_e$ transformed data when it improved normality (for data with zero values, a 1 was added to each point if the data were $\log_e$ transformed). If an ANOVA was significant, we used a Tukey's multiple comparisons test to evaluate which groups significantly differed. All tests were considered significant at the $\alpha = 0.05$ level. All tagged American shad not found by at least one stationary receiver or by manual tracking outside of their general site of release were eliminated from analyses, as they may have died or dropped their tags just after release.

Assessment of fallback.—After handling and tagging, some anadromous fishes experience a period of "fallback" when they move back downstream towards marine waters (Moser and Ross 1993). Tagged American shad often experience fallback and some subsequently do not continue upstream migration, even when no barriers exist (Barry and Kynard 1986; Beasley and Hightower 2000; Moser et al. 2000; Hightower and Sparks 2003; Bailey et al. 2004; Sprankle 2005; Olney et al. 2006; Aunins and Olney 2009). We considered a fish to have experienced fallback if it was first recorded by a stationary receiver downstream of the release site. In 2008, we evaluated the degree of fallback as a result of our tagging and transport procedures. To evaluate fallback associated with our tagging procedures, six American shad were collected by electrofishing, tagged, and immediately

released at Roanoke Rapids. To evaluate fallback as a result of both tagging and transport combined, we collected approximately 50 fish and tagged six individuals. All fish were put in the hauling tank, driven around for over 1 hour, placed in net pens set at Roanoke Rapids overnight and released the next morning, similar to fish transported to upstream habitats. We placed stationary receivers near the collection site and about 2.7 rkm downstream (Figure 4.1) to assess the percentage of tagged fish that experienced fallback and the percentage of those that returned to the main spawning grounds.

Downstream passage and survival.— To evaluate some effects of transporting wild fish on the number of repeat spawners in the population, we estimated mortality associated with downstream passage through Gaston and Kerr dams. There are no bypass facilities at these dams, so downstream passage occurs through the turbines. A fish was presumed alive after movement through a dam if it was later manually identified at two or more locations, detected at two or more stationary receivers, detected by one stationary receiver at least twice separated by over 24 hours, or a combination that suggested that the fish moved. Separation in space of relocations would document that the fish moved, whereas separation in time would imply that the fish moved away from the stationary receiver and later moved back. Changes in flow releases from dams could potentially also result in separations in detections, since the ranges for stationary receivers are affected by depth and bathymetry; however, the environmental conditions where our receivers were located and the specific detection patterns (i.e., when a specific fish was and was not detected in relation to flow changes) made this type of bias unlikely. A fish was presumed dead if it was located in the same place

by manual tracking on multiple sampling dates. A fish's fate was considered unknown if it was only detected once after passage through a dam. In 2008, when receivers were placed at Roanoke Rapids, we also examined if any tagged American shad made it past the series of dams to migrate back to the ocean.

Sampling for American shad eggs.— To examine for spawning in upper rivers, we completed plankton tows. Plankton tows have successfully collected American shad eggs in numerous previous studies (Bilkovic et al. 2002; Hightower and Sparks 2003; Burdick and Hightower 2006; Chapter 2). Fifteen minute oblique plankton tows using a bongo frame with two 0.3-m diameter plankton nets with 6:1 tail to mouth ratios and 500-um mesh were completed weekly from three stationary locations (near VR2s 10, 13 and 14) in the Staunton River from mid-May to late June in 2007 (Figure 4.1). In 2008, four additional plankton sampling locations were added, one in the Staunton River near VR2 12 and three in the Dan River (Figure 4.1). Plankton tows were also completed weekly in 2007 during the evening from early April to early July at the primary spawning area in Roanoke Rapids (Figure 4.1; Hightower and Sparks 2003) to determine the timing and temperature range when spawning occurred. At each plankton tow site, water temperature and DO were recorded from ~0.5 m below the surface of the water using a YSI85. A standard General Oceanics Environmental flow meter was deployed adjacent to the net to estimate the volume of water filtered during each tow so that the volume could be standardized for all samples. Eggs were fixed in 5-10% buffered formalin in the field and American shad eggs were later identified and counted (Jones et al. 1978; Burdick 2005).

Results

Trap and transport

A total of 738 American shad (313 in 2007 and 425 in 2008) were transported and released in lakes Gaston (n = 294) and Kerr (n = 313) and the lower Staunton River (n = 131). American shad females ranged in total length (TL) from 422 to 556 mm (average = 495 mm) and males ranged from 331 to 526 mm TL (average = 435 mm). Of the 738 American shad released into upstream habitats, 160 received sonic tags (62 in Lake Gaston, 66 in Kerr Lake and 32 in the lower Staunton River; Table 4.1). The majority of collected (78%) and tagged (72%) American shad were males.

Survival of transported American shad was generally high for tagged and untagged fish in 2007 and 2008 (Table 4.1). The only exception was on 4/24/2007, when the net pen at Summit was mostly removed from water overnight, resulting in very high mortality. Fish alive the next morning were released and tagged fish were included in the movement portions of this paper; however, data from this date were not included in analyses of mortality since the outcome was a result of human interference, rather than transport procedures. Excluding that date, the average rate of survival to release during both years was 85% (81% for females, 86% for males). It was not possible to compare survival of tagged and untagged fish in 2007, since fish were tagged at the release site, but in 2008, 91% of tagged and 87% of untagged American shad survived to release.

Logistic regression analysis suggested that survival to release was influenced by river water temperature, transport time, and the fish's total length (Table 4.2, Figure 4.2); the best

model according to AIC included temperature and total length. Models with delta AIC values within 2 of the selected model are considered to have substantial support (Burnham and Anderson 2002) and three models fell within this range (Table 4.2). All substantially supported models contained river temperature as a covariate with survival declining with increasing river water temperature (Table 4.2, Figure 4.2A). Survival also generally declined with increasing time in the haul tank and total length (Figures 4.2B and 4.2C).

Telemetry

Most tagged American shad left the immediate site of release and were later detected by stationary receivers (VR2s) in riverine and reservoir habitats. In Lake Gaston, 55 of the 62 tagged American shad (13 females and 42 males) left the site of release and were located by VR2s or manual tracking at least once during the season. Of the remaining seven, two were found near their release site and four were not relocated; these seven were removed from further analyses. Eighty percent of all tagged fish located in Lake Gaston were detected at least once by VR2 4 in the middle of the reservoir (See Figure 4.1). Specific movement patterns and the amount of time spent in Lake Gaston by tagged individuals varied (Figure 4.3). Approximately 31% of tagged American shad released in Lake Gaston (15% in 2007 and 46% in 2008) migrated to the tailrace of Kerr Dam (past VR2 5). Tagged fish passed VR2 5 from late April to early July, with most passing the stationary receiver in late April to late May (Figure 4.4). It is not known why more fish moved into the Kerr tailrace in 2008 as compared to 2007. Annual differences were not apparently related to average daily discharge rates from Kerr Dam, temperature, or dissolved oxygen (Figures 4.4 and 4.5); however, these

environmental factors may have affected movement on a smaller scale, since temperature and dissolved oxygen can change dramatically with water releases from Kerr Dam. The distance between VR2 4 and VR2 5 is almost 29 km and 15% of tagged fish in Lake Gaston moved repeatedly between these two stationary receivers and two fish completed this migration four times (Figure 4.3B). Tagged fish released in Lake Gaston were located in this reservoir for between 3 and 69 days, with an average total duration of 23 days (standard error (SE) = 2.77 days). Overall, 49% of tagged fish released in Lake Gaston passed downstream through Gaston Dam into Roanoke Rapids Lake (56% in 2007 and 43% in 2008). Of those that passed downstream through Gaston Dam, 59% first made observable upstream migrations, some to VR2 5 in the tailrace of Kerr Dam. Downstream passage occurred from late April to late May in both 2007 and 2008. Also, 32% of the tagged fish that did not pass downstream into Roanoke Rapids Lake during the season were last located by manual tracking just above Gaston Dam during June.

Similar to fish released in Lake Gaston, most tagged American shad released in Kerr Lake were detected by stationary receivers in the middle of the reservoir (Figure 4.6). Of the 66 tagged American shad released in Kerr Lake, 54 (18 females and 36 males) left the site of release and were located by either manual tracking or stationary receivers, eight were not located and four were only found near the site of release. Of the 54 tagged fish that actively migrated, 96% were located in the middle of Kerr Lake on VR2 6, VR2 7, or more commonly (81%), both stationary receivers (Figure 4.6). In fact, many tagged fish released in Kerr Lake moved back and forth (up to four times) between VR2 6 and 7 in the middle of

the reservoir without passing another stationary receiver (Figure 4.6C). Twenty-six percent of tagged fish passed VR2 8 in Clarkesville, Virginia, one or more times (Figure 4.6B). Tagged American shad released in Kerr Lake were located from 3 to 77 days post release, for an average total duration of 29 days (SE = 2.78 days). Approximately 9% of tagged fish released in Kerr Lake (12% in 2007 and 7% in 2008) migrated into riverine habitat in either the Staunton or Dan rivers (these fish migrated past VR2 9 or 10; see Figure 4.1). Tagged American shad entered the lower Staunton River in mid-May and the lower Dan River in late April and early May (Figures 4.7 and 4.8). Fish that entered riverine habitat, spent between 2 h and 30 days there, for an average riverine duration of seven days (SE = 5.81 days). The small percentage of tagged fish from Kerr Lake that entered riverine habitat spent from 0.5 to 51% of their time there, for an average of 16% (SE = 8.94). Only three tagged American shad (6%) migrated downstream through Kerr Dam, none after perceivable upstream movement. Also, 27% of all tagged American shad that did not pass downstream through Kerr Dam were last found just upstream of the dam in June.

Tagged American shad released in the Staunton River in 2008 behaved differently from those released in either reservoir (Figure 4.9). Thirty-one of 32 tagged fish (9 females and 22 males) released in the Staunton River left the immediate release site. Ninety-four percent of those individuals first conducted a rapid downstream movement (i.e., fallback; Figure 4.9B and C) and 6% (two fish) first moved upstream (Figure 4.9A). Of the tagged fish that exhibited fallback in the river, 59% later conducted upstream movements back to riverine habitats in the Staunton or Dan rivers (later passing VR2 9 or VR2 10, again),

whereas other fish were only detected later in Kerr Lake. Excluding the fallback period, tagged American shad released in the Staunton River were found in the Staunton and Dan rivers from mid-April to mid-May, which appears to correspond to the period of the sampling season that had the highest water flow rates (Figures 4.7 and 4.8). Most fish that were detected in June had left the Staunton River and were in Kerr Lake. Tagged American shad released in the Staunton River were found in upstream habitats for 12 h to 72 days post release, with an average duration of 21 days (SE = 3.83 days). Each fish spent between 5 h and 23 days in either the Staunton or Dan rivers, for an average of 4 days (SE = 0.91 days). Thus, these fish spent between 0.5 and 100% of their time in riverine habitat, with an average riverine duration of 27.8% (SE = 6.02%). The two fish that did not exhibit fallback experienced a longer average riverine duration than those that did fallback (non-fallback average = 7 days (SE = 2.8 days), fallback average = 3 days (SE = 1.1 days)). There was not a significant difference in riverine duration for males and females ($t = 0.85$, $p = 0.4002$). Tagged American shad released earlier appeared to spend more time in riverine habitat than those released later in the season, although differences were marginally insignificant ($F = 3.02$, $p = 0.065$; Figure 4.10). No fish released in the Staunton River passed downstream through Kerr Dam during the study; however, 13% were last found just above Kerr Dam in June. Although manual tracking was completed in the lower Staunton River regularly (~once/week in May and June of each year), only one tagged fish was located repeatedly at the same location, suggesting that it died in the river.

Minimum total and minimum upstream migration distances varied greatly among individuals and groups of tagged fish released in different areas (Table 4.3). There was a significant difference in minimum total distance and minimum upstream distance moved by tagged fish released in different upper basin areas ($F = 7.99$, $p < 0.001$ and $F = 24.37$, $p < 0.001$). Tukey's multiple comparisons tests found that fish released in the Staunton River moved significantly more than those in either lakes Gaston ($p = 0.002$) or Kerr ($p < 0.001$) and that fish released in Lake Gaston moved farther upstream than those in either the Staunton River or Kerr Lake (both $p < 0.001$), but no other comparisons were significant (Table 4.3). Despite differences, some tagged American shad released in all areas were found to move between specific stationary receivers multiple times, leading to high total migration distances for some individuals. Tagged fish released in Kerr Lake and the Staunton River combined passed VR2s in the Staunton and Dan rivers at all hours, with no obvious diel peaks (Figure 4.11; fallback periods excluded).

Fallback at Roanoke Rapids

Of the 12 tagged American shad released at Roanoke Rapids, four (33%) experienced fallback past VR2 1, which was ~2.7 rkm below the release site. Of those four, one (17%) was in the net pen overnight and the other three (50%) were immediately released after tagging. Fallback to VR2 1 occurred between 3 h and 2 days after release, with an average of 1 day (SE = 0.38 days). Of the four fish that exhibited fallback, three returned to the main spawning area and the fourth was not detected again. Four tagged fish later out-migrated

past VR2 1, whereas three others remained on the spawning grounds at the end of June, over 50 days post-tagging.

Downstream passage and survival

Estimated immediate survival after downstream passage through any dam was high. Three tagged fish (3.5%) passed downstream through Kerr Dam and all appeared to survive. All three fish were located on VR2 5 on a few sampling occasions, two fish were found to later pass VR2 4 in the middle of Lake Gaston, and one was found in Roanoke Rapids Lake and thus migrated downstream passed both Kerr and Gaston dams (Figure 4.1). For tagged fish in Lake Gaston (including those originally from Kerr Lake), 48% passed downstream through Gaston Dam to Roanoke Rapids Lake. Of those that passed downstream, ~71% appeared to survive, ~21% had unknown fates, and ~7% (2 fish) died. The two fish categorized as definite turbine mortalities were found in the same location (one in 2007 and the other in 2008) on multiple manual tracking occasions in the tailrace of Gaston Dam in Roanoke Rapids Lake. Most fish with unknown fates were those that passed downstream in 2007 and were only detected on one date and either may have suffered delayed mortality in Roanoke Rapids Lake or may have out-migrated through Roanoke Rapids Dam to the lower Roanoke River. Roanoke Rapids Lake was manually searched infrequently, making it difficult to determine the fates of fish only detected once. In 2008, VR2s were placed at Roanoke Rapids to identify downstream passage from Roanoke Rapids Lake to the lower Roanoke River. Between 55% and 67% of tagged fish in Roanoke Rapids Lake in 2008

passed downstream to the lower Roanoke River, with apparent survival of 83% and 17% with unknown fates.

Sampling for American shad eggs

American shad eggs were collected at Roanoke Rapids below the Roanoke Rapids Dam from 10 May 2007 to 9 July 2007, at temperatures ranging from 17.9 to 25.5 ºC (Figure 4.12A). The highest number of eggs/m^3 occurred on 7 June 2007, when the water temperature was 24.3 ºC (Figure 4.12A). No American shad eggs were collected from any plankton samples in the Staunton River. Temperatures between 18 and 25 ºC, when spawning would be expected, generally occurred in the upper Staunton and Dan rivers during late April, May, and sometimes early June (Figure 4.12). Temperatures appeared generally more variable in upper river areas, as compared to at Roanoke Rapids (Figure 4.12), although this may be a function of the times when sampling was completed, as samples were collected between 20:00 and 22:00 EST at Roanoke Rapids and throughout the day at upper river sites.

Telemetry Summary

Most sonic-tagged adult American shad transported to the upper basin of the Roanoke River were later detected migrating within reservoir and riverine habitats. Most tagged fish spent the majority of their time moving back and forth between stationary receivers within a reservoir. Thirty-one percent of tagged fish released in Lake Gaston reached the tailrace of Kerr Dam and 9% of those released in Kerr Lake reached the lower Staunton or Dan rivers. Ninety-four percent of tagged American shad released directly into flowing waters in the lower Staunton River experienced fallback into Kerr reservoir;

however, 59% of those that first migrated downstream later moved back into riverine habitat. Tagged fish released in the Staunton River spent an average of 4 days in riverine habitat. The few tagged individuals that did not suffer fallback spent a longer average amount of time in riverine habitat. American shad were detected in the Staunton and Dan rivers mainly during April and May, the seasonal time period when flows were the highest and temperatures were appropriate for spawning. No American shad eggs were collected to document spawning in upper basin rivers; however, our sample size of plankton tows was fairly small. Although there were only two documented turbine mortalities, the downstream passage rate was not high at any dam (all < 60%). The downstream passage rate through Kerr Dam was < 4%, and no tagged American shad were documented to move downstream through all three dams. Some tagged individuals were located just above both Kerr and Gaston dams in June.

Discussion

Adult American shad can be successfully collected and transported for release into upstream habitats with low overall mortality. As observed in other studies, we found that survival was highest when fish were transported at cooler water temperatures (Layzer 1979; Hendricks 2003). Cooler temperatures generally occurred earlier in the spawning season and were associated with higher levels of dissolved oxygen, which may lead to lower physiological stress for transported fish. In transport studies on two other Atlantic Coast rivers, Walburg (1954) and Layzer (1979) noted that transported females suffered higher mortality than did males. Our most parsimonious model did not contain sex as a factor but

did include total length. The model predicted higher mortality for larger fish which accounts for the same effect because females were generally larger than males. Since mortality was lowest early in the season, fish released early appeared to spend comparably more time in riverine habitat, and most detections in rivers occurred during April and early May, we suggest that it would be best to transport American shad at the start of the spawning season. We collected American shad on their spawning grounds at Roanoke Rapids (Figure 4.1), because fish accumulate there and can be caught and transported more quickly; however, collecting American shad earlier at a more downstream location might result in even lower mortality and better upstream migration, although transport duration would also increase.

Although tagged American shad were successfully transported upstream with low mortality, they spent relatively little time in habitats considered suitable for spawning. American shad typically spawn in the main channels of rivers in areas of shallow depth (generally < 5 m, often much less), with suitable temperature (often between 14 and 24 ºC) and dissolved oxygen (generally > 5mg/L), moderate water velocity (generally 0.3-0.9 m/s), and substrates free from silt (Williams and Bruger 1972; Stier and Crance 1985; Ross et al. 1993; Beasley and Hightower 2000; Bilkovic 2000; Bilkovic et al. 2002; Hightower and Sparks 2003; Burdick and Hightower 2006). The riverine habitat upstream of Kerr Lake met these conditions, but most transported American shad, including most individuals released in the Staunton River, spent much of their time in Kerr Lake. Kerr Lake is a large (22,234 ha), deep (average ~9 m), reservoir that lacks adequate flow to provide suitable habitat for spawning American shad.

It could be speculated that some tagged American shad released in Kerr Lake could not complete the longer-distance migration to reach riverine habitat. Historically, American shad in the Roanoke River and other rivers completed even longer migrations upstream to spawning habitats (Limburg et al. 2003), so the distance from stocking locations to riverine habitat should not be a factor. In addition, some tagged American shad moved considerable distances after transport; however, much of the movement was back-and-forth within a reservoir (see Figures 4.3 and 4.6), rather than a directed movement upstream. Also, our estimates of total movement were likely lower than actual values since they were calculated mainly from detections on stationary receivers (some over 30 km apart) and take no smaller scale movements between receivers into account. Therefore, the relatively small amount of time spent in upstream riverine habitats by tagged American shad was not likely due to an inability to migrate that far upstream.

Another possible cause for the short duration in the riverine habitat was the adverse effects of handling, tagging, and transport on American shad behavior. Numerous studies have shown that American shad subjected to tagging suffer a "fallback" response (Moser and Ross 1993) where they discontinue upstream migration and instead initiate a rapid downstream migration just after tagging (Barry and Kynard 1986; Beasley and Hightower 2000; Moser et al. 2000; Hightower and Sparks 2003; Bailey et al. 2004; Olney et al. 2006; Aunins and Olney 2009). It has been suggested that fallback behavior in alosines may be a response to the stress associated with handling and tagging procedures (Acolas et al. 2004; Olney et al. 2006) and possibly the sound pulses made by sonic tags (Mann et al. 2001;

Popper 2003). During tagging, Sprankle (2005) collected no information on an individual's size or sex to reduce handling time and fallback was only observed for 10% of the tagged fish. Frank et al. (2009) examined chemical levels in blood plasma associated with stress (cortisol, glucose, and chloride ions) in alewife *A. pseudoharengus* under conditions of handling and tagging. Their data suggest that just handling or handling combined with tagging result in similarly elevated stress levels, compared to unhandled fish (Frank et al. 2009). They also observed that alewife transported for 2 hours experienced even greater changes in chemical levels, suggesting more highly elevated stress levels associated with transport. American shad may also be negatively affected by handling and transport. Evaluation of stress levels under different environmental conditions during transport (i.e. temperature, dissolved oxygen, tank size, fish density, etc.) could help define hauling methods that would result in the least impact on fish behavior. Compared to fish released in the Staunton River, fallback was not as well defined for fish released in reservoirs. Possibly, fish released in reservoirs could not orient because of the lack of current or were simply less constrained in the direction of their movements than those in the Staunton River. Also, the sequence of receivers in the river could provide good documentation of fallback behavior. We suspect that handling, tagging, and transport also affected the movements of fish released at reservoir sites. Although our sample size was very small, it was observed that a lower proportion of American shad tagged and transported, but released on the spawning grounds at Roanoke Rapids, experienced fallback. Barry and Kynard (1986) noticed that when tagged American shad returned upstream after fallback, they were in schools with other untagged

American shad. Individuals released on spawning grounds may have suffered lower amounts of fallback, since other American shad were present to form schools. We transported 50-60 American shad at a time since that was the suggested maximum density to transport in our hauling tank (Hendricks 2003). Possibly, transporting larger groups of American shad would reduce fallback and improve behavior.

Environmental conditions in the upper rivers or reservoirs may also have reduced the amount of time that individuals spent in riverine habitat. Fish released in Kerr Lake and those in the Staunton River that experienced fallback into Kerr Lake may not have spent considerable time in rivers because there was not enough flow or temperatures were too warm when fish reached river entrances to attract further upstream migration. Both 2007 and 2008 were drought years and flows in the Staunton and Dan rivers may have been lower than experienced normally, which could affect the amount of time spent in riverine habitats. Also, water temperatures over 25 ºC occurred in the Staunton and Dan rivers in late May and many fish may not have been able to navigate to suitable riverine habitat before temperatures became warmer than expected for spawning (Leim 1924; Leggett and Whitney 1972; Stier and Crance 1985; Ross et al. 1993). Leggett and Whitney (1972) suggested that water temperature may cue the start of the spawning run and warm water temperatures along with reproductive condition may signal out-migration for iteroparous populations. Most tagged fish detected in the upper rivers were there when flows were the highest and temperatures were the coolest seasonally, possibly suggesting that increased rainfall and discharge rates could aid in migration into rivers.

Regardless of the cause, the short duration in suitable spawning habitat could reduce a transported individual's annual reproductive output. American shad are batch spawning fish (Olney et al. 2001; Olney and McBride 2003; Hyle 2003) and studies from American shad populations in Virginia suggest that females spawn every 2 to 4 days, with fish spending about a month in riverine spawning habitats (Olney et al. 2001; Hyle 2003; Olney et al. 2006; Aunins and Olney 2009). Sparks (1998), found that most American shad tagged in the lower Roanoke River spent between 20 and 30 days on the spawning grounds near Roanoke Rapids and we observed that some fish tagged on the spawning grounds remained there for over 50 days. Using this information on spawning frequency and duration, it seems very unlikely that many of our tagged American shad could have spawned multiple batches of eggs during their forays into the upstream rivers. We also found no evidence of spawning from plankton tow samples in upper basin rivers, although these data should be evaluated with caution since our sample sizes were small relative to the size of the system, we did not find any areas where fish were concentrated to guide sampling site selection, and we did not transport a large number of females.

In addition to spending less time in suitable spawning habitat, transported American shad had a lower probability of repeat spawning, compared to fish below the Roanoke Rapids Dam. Of the tagged fish released in either Kerr Lake or the Staunton River, less than 4% (3 fish) passed downstream through Kerr Dam and none appeared to complete the entire migration back to the lower Roanoke River. It is possible that some tagged fish passed downstream after the study or the tag's battery life ended. Tagged fish located just above

dams late in the season could also suggest that some individuals were attempting to outmigrate, but were unable to pass downstream through turbines. In the River Gudbrandsdalslagen, a regulated river in Norway, post-spawning brown trout *Salmo trutta* L. kelts moved back and forth within a reservoir until spillway releases began, when they moved near the dam, possibly searching for a way to pass downstream. These brown trout only outmigrated through the spillways during periods of surface releases (Arnekleiv et al. 2007). American shad consume very little food in freshwater and generally lose considerable weight during spawning runs (Liem 1924; Chittenden 1974; Walter and Olney 2003; Harris and McBride 2009); therefore, the combination of longer migration distances, delayed or ceased outmigration, and turbine mortality (Chittenden 1974; Kynard and Buerkett 1997; Limburg et al. 2003; Leggett et al. 2004) could cause increased mortality and reduced numbers of repeat spawners. Although highly variable, the estimated percentage of repeat spawners in the Roanoke River averages 55% and some individuals spawn during more than two years (Burgess et al. 2007); thus, fish transported above Kerr Lake likely have a reduced chance of repeat spawning compared to fish in the lower Roanoke River.

In contrast to the low passage rates at Kerr Dam, about 50% of fish passed downstream through Gaston and Roanoke Rapids dams. Differences in passage rates may be a result of turbine type and location of input water within the water column. Roanoke Rapids Dam has four adjustable blade propeller-type Kaplan turbines (36,000 horsepower, 20.7-m head and 128.6 rotations per minute) and Gaston Dam has one adjustable and three fixed blade Kaplan turbines (70,000 horsepower, 20.4-feet head and 100 rotations per

minute). Turbines in the Gaston and Roanoke Rapids dams pull input water across a sub-surface weir, so surface withdrawals are generally well oxygenated during the alosine spawning season. In contrast to Gaston and Roanoke Rapids dams, Kerr Dam has nine vertical-shaft Francis turbines (six with 45,000 horsepower, 90-feet head, and 85.7 rotations per minute; one with 17,000 horsepower and 27.4-m head, and 138.5 rotations per minute; and two with 1,600 horsepower, 27.4-m head and 450.0 rotations per minute) and pulls water from the hypolimnion, which is poorly oxygenated. Thus, our results suggest that, like other systems, downstream passage through dam turbines can result in low mortality for American shad, but rates may vary as a result of the dam's configuration and power output (Bell and Kynard 1985; St. Pierre 2003; Sadzinski and Hendricks 2007; Heisey et al. 2008). Structures to increase downstream passage would be expected to improve the proportion of transported fish able to return to the ocean post-spawning, which could reduce the effects of transport on the proportion of repeat spawners in the population.

Environmental conditions appear to affect the annual results of a trap and transport program. Dominion contracted the transport of additional sonic-tagged American shad during the spring of 2009 and preliminary results from their work suggest that more tagged American shad migrated into riverine habitat during a year with higher water volume. During 2009, tagged American shad were released in the Staunton River and Kerr Lake and their movement patterns were identified by detections on stationary receivers placed in the same locations as they were in 2008. However, in contrast to the drought conditions in 2007 and 2008, rainfall in the upper Roanoke River basin during 2009 was similar to historic

averages. The tagged individuals released in the lower Staunton River in 2009 had high levels of fallback, but later moved more frequently between stationary receivers in the Staunton and Dan rivers and spent over twice as much time in riverine habitat (between 9 and 10 days), as compared to tagged fish in 2008. Of the tagged American shad that they released in Kerr Lake in 2009 and were later detected on a stationary receiver, almost 35% entered either the Staunton or Dan rivers, compared to only 9% of the tagged fish released in Kerr Lake in 2007 and 2008. Continued research would help evaluate the relationship between movement patterns and water flow for American shad in upstream habitats and help determine when and how to best transport American shad to upstream habitats.

The overall success of a trap and transport program in a river system is likely affected by release site and upper basin characteristics. American shad released directly into riverine habitat spent more time in riverine habitat than did tagged fish released in Kerr Lake. In addition, a higher percentage of tagged fish in Lake Gaston, the smaller reservoir, reached the tailrace of Kerr Dam, than the percentage of tagged fish released in Kerr Lake that reached the lower Staunton or Dan rivers. Possibly, Lake Gaston is easier for American shad to navigate since it is much smaller and may have detectable flow throughout. Barry and Kynard (1986) observed that American shad schooling and swimming behavior in a dam's tailrace appeared altered when water discharge stopped and suggested that these fish were moving "rapidly back and forth upstream and downstream in an attempt to locate flow" (Barry and Kynard 1986, p. 237). American shad may have a similar difficulty locating flow in large reservoirs, such as Kerr Lake, especially during drought years when annual flows are

comparatively low. However, American shad in the St. Johns River, Florida, successfully migrate through a few natural lakes to reach spawning areas (Williams and Bruger 1972), suggesting that adult American shad can navigate through areas with little or no flow, although lakes on the St. Johns River are smaller and shallower than either Kerr or Gaston reservoirs. Arguably the largest American shad population is found in the highly regulated Columbia River on the Pacific Coast of North America. Columbia River American shad are an introduced species and no restoration is focused on them; however, fish ladders, created to aid Pacific salmon recovery have also increased American shad populations, giving them access to quality spawning habitat upstream of large hydroelectric dams (Petersen et al. 2003). Columbia River dams produce run-of-river reservoirs and fish appear to pass effectively both up and downstream, some fish passing dams over 600 rkm from the river mouth (Petersen et al. 2003). Based on our results and those of other studies, we speculate that transport would be most beneficial for American shad in systems with both small impoundments and large amounts of high quality spawning habitat upstream.

In conclusion, adult American shad can be successfully collected and transported for release into upper basin habitats. Potential concerns about the effectiveness of a transport program include fallback, the low fraction of fish from reservoirs later located in riverine habitat, and the relatively few days spent in riverine spawning habitat, all of which may lead to reduced reproductive output for transported individuals. The effects of handling, tagging, and transport on our results cannot be determined with certainty; however, it could be speculated that American shad would perform better in a large scale transport program, when

fish were handled less, left untagged, and moved in larger groups, than in our small experimental program. Other potential concerns associated with transport are mortality and delays associated with downstream passage through dams, which might be reduced by structures to aid downstream migration. Overall, a transport program would likely be most effective if fish were collected and moved early during the spawning season and were released into areas with high quality, accessible spawning habitat during periods of appropriate spawning temperatures.

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Tables

Table 4.1. Summary of American shad collected and transported to upstream habitats of the Roanoke River, by collection date, including the number collected by electrofishing, the number released alive the following morning from net pens in upstream habitats, the upstream site of release, and the number with sonic tags. "*" illustrates when the pen placed at the Summit release site was removed from the water by people and as a result, most fish died. This sampling date (4/24/2007) was removed from further analyses of mortality rates during transport, since most mortality was not a response to our transport procedures. Parentheses illustrate the number of fish placed in a pen and released from each site in 2007.

Date	Location	# Collected	# Released	# with a tag
4/10/2007	Gaston (Stonehouse)	25	23	5
4/17/2007	Gaston (Stonehouse/Summit)	53 (27/26)	53 (27/26)	10 (4/6)
4/19/2007	Kerr (Island Creek/County Line)	45 (22/23)	42 (22/20)	10 (5/5)
4/24/2007	Gaston (Stonehouse/Summit)	53 (25/24)	28 (22/6)*	5 (4/1)
4/26/2007	Kerr (Island Creek/County Line)	57 (27/17)	38 (22/16)	5 (3/2)
5/1/2007	Gaston (Stonehouse/Summit)	59 (25/28)	46 (22/24)	9 (4/5)
5/3/2007	Kerr (Island Creek/County Line)	59 (23/22)	36 (21/15)	8 (4/4)
5/8/2007	Kerr (Island Creek/County Line)	59 (26/27)	47 (22/24)	8 (4/4)
4/9/2008	Kerr (Island Creek)	53	52	12
4/11/2008	Gaston (Stonehouse)	53	50	11
4/14/2008	Staunton	53	49	11
4/16/2008	Kerr (Island Creek)	51	51	12
4/18/2008	Gaston (Stonehouse)	52	49	12
4/21/2008	Staunton	54	45	10
4/23/2008	Kerr (Island Creek)	54	47	11
4/25/2008	Gaston (Stonehouse)	56	45	10
4/29/2008	Staunton	56	37	11
Total	All sites	892	738	160

Table 4.2. Candidate models for logistic regression of the probability of survival for transported American shad in relation to examined covariates, including the number of parameters in the model, deviance (-2 log-likelihood), AIC and delta AIC values. Temperature = temperature in the river at collection, Time in tank = the number of minutes during transport, TL = fish's total length.

Model	Parameters	Deviance	AIC	Delta AIC
Temperature, TL	3	638.5519	644.5519	0
Temperature, Time in tank, TL	4	637.5423	645.5423	0.9904
Temperature	2	642.4234	646.4234	1.8715
Temperature, Time in tank	3	640.9917	646.9917	2.4398
Temperature, Sex	3	641.8091	647.8091	3.2572
Temperature, Time in tank, Sex	4	640.5021	648.5021	3.9502
Time in tank, TL	3	711.4431	717.4431	72.8912
TL	2	716.8587	720.8587	76.3068
Time in tank	2	717.0687	721.0687	76.5168
Time in tank, Sex	3	715.9137	721.9137	77.3618
Sex	2	721.6662	725.6662	81.1143

Table 4.3. Minimum total and minimum upstream migration distances (km) for tagged American shad released in different areas in the upper basin. Distances are minimum because they were calculated from linear distances between stationary receivers only and do not include any non-straight line movement between stationary receivers.

Release site	Total range	Total average (SE)	Upstream range	Upstream average (SE)
Lake Gaston	5.7 – 311.0	57.9 (10.3)	0 – 44.3	14.2 (2.0)
Kerr Lake	6.0 – 276.3	41.2 (6.4)	0 – 47.3	8.0 (1.8)
Staunton River	21.2 – 212.3	77.1 (9.5)	0 – 57.5	4.1 (2.1)

Figures

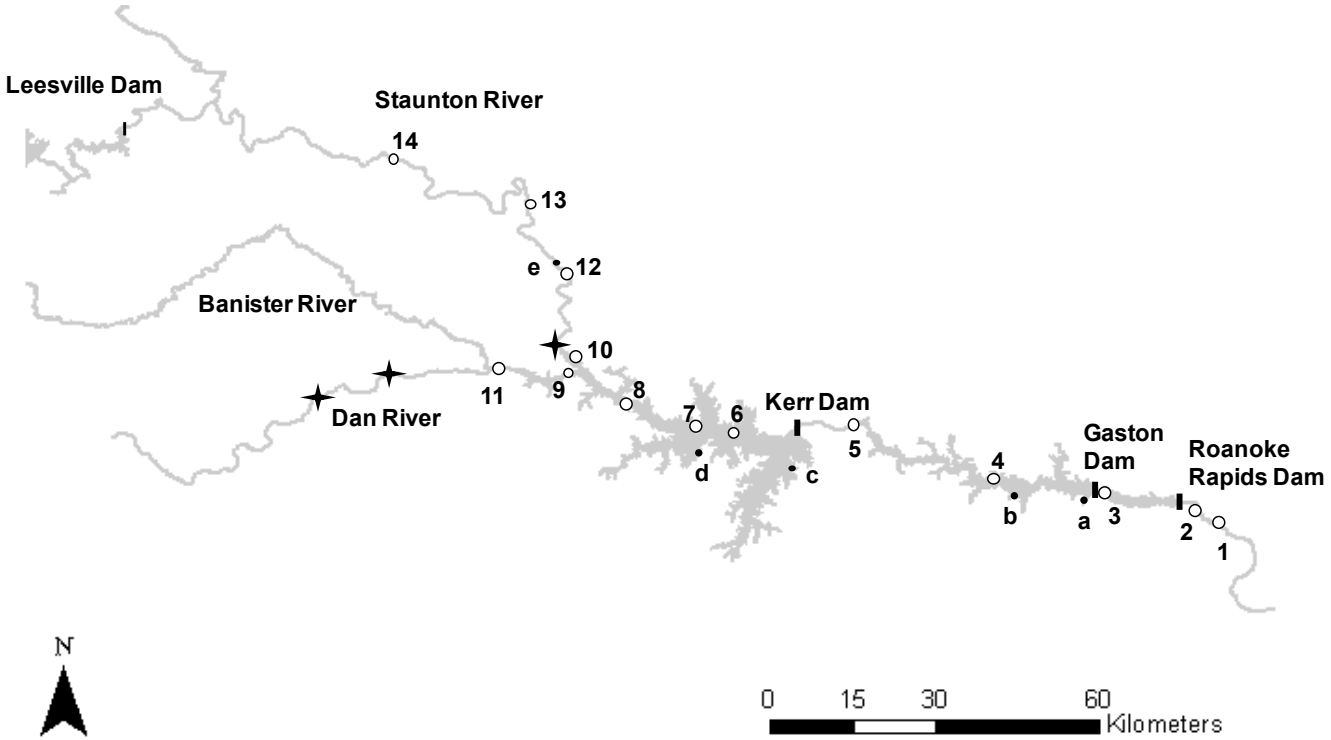


Figure 4.1. Map of the Roanoke River basin in North Carolina and Virginia, including sampling sites, tributary rivers and dams. Filled circles accompanied by letters illustrate release sites (a = Summit, b = Stonehouse, c = County Line, d = Island Creek, e = Staunton River) and open circles with numbers represent VR2 stationary receivers (3, 4, 5, 6, 7, 8, 9, 10, 13, and 14 were used in both years and 1, 2, 11, and 12 were used in 2008 only). Plankton sampling was completed near VR2s 11, 12, 13, and 14, and at sites denoted by filled stars. Impounded lakes are located above the dam with the same name.

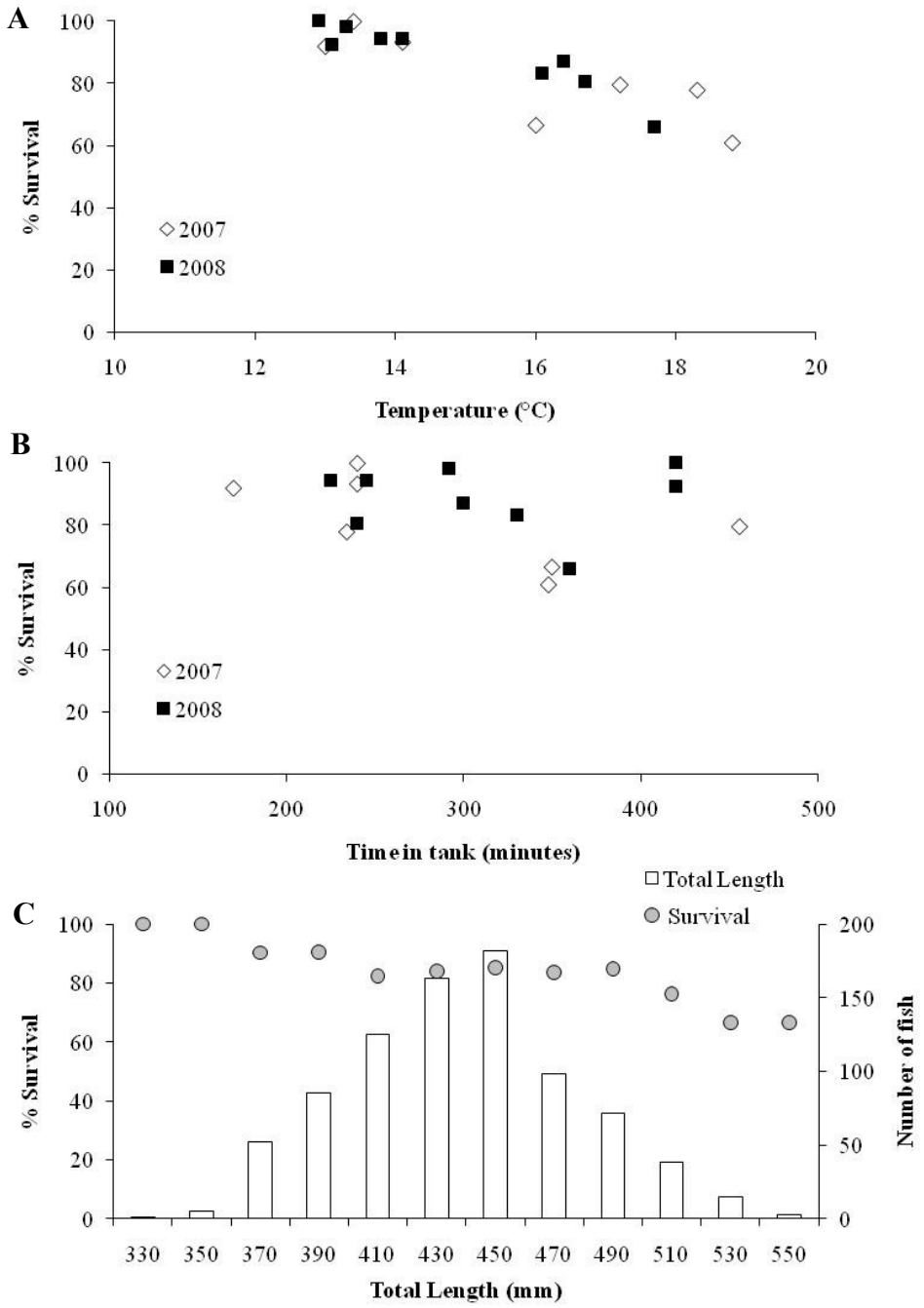


Figure 4.2. Percent survival in transport in relation to parameters found in models with delta AIC scores ≤ 2 (See Table 4.2), including (**A**) river temperature at collection, by collection date and year, (**B**) number of minutes in the haul tank during transport, by collection date and year, and (**C**) the fish's total length, by size class.

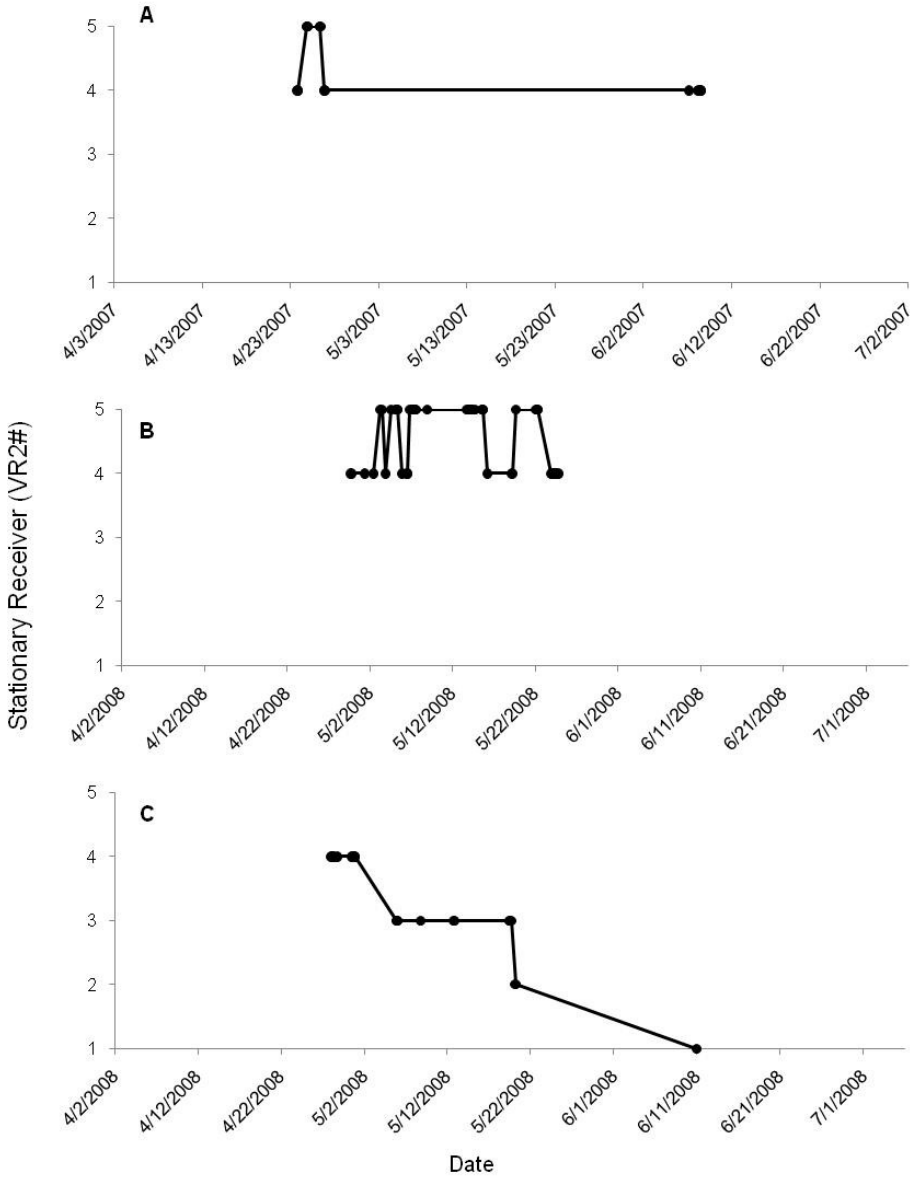


Figure 4.3. Three specific examples representing the different movment patterns of tagged American shad released in Lake Gaston determined by detections at stationary receivers (see Figure 4.1 for the locations of VR2 stationary receivers). Each panel illustrates the detection history of one fish over the season: (**A**) spent time in the middle of Lake Gatson, but migrated once to the tailrace of Kerr Dam, (**B**) migrated multiple times to the tailrace of Kerr Dam, (**C**) detected in the middle of the Lake Gaston then out-migrated to the lower Roanoke River. Dots represent the individual detections on the stationary receiver.

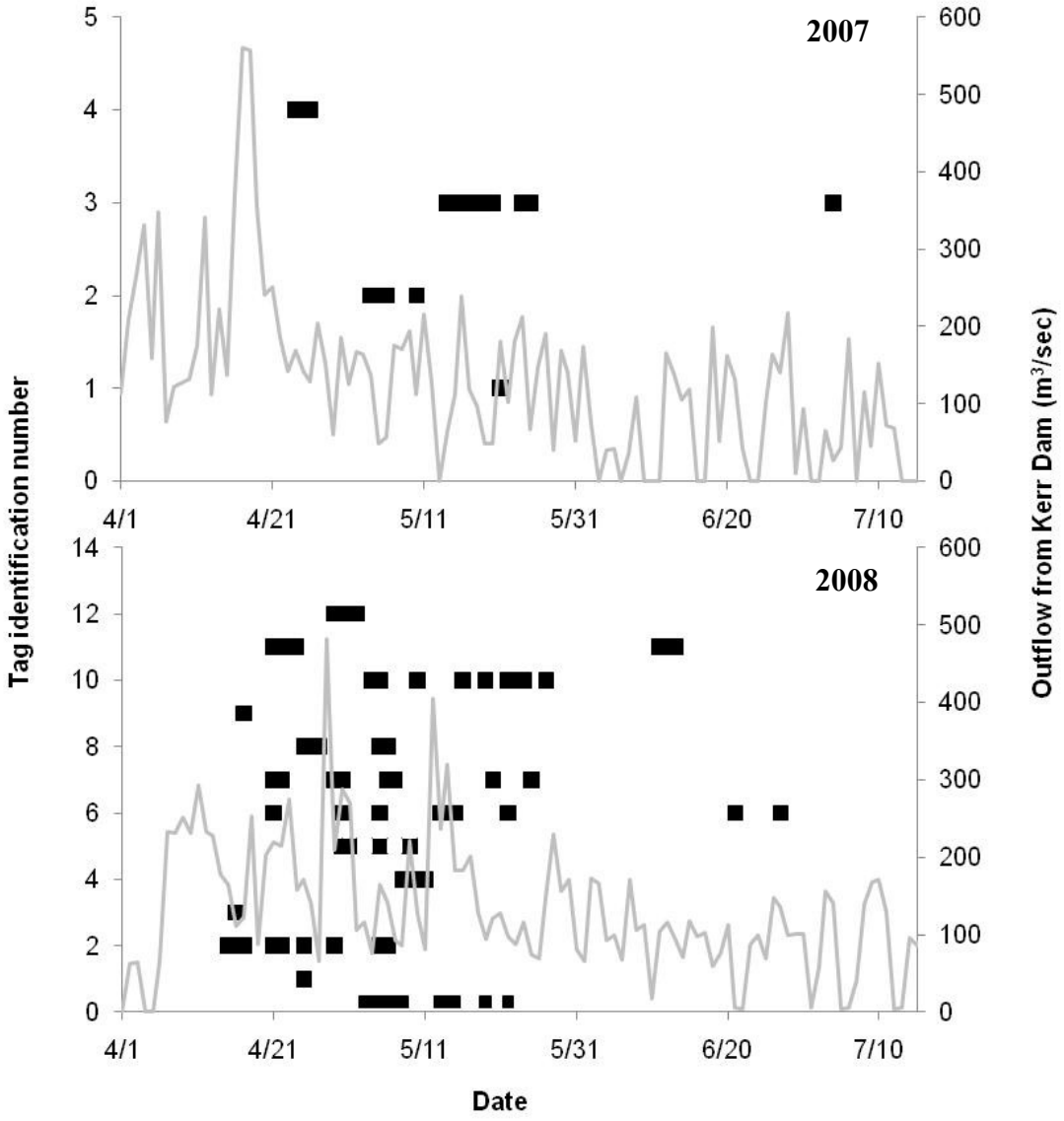


Figure 4.4. Dates in 2007 and 2008 when American shad released in Lake Gaston were detected by VR2 5 (see Figure 4.1) in the tailrace of Kerr Dam, in relation to daily outflow from Kerr Dam. Filled black bars represent the dates when a specific American shad (assigned an arbitrary tag identification number on the Y-axis) was detected. Average daily outflow values (grey lines) are from the USGS gauging station in the Kerr tailrace (02079500).

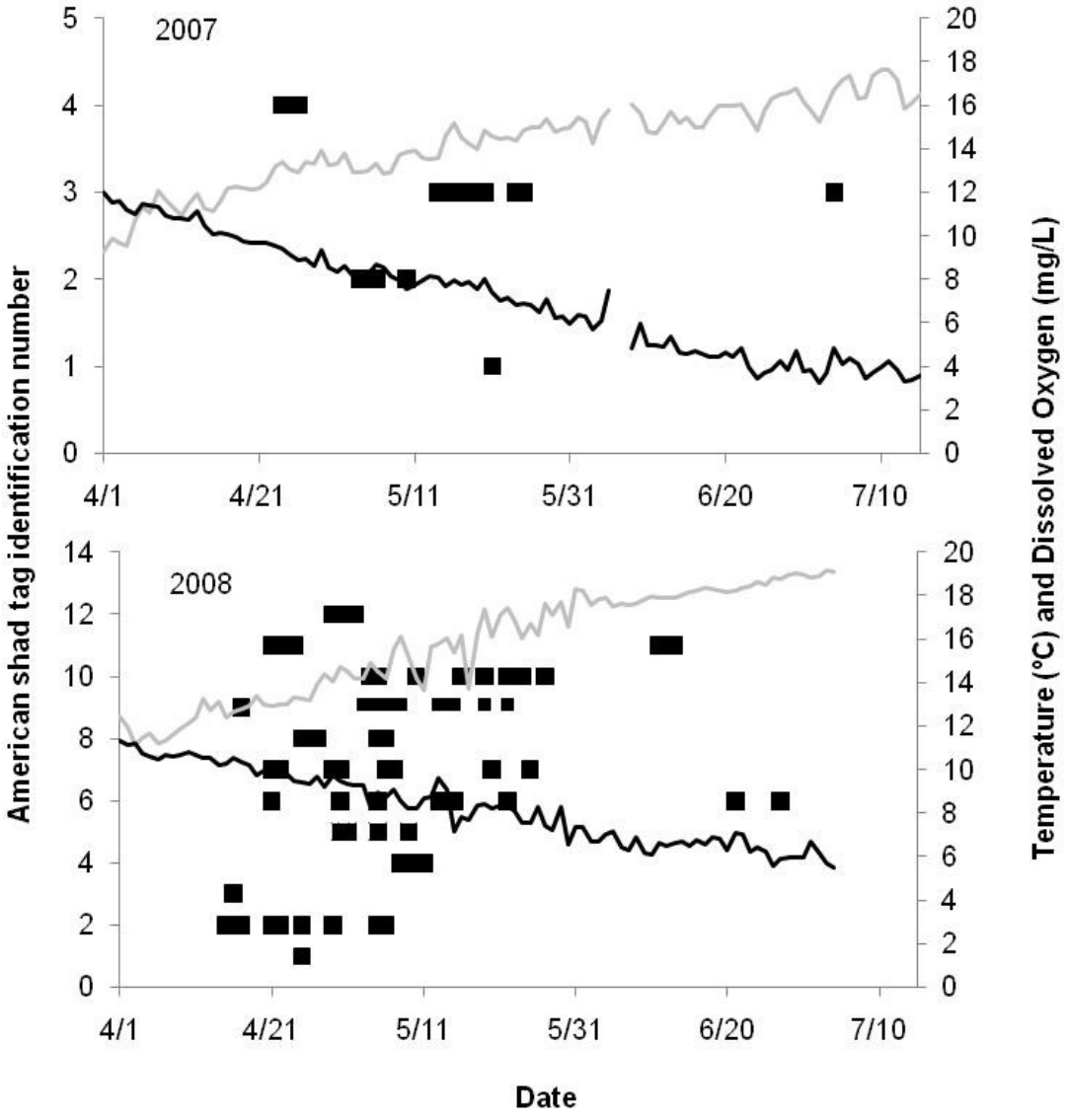


Figure 4.5. Dates in 2007 and 2008 when American shad released in Lake Gaston were detected by VR2 5 (see Figure 4.1) in the tailrace of Kerr Dam, in relation to water temperature and dissolved oxygen. Filled black bars represent the dates when a specific American shad (assigned an arbitrary tag identification number on the Y-axis) was detected. Average daily water temperature (grey lines) and dissolved oxygen (black lines) are from the USGS gauging station in the Kerr tailrace (02079500).

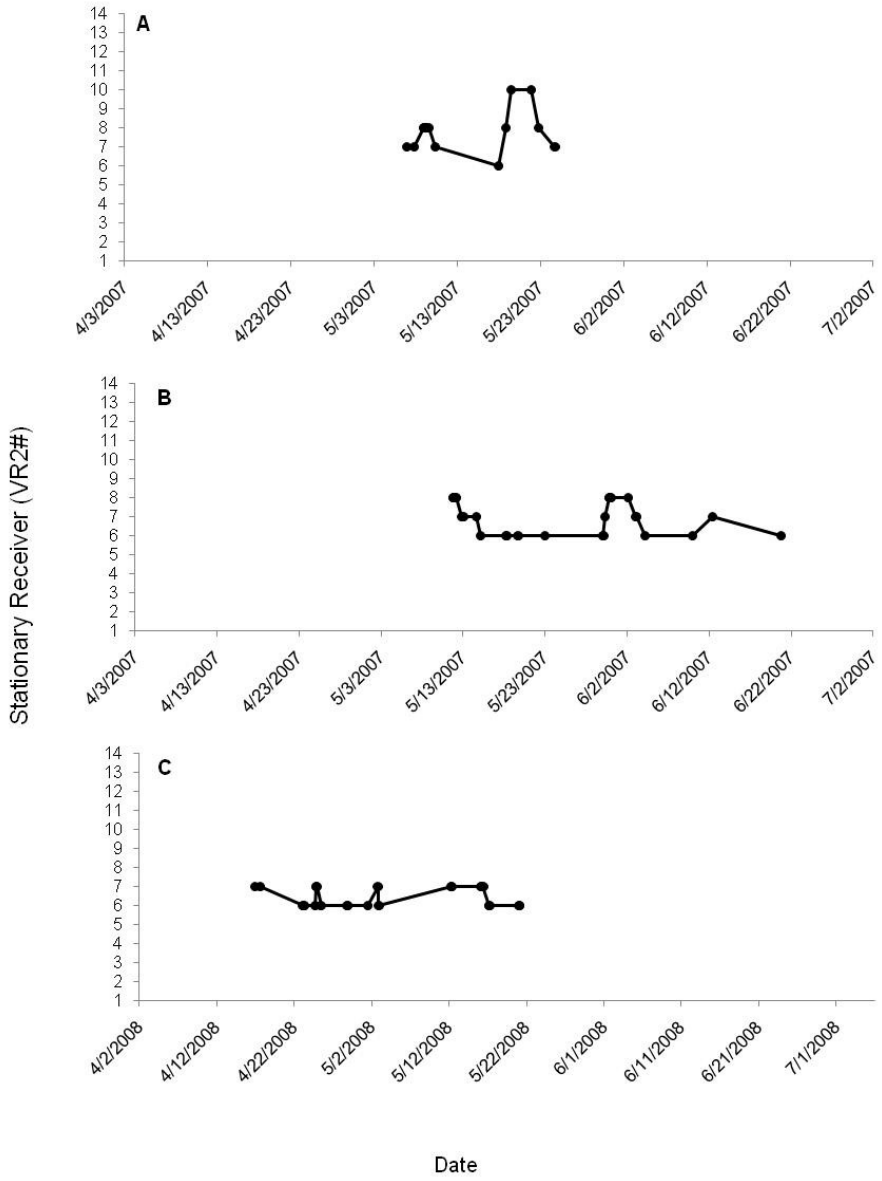


Figure 4.6. Three specific examples representing the different movement patterns of tagged American shad released in Kerr Lake determined by detections at stationary receivers (see Figure 4.1 for the locations of VR2 stationary receivers). Each panel illustrates the detection history of one fish over the season: (**A**) completed a foray into the Staunton River (**B**) meandered within Kerr Lake, (**C**) detected multiple times on VR2 6 and 7, sometimes moving from one to the other in < 3 hours. Dots represent the individual detections on the stationary receivers.

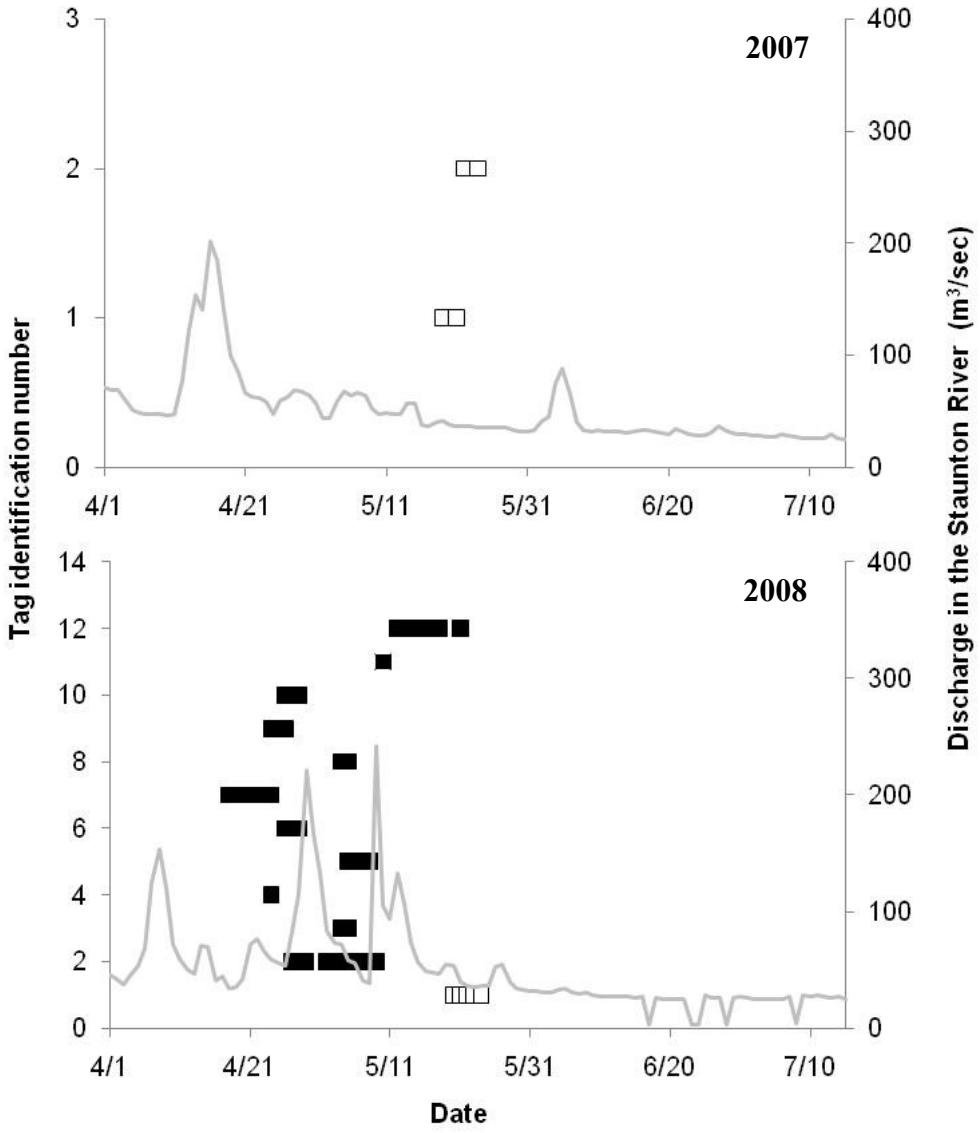


Figure 4.7. Dates in 2007 and 2008 when American shad released in Kerr Lake (open bars) and the lower Staunton River (black bars) were detected by a VR2 in the Staunton River (VR2 10, 12, 13, 14; see Figure 4.1) in relation to discharge in the Staunton River (periods of fallback were excluded). Filled black bars represent the dates when a specific American shad (assigned an arbitrary tag identification number on the Y-axis) was detected. Average daily discharge rates (grey lines) are from USGS gauging station in the Staunton River at Brookneal (02062500).

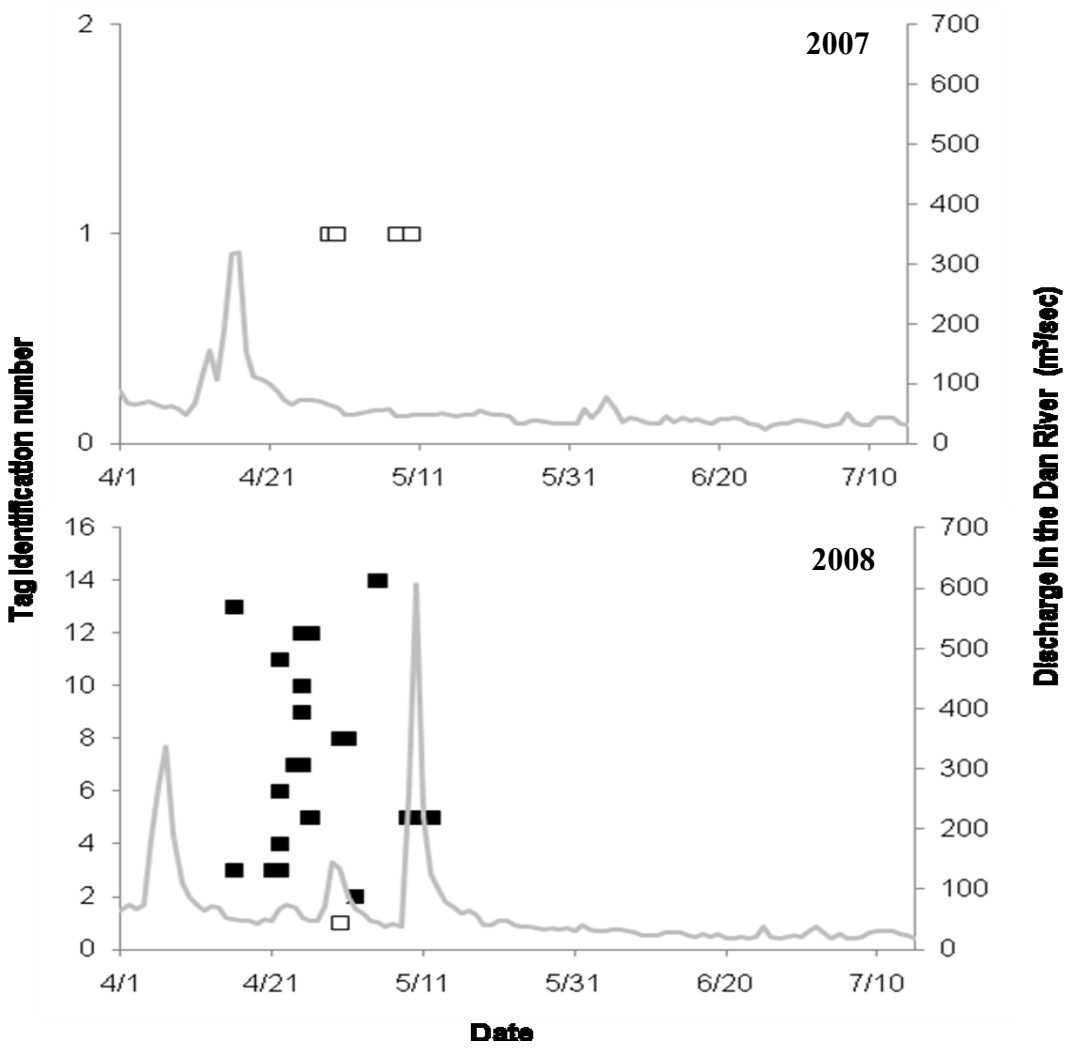


Figure 4.8. Dates in 2007 and 2008 when American shad released in Kerr Lake (open bars) and the lower Staunton River (black bars) were detected by a VR2 in the Dan River (VR2 9, 11; see Figure 4.1) in relation to discharge in the Dan River (periods of fallback were excluded). Filled black bars represent the dates when a specific American shad (assigned an arbitrary tag identification number on the Y-axis) was detected. Average daily discharge rates (grey lines) are from USGS gauging station in the Dan River at Paces (02075500).

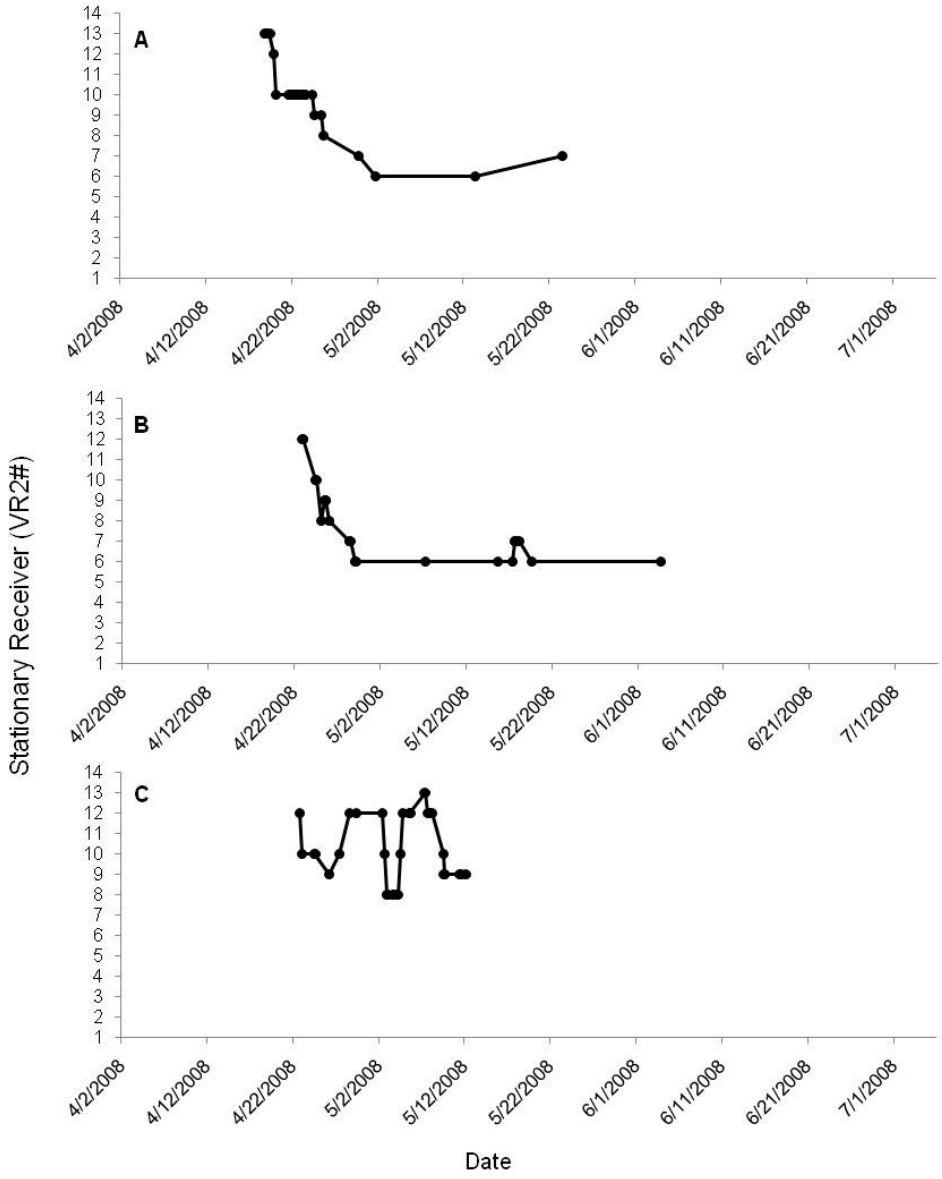


Figure 4.9. Three specific examples representing the different movment patterns of tagged American shad released in the lower Staunton River determined by detections at stationary receivers (see Figure 4.1 for the locations of VR2 stationary receivers). Each panel illustrates the detection history of one fish over the season: (**A**) first made an upstream migration to VR2 13, but spent most time in Kerr Lake (**B**) experienced fallback and spent most time in Kerr Lake (**C**) first expereinced fallback, but then migrated within the Staunton and Dan rivers between late April and mid-May.

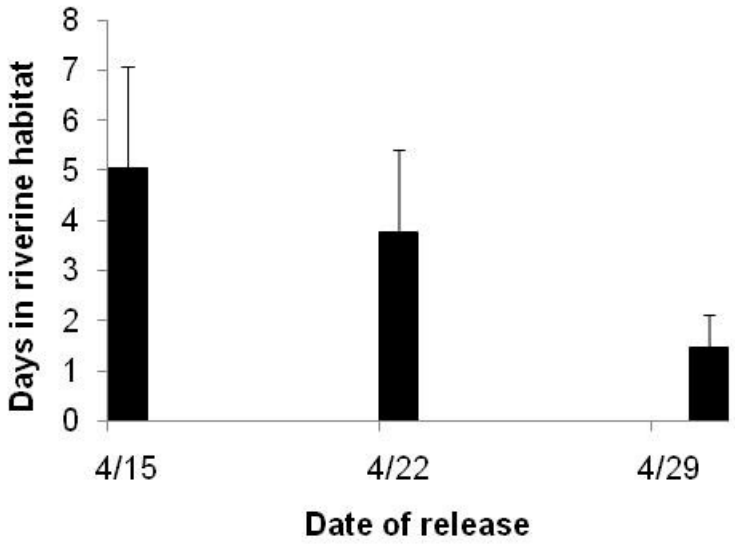


Figure 4.10. Average (+1 SE) number of days spent in riverine habitat by tagged American shad released in the Lower Staunton River in 2008, by release date.

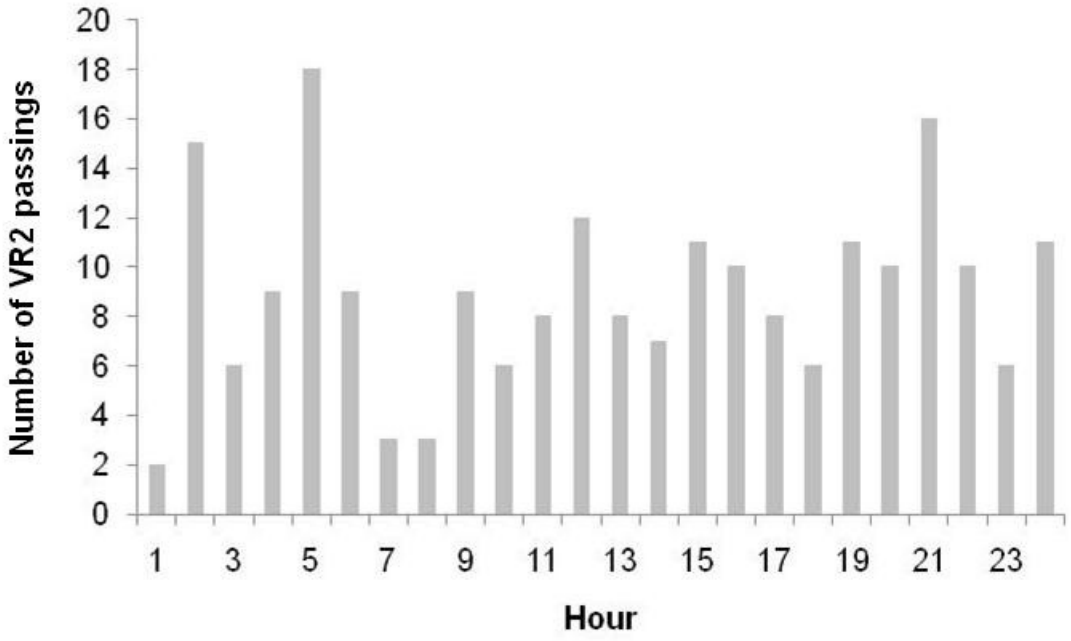


Figure 4.11. The number of times an American shad passed a stationary receiver (VR2) in either the Staunton or Dan rivers (VR2 9 and higher) by hour (Eastern Standard Time). When a specific fish passed a VR2, only the first and last detections were included to reduce the influence of any one time when a specific fish passed a VR2.

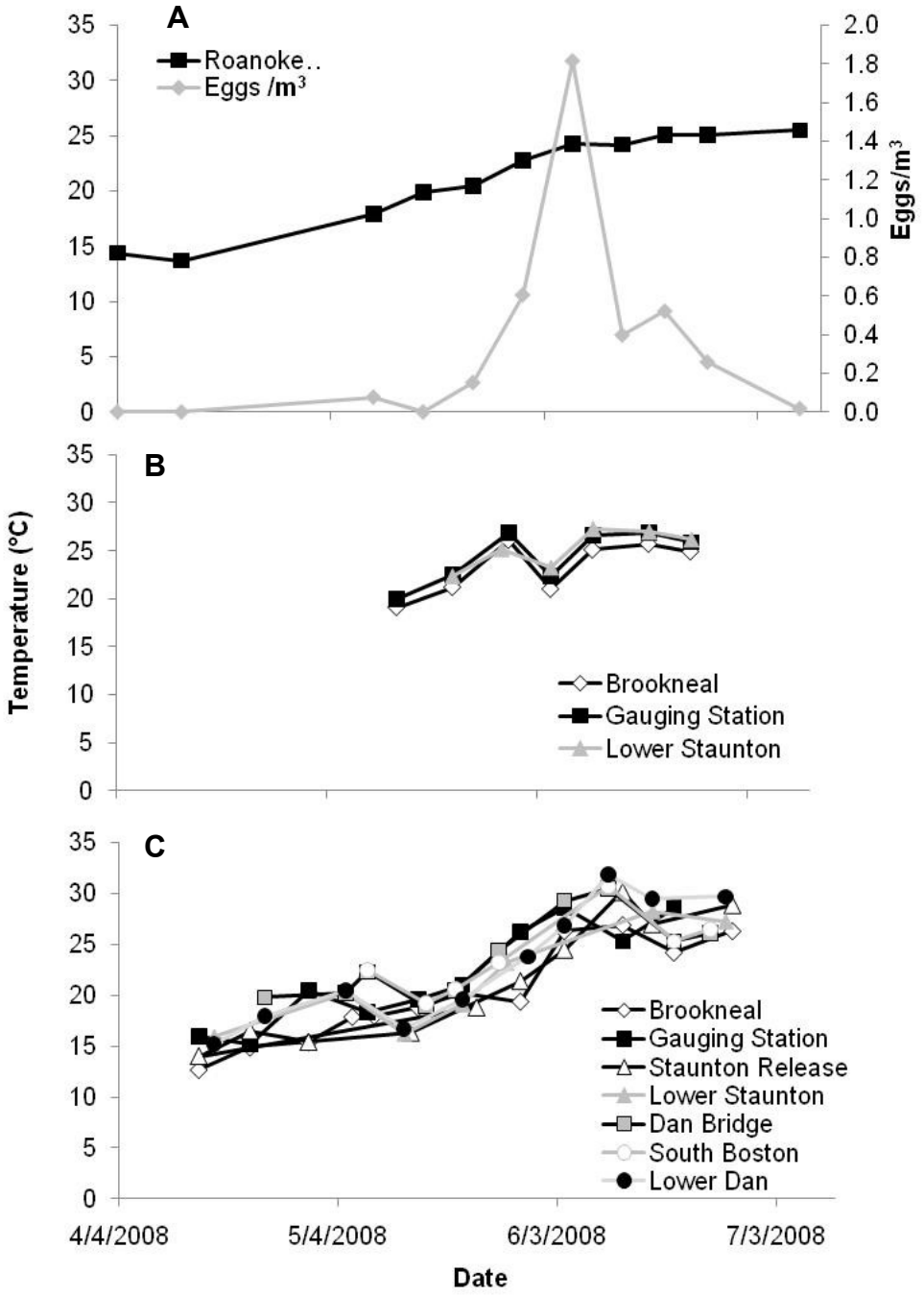


Figure 4.12. Temperature (ºC) and American shad eggs/m^3 by date and collection site at (**A**) Roanoke Rapids in 2007, (**B**) the Staunton River in 2007, and (**C**) the Staunton and Dan rivers in 2008 (see Figure 4.1).

CHAPTER 5. DEMOGRAPHIC POPULATION MODEL FOR AMERICAN SHAD: WILL ACCESS TO ADDITIONAL SPAWNING HABITAT UPSTREAM OF DAMS INCREASE POPULATION SIZES?

Abstract

American shad are in decline in their native range and modeling possible management scenarios could help guide restoration efforts. We developed a density-dependent, deterministic, stage-based matrix model to predict the population-level results of transporting American shad to suitable spawning habitat upstream of dams on the Roanoke River, North Carolina and Virginia. We used data from studies on behavior of sonic-tagged adult American shad and oxytetracycline-marked American shad fry released above and below dams on the Roanoke River, as well as information from other systems, to estimate a starting population size for the Roanoke River and all vital rates. We then modeled the adult population size over 30 years under different plausible scenarios for adult transport, effective adult fecundity, and outmigration survival for adults and young. We also evaluated changes as a result of increased survival rates for either young or adults. The adult female population size in the Roanoke River was estimated to be 5,224. Under present conditions, the model predicted that the American shad population will increase slowly over the next 30 years. Predicted population increases were highest when survival was improved during the first year of life. Transport was predicted to benefit the population only if high rates of egg production and young survival to outmigration could be achieved. Presently, the estimated adult population size is much smaller than either of two assumed values of carrying capacity for

the lower Roanoke River and, as a result, predicted population-level effects of access to additional habitat were lower than they would be if the population was nearing carrying capacity. Better information about natural mortality and carrying capacity for American shad in regulated rivers would improve the model and its evaluation of the benefits of access to additional spawning habitat upstream of dams.

Introduction

American shad *Alosa sapidissima* is the largest herring native to the Atlantic coast of North America from Quebec, Canada, south to Florida, USA (Limburg et al. 2003). Historically, American shad supported valuable commercial and recreational fisheries (Smith 1894; Walburg and Nichols 1967); however, more recently many stocks have suffered declines as a result of dams, habitat change, overfishing, and poor water quality (Rulifson 1994; Hightower et al. 1996; Limburg et al. 2003). Reductions in fishing pressure in some systems and moratoria in others have not resulted in large population increases, prompting research on additional management options, such as population enhancement and improved access to spawning habitat, to improve stocks (ASMFC 2007).

American shad are anadromous and spawn in coastal rivers during the spring and early summer, when temperatures are appropriate (Stier and Crance 1985). Studies suggest that individuals spawn in their natal rivers and some life history traits, such as the percentage of repeat spawners, are river specific (Carscadden and Leggett 1975; Leggett and Carscadden 1978; Melvin et al. 1986). Repeat spawning is observed for populations north of and including the Neuse River, North Carolina, and semelparity is suggested for populations

farther south (Facey and Van Den Avyle 1986). For iteroparous populations, a higher percentage of repeat spawners may be linked to higher lifetime fecundity rates and reductions in annual variability in spawning stock sizes (Leggett 1977).

Dams contribute to American shad population declines by blocking access to suitable spawning habitat upstream and altering flow and habitat downstream (Rulifson 1994; Freeman et al. 2003; Limburg et al. 2003). To mitigate the effects of dams, fish passageways have been constructed to allow individuals volitional upstream passage and both wild and cultured fish have been released in upstream habitats (Cooke and Leach 2003; Hendricks 2003; St. Pierre 2003; Weaver et al. 2003; ASMFC 2007). In some systems, passage of adult American shad along with stocking of young appears to have improved populations (Cooke and Leach 2003; St. Pierre 2003; Weaver et al. 2003). It has been suggested, however, that populations with high percentages of repeat spawners may be negatively affected by access to habitat upstream of dams because they may have higher post-spawning mortality (Leggett et al. 2004). Habitat above dams may also be highly altered and fish must sometimes migrate through large reservoirs; thus, the quantity, quality, and likelihood of reaching suitable spawning habitat at upstream sites may be lower than it was pre-dam construction. Increased mortality passing downstream through dam turbines would cause population reductions, whereas access to upstream spawning habitat might lead to higher production of young, which would lead to population increases. The balance between negative and positive factors would likely be system-specific and would determine whether access to upstream habitats would benefit the population in question.

We developed a density-dependent, deterministic, stage-based matrix model for American shad on a river regulated by dams, but having suitable upstream spawning habitat. We used the model to predict the effects of transporting American shad upstream of dams in the Roanoke River, North Carolina and Virginia, under a few different plausible levels of survival and effective fecundity, and to compare such outcomes to those of increasing survival rates of adults or young. The Roanoke River appears ideal for examining opportunities for transport to upper basin habitats because the population is depressed, upstream habitat appears suitable for spawning, data from stocking and trap and transport programs can be used to evaluate spawning and survival in upstream habitats, and the population experiences moderate (although variable) levels of repeat spawning. This model was developed for the American shad population in the Roanoke River, but after modification of some vital rates, could be useful for evaluating the effects of transport in other regulated rivers.

Methods

American shad in the Roanoke River.—Equations to estimate the carrying capacity of American shad in a river system have been developed using information on the total size of the river, along with historic and current American shad run-size estimates (Hightower and Wong 1997). St. Pierre (1979) developed what is often considered the "rule of thumb" equation for American shad carrying capacity of 124 individuals per hectare of river (124/ha; Hightower and Wong 1997; Weaver et al. 2003) from historic data on the Connecticut River. Water flow on the Roanoke River is regulated by six dams, with the most downstream

located in Roanoke Rapids, North Carolina (river kilometer (rkm) 221; Rulifson and Manooch 1990; Walsh et al. 2005). Other dams on the river's main stem include Gaston Dam at rkm 233 and Kerr Dam at rkm 288. Historically, American shad migrated as far upstream as Salem, Virginia (McDonald 1878); however, the dams provide no fish passage, so spawning is presently restricted to the lower 221 rkm. Assuming 124/ha as the density for carrying capacity and assuming a river length of 221 km with an average width of 100 m, the lower Roanoke River would be expected to support ~273,100 spawning American shad annually. Despite large amounts of riverine habitat, telemetry and egg collections in the Roanoke River (Sparks 1998; Hightower and Sparks 2003) suggest that most spawning by American shad presently occurs in an approximately 90-ha area just below the Roanoke Rapids Dam.

Recently, transport of American shad upstream of dams on the Roanoke River has been considered to improve access to historic spawning sites in the upper basin. The Federal Energy Regulatory Committee (FERC) license for Roanoke Rapids and Gaston dams specifies that Dominion/North Carolina Power must be prepared to move American shad above dams, once the population reaches 20,000 individuals in two years. The intent of the fish passage program was to provide access to riverine habitat above Kerr Dam, the third dam in the Roanoke River system. To help evaluate possible outcomes of access to upstream habitats on the Roanoke River, various studies have been completed. Read (2004) examined habitat features and environmental parameters in main channel and tributary sections of these upper basin rivers to evaluate their suitability for spawning American shad. She used three

models to estimate suitability and found that even with the most conservative model, at least 62 rkm and 39 rkm of habitat would be suitable for spawning during May and June, respectively. Read (2004) also found that American shad eggs in incubators at riverine sites above Kerr Dam successfully hatched, demonstrating that water quality was adequate for spawning. We recently characterized migration, spawning, and survival downstream past dams for sonic-tagged adult American shad released into upstream habitats (Chapter 4). In addition, data on the outmigration of oxytetracycline (OTC)-marked American shad fry released in the main river upstream of Kerr Dam is presently being collected (North Carolina Wildlife Resources Commission (NCWRC) study).

The American shad spawning run in the lower Roanoke River is limited by commercial take in the Albemarle Sound, which includes individuals that spawn in both the Roanoke and Chowan rivers. Commercial harvest in Albemarle Sound averaged approximately 58,000 kg per year between 1972 and 2005 and 75,000 per year between 2000 and 2005 (from Burgess et al. 2007). Using the average weight of an American shad collected each year (Burgess et al. 2007), the commercial fishery was estimated to harvest approximately 38,000 individuals per year from 1972 to 2005 from the Albemarle Sound.

Matrix model development.—Our model includes five stages and uses data evaluated in the form of a pre-breeding census (Caswell 2001; Gotelli 2001; Cooch et al. 2003). American shad have one annual spawning period and all data on adults were collected before the spawning migration in the Albemarle Sound; thus, a model using data in the form of a pre-breeding census (i.e. data collected just prior to the onset of spawning) with an annual

time step, appeared appropriate. The five stages included are: yearlings (age-1) produced below Roanoke Rapids Dam (Yl); yearlings (age-1) produced in riverine habitat above Kerr Dam (Yu); sub-adults (age-2 years and older; SUB); adults (age-3 years and older) spawning below Roanoke Rapids Dam (Al); and adults (age-3 years and older) spawning above the dams (Au; Table 5.1; Figure 5.1). The model was run under a variety of transport scenarios through iteration of the following equation:

$$N(t+1) = AN(t)$$

where $N(t)$ is a vector of the number of American shad in each stage in one time step, A is the population projection matrix (Table 5.1) and $N(t+1)$ is the number of American shad in each stage in the next time step (Caswell 2001).

Density dependence.—Both density-dependent and density-independent factors impact survival for young American shad (Leggett 1976; Leggett 1977; Crecco and Savoy 1984; Crecco and Savoy 1985; Savoy and Crecco 1988; Leach and Houde 1998). To incorporate density dependence into this population model, we modified the production of yearlings below Roanoke Rapids Dam by the number of spawning females there, as it related to an estimate of carrying capacity for the lower Roanoke River:

$$Yl(t+1) = F_{Al} S_{Yl} \left(\frac{K - Al(t)}{K} \right)$$

where $Yl(t+1)$ is the number of female yearlings produced below the Roanoke Rapids Dam in year $t+1$, F_{Al} is the adult fecundity below the Roanoke Rapids Dam, S_{Yl} is the survival rate to become a yearling (age-1) when produced below the Roanoke Rapids Dam, K is carrying capacity below Roanoke Rapids Dam, and $Al(t)$ is the number of adult females at

Roanoke Rapids in year t. While density dependence can be incorporated into matrix models in a variety of ways (Jensen 1995; Caswell 2001, Miller et al. 2002; Rintala and Tianen 2008), using an estimate of carrying capacity to impact the survival rate of yearlings appears reasonable for American shad since riverine spawning and nursery habitats likely limit population growth, whereas oceanic habitat does not likely impact stocks at their current sizes. Yearlings produced above dams were not assumed to be affected by density dependence as habitat is not expected to limit population growth at current stock sizes. We used the more common density equation (124/ha) to estimate the carrying capacity of the lower Roanoke River (273,100/2 for females). However, we also examined results assuming a different density calculation (49/ha) to produce an alternative estimate of carrying capacity for the Roanoke River (109,200/2 for females). This alternative rule-of-thumb was developed by Savoy and Crecco (1994) from more current estimates of population size in the Connecticut River.

Estimation of vital rates.—Vital rates and starting population sizes were generated from data on American shad in the Roanoke River and Albemarle Sound along with literature on other American shad populations. The model includes female American shad only and represents the production of females by females. Whenever possible, information specific to female Roanoke River or Albemarle Sound American shad was used. Vital rates were estimated for the present population spawning below the Roanoke Rapids Dam (lower River) and then modified to include transport to upstream habitats (upper River).

Fecundity.—Data in Holland and Yelverton (1973) suggest that the average female American shad in the Albemarle Sound produces ~272,700 eggs to be spawned annually. More recently, it has been determined that American shad are batch spawners and likely have indeterminate fecundity, thus estimates of fecundity made by counting yolked oocytes in the ovary at the start of the spawning season may be biased (Olney et al. 2001; Olney and McBride 2003; Hyle 2004). To more accurately estimate annual fecundity, estimates of batch size, spawning frequency, and spawning duration for the average female are required (Olney et al. 2001). As for most stocks, these values are unavailable for the Roanoke River population; therefore, the average value from Holland and Yelverton (1973) was used. Average fecundity estimates for the York River generated by Hyle (2004) were higher than previous estimates generated for that system.

Survival to become a yearling.—To estimate survival from spawned egg to age-1, we used data from a variety of sources in the literature. We included egg ripening (50%) and fertilization (90%) rates from hatchery data on the Susquehanna River (Sadzinski and Hendricks 2007). The proportion of American shad eggs to hatch is highly variable and dependent on temperature (Crecco et al. 2007). Limburg (1996) developed the following equation to estimate the duration of time to hatch for American shad eggs as a function of temperature:

$$\ln(EDT) = 8.9 - 2.484 * \ln(T)$$

where EDT is egg development time in days and T is temperature in ºC (See Limburg 1996 for more information on this equation). We used our plankton sampling data at the main

spawning site at Roanoke Rapids from 2005 to 2007 (Chapters 2 and 4) to determine the temperatures experienced by American shad eggs in the Roanoke River and used the model by Limburg (1996) to estimate their duration to hatch. We used the average duration to hatch experienced by a Roanoke River American shad egg (3 days) and the median survival rate for eggs to hatch (66% per day) from Crecco et al. (2007) to estimate egg survival to hatch. We used average survival rates from hatch to 9 days old, from 10 to 18 days old, and from 19 to 35 days old, from Crecco and Savoy (1987), as also used by Limburg (1996). Young American shad spend a variable amount of time in riverine and estuarine habitats before migrating to the ocean (Limburg 1996; Limburg et al. 2003; Hoffman et al. 2008). We assumed that from age 35-150 days, young American shad were in Albemarle Sound and used the average of the two survival estimates developed for American shad juveniles in the Albemarle Sound from Tuomikoski et al. (2008). To estimate survival for American shad age 150-365 days, we used the Lorenzen (1996) equation for oceanic fish. Lorenzen's (1996) equation estimates instantaneous natural mortality as a function of weight. We assumed that American shad in this age range were approximately 100 mm in total length, since most fish collected in September in the Albemarle Sound were slightly smaller (Tuomikoski 2004). In addition, American shad emigrating from the Hudson River between 120 and 200 days in age appeared to be around 100 mm (From Figure 4 in Limburg 2001). We used a length-weight equation in Hoffman and Olney (2005) for juvenile American shad in the Chesapeake Bay to estimate the expected weight of a 100-mm total length American

shad. To estimate annual survival (S), we transformed the instantaneous natural mortality rate (M):

$$S = e^{-M}$$

This annual survival rate was converted to a daily rate and applied to fish aged 150-365 days. We assumed that half of the yearlings produced by each female were females.

Survival to become a sub-adult.—American shad spend most of their lives in the ocean and return to their natal rivers to spawn annually after they mature (Limburg et al. 2003). Very little is known about the oceanic phase of their life history and especially little is known about oceanic survival rates before maturity. We assigned instantaneous natural mortality rates for immature fish, by age, using the same Lorenzen (1996) equation. We assumed no harvest on immature fish and again estimated annual survival rates through the following equation:

$$S_x = e^{-M_x}$$

where S_x is annual survival rate at age x, and M_x is the instantaneous natural morality at age x. Age-specific weights generated by a Gompertz equation for American shad in Albemarle Sound (Hattala et al. 2007) were used as estimates of the average weight at age. Since the survival rate assigned to an age-x fish is survival for the period from age $x-1$ to age x, we used the average of the estimated survival rates for fish age $x-1$ and age x. All surviving yearlings move into the sub-adult stage after one annual time step, as they approach two years in age. The annual survival rate to become a sub-adult (S_2) was therefore the average annual survival of an age-1 and an age-2 female.

Maturation and adult survival.—Within a population, individual American shad mature at different ages (Maki et al. 2001, 2002). In addition, American shad in different systems mature over different age ranges (ASMFC 2007). Therefore, to determine the proportion of sub-adult females that become adults annually, as well as the average annual survival rate for sub-adults and adults in our model, we needed a maturity schedule for American shad specific to the Roanoke River. Maturity schedules for American shad are difficult to estimate, since immature fish cannot be sampled with adults during spawning runs in rivers (Maki et al. 2001, 2002). Estimation can be particularly problematic for stocks with unknown rates of mortality associated with harvest and spawning, as in the Roanoke River, since mortality rates are different for mature and immature fish of the same age (Maki et al. 2002).

For American shad, maturity schedules are generally estimated from age and spawning history information identified on their scales. Two scale marks, both representing a year of age, can be observed on American shad scales: annuli, which represent a year spent in the ocean, and spawning marks, which represent a spawning migration (Cating 1953; Judy 1961; Maki et al. 2001; Olney 2007; ASMFC 2007). When fish are collected in estuaries or rivers during the spawning migration, the edge is also considered a spawning mark (Cating 1953; Judy 1961). From known-aged American shad in the Delaware River, McBride et al. (2005) showed that using Cating's (1953) method to estimate age from scales was biased, suggesting that the ageing method, the hard part, or both, resulted in inaccurate age estimates

for American shad, at least in that specific river. However, ageing by scale marks using Cating's (1953) method is still commonly used in other systems (ASMFC 2007).

To determine a maturity schedule and a survival rate for adults, we used scale ages and spawning histories for American shad females collected from 2000 to 2005 in the Albemarle Sound (from Burgess et al. 2007; Table 5.2). We used scale data from fish collected in the Albemarle Sound, rather than the Roanoke River, since McBride et al. (2005) and Olney (2007) suggest that scales from fish collected in estuaries may be less eroded and more readable than those from fish after the long riverine migration. We assumed that once a female reached maturity, she would spawn each year until she perished. The assumption that spawning occurs each spring after maturity is suggested by scales, since they appear to lack annuli between spawning marks (Maki et al. 2001). To determine a maturity schedule and annual survival rate for mature fish, we used a modified version of the maximum likelihood method developed by Maki et al. (2002) to estimate the maturity schedule for American shad in the York River under conditions of commercial harvest. Conditional maturity by age (π_j) is defined as the following:

$$\pi_j = \text{(number maturing at age j) / (number maturing at age j + number age j remaining immature)}$$

The Maki et al. (2002) model estimates conditional maturity rates by age based on the likelihood of collecting an age-i fish that matured at age-j given spawning histories of all age-i fish. The model accounts for differential survival of mature and immature fish, by including the ratio of mature to immature survival (R) in likelihood components for fish that

matured before the age of collection (i.e. fish that suffered comparatively lower survival to age since they matured earlier). The model does not require the user to assume specific values for immature and mature survival, only to define the ratio between the two rates. We used our assumed estimates of immature survival at age (calculations described above), to estimate both conditional maturity at age and adult survival, by modifying R in the model to be a ratio of adult survival to immature age-specific survival. As an example, Maki et al. (2002) estimated the likelihood of collecting an age-5 American shad (Λ_5) during the spawning migration by the following:

$$\Lambda_5 \propto \left[\frac{A}{A+B+C}\right]^{x_{5,3}} * \left[\frac{B}{A+B+C}\right]^{x_{5,4}} * \left[1-\frac{A+B}{A+B+C}\right]^{x_{5,5}}$$

where

$$A = R^2\pi_3$$

$$B = \pi_4(1-\pi_3)R$$

$$C = \pi_5(1-\pi_3)(1-\pi_4)$$

and $X_{i,j}$ is the number of age-i fish collected that matured at age j. (The likelihood model depiction above was corrected for a typographical error in the publication by Maki et al. (2002), Kristin Maki, personal communication). We modified the following definitions of A, B and C as the following:

$$A = \left(\frac{S_{Al}}{S_4}\right)\left(\frac{S_{Al}}{S_5}\right)\pi_3$$

$$B = \pi_4(1-\pi_3)\left(\frac{S_{Al}}{S_5}\right)$$

$$C = \pi_5(1-\pi_3)(1-\pi_4)$$

where S_{Al} is the annual survival rate for mature fish, and S_x is the annual survival rate for immature fish at age X. All females mature between ages 3 and 8 (Burgess et al. 2007), so likelihood equations were similarly modified for American shad females aged 4 to 8. All conditional maturation rates and S_{Al} were constrained between 0.01 and 1.00. We also required that $\pi_j \leq \pi_{j+1}$ for all conditional maturity rates. This additional constraint seems reasonable considering that with each additional year in age, conditional maturity values should increase. As in Maki et al. (2002), we maximized the overall likelihood (Λ), which is the product of all individual likelihoods:

$$\Lambda = \prod_{i=4}^{8} \Lambda_i$$

Transition and survival rates for sub-adults.—Sub-adults transition to adulthood if they survive to maturity. The proportion of sub-adults that transition at each time step is the sum of the individual proportions of sub-adults that mature at each age, which is a function of conditional maturity and survival rates at and before that age. As an example, the proportion of sub-adult fish that will mature at age-5 had to survive to become age-4 and to not mature until age-5, as illustrated in the following equation:

$$D_5 = (1-\pi_3)(1-\pi_4)\pi_5 * S_3 * S_4$$

where D_5 is the proportion of age-4 sub-adults that will mature at age-5. The total proportion (D) of sub-adults that will mature at each time step is the sum of all (similarly calculated) individual proportions:

$$D = \sum_{j=3}^{8} D_j$$

Because the model is in the form of a pre-breeding census, those that mature and migrate for the first time will have suffered mortality associated with harvest in the estuary, but not associated with the spawning migration. It is unknown what proportion of the added mortality associated with being an adult is due to the spawning migration, compared to the commercial fishery. As a survival rate, we assigned maturing fish the average mortality rate they would experience as an immature fish at age and that of a mature fish (S_{Al}). Thus, the total proportion of sub-adults that mature at each age (DS_t) is the product of the age-specific maturity proportion (D_j), and the average of the age-specific immature survival rate (S_j) and the adult survival rate (S_{Al}). The total proportion to mature and survive to the adult stage is the sum of each individual age specific proportion:

$$DS_t = \sum_{j=3}^{8} \left(D_j \left(\frac{S_j * S_{Al}}{2} \right) \right)$$

where, S_t is the proportion that survive from the sub-adult to adult stage.

The proportion of fish in the sub-adult stage that remain immature is $(1 - D)$. The rate to survive and stay as a sub-adult in the next time step is the product of the proportion of fish that remain immature $(1 - D)$ and the average survival rate of a remaining sub-adult fish. To calculate the average survival rate for remaining sub-adults, the proportion of fish remaining sub-adults at each age must be estimated. For an age-5 fish, the proportion to survive and remain immature ($S(1 - D)_5$) would be estimated by the following:

$$S(1-D)_5 = (1-\pi_3)(1-\pi_4)(1-\pi_5) * S_3 * S_4 * S_5$$

To estimate the average survival rate of a remaining fish, we summed the multiple of each age-specific proportion to remain immature, by its age-specific survival rate, and divided by the sum of the proportions to remain immature using the following equation:

$$S_{SUB} = \sum_{j=3}^{8} \left[\frac{S(1-D)_j \, S_j}{\sum_{j=3}^{8} S(1-D)_j} \right]$$

where, $S(1-D)_j$ is the proportion to remain immature at age j and S_{SUB} is the average survival rate of a sub-adult. Thus, the proportion to survive and remain a sub-adult is the product of the proportion remaining immature $(1-D)$ and the average survival rate for immature fish (S_{SUB}).

Vital rates for transported American shad.—To estimate vital rates for American shad transported to the upper Roanoke River basin, we used data on sonic-tagged adults transported to upstream habitats in 2007 and 2008 (Chapter 4), OTC-marked American shad fry released by the NCWRC in riverine habitats just below the spawning grounds at Roanoke Rapids and also upstream of Kerr Dam (Kevin Dockendorf NCWRC, personal communication; NCDMF and NCWRC 2006), and literature on other American shad populations (Bell and Kynard 1985; Sadzinki and Hendricks 2007).

Behavior of transported sonic-tagged adult American shad in habitats above Kerr Dam and below Roanoke Rapids Dam suggests differential spawning effort and post-spawning survival in the two areas. Our results suggest that most transported American shad spent less time in riverine habitat, compared to tagged fish at Roanoke Rapids (Sparks 1998;

Chapter 4). The reason for the reduced time in riverine habitat upstream may be a result of environmental conditions in the upper rivers, fish being unable to find suitable spawning habitat, or the effects of transport, and may vary annually with environmental and transport conditions. We compared time spent on the Roanoke River spawning grounds from telemetry data in Sparks (1998) to time spent in upstream riverine habitats by transported American shad that did not exhibit a downstream movement just after release (Chapter 4) to estimate the fraction of spawning expected in suitable upstream habitat. American shad are batch spawners (Olney et al. 2001; Olney and McBride 2003; Hyle 2004), and female spawning frequency has been estimated to be approximately 2-3 days (Olney et al. 2001; Hyle 2004); thus, it is unlikely that annual fecundity could be as high for females found in suitable spawning habitat for only a fraction of the spawning period. We evaluated the results assuming that transported American shad were only able to spawn 1/3 as many eggs as those left in the lower Roanoke River and also assuming that they spawned the same number of eggs.

We also used data on outmigration behavior and downstream dam passage mortality from our sonic-tagged adults to estimate the proportion of transported American shad expected to be repeat spawners. We evaluated three different survival rates for transported females. First, we examined predictions assuming no survival of transported fish. No sonic-tagged fish transported upstream of all three dams in 2007 or 2008 were documented to return to the lower Roanoke River (Chapter 4) and assuming that they cannot survive in the reservoir over the rest of the year, almost no transported individuals would be expected to

become repeat spawners. Second, we evaluated the survival rate expected if all females located near the dam were able to outmigrate. We observed that some females were located near the upstream ends of dams near the end of season, possibly illustrating that individuals were unable to pass downstream through the turbines, but were available to outmigrate. For this rate, we assumed that the survival rate for adults above the dam was that of adults below the dam, but reduced by 10% for each of the three dams (i.e. proportion near the dam * survival below the dam * 0.9^3), as appears reasonable, since some mortality is associated with downstream passage (Bell and Kynard 1985; Sadzinski and Hendricks 2007; Chapter 4). The third rate examined would be considered optimal; it assumed that all fish outmigrated, but the survival rate again was that for fish below the dam reduced by 10% for each dam passed to account for downstream passage mortality.

To improve the American shad stock in the Roanoke River, the NCWRC has released a known number of known-age OTC-marked American shad fry annually from 2002 to 2008 into suitable riverine habitat above Kerr Dam and below Roanoke Rapids Dam. Ages at marking varied annually (3 to 9 days in age) and double marks were given to fry released in riverine habitat above Kerr Dam and a single mark to those released below Roanoke Rapids Dam. Fry were generally released the day after the final marking. In the fall, the NCWRC collects juvenile American shad in the lower Roanoke River and examines a proportion for the presence and number of OTC marks (Table 5.3). Assuming that all OTC marked individuals were the same age at capture in the lower river, the number collected from each release location (N_{Loc} ; either upper (u) or lower (l) river) would be a function of the number

of OTC marked fry released there (R_{Loc}), the location specific survival (S_{Loc}), and catchability (C):

$$N_{Loc} = R_{Loc} * S_{Loc} * C$$

Using age-specific survival rates for fry below Roanoke Rapids Dam (stated above), we estimated catchability and from that, we estimated survival for fry released above Roanoke Rapids Dam. Recent catches of OTC-marked American shad older than one year in age in lakes Gaston and Roanoke Rapids suggest that some young did not emigrate during their first fall (Kevin Dockendorf NCWRC, personal communication). Downstream passage structures for juveniles might induce more juveniles to outmigrate. To evaluate possible outcomes with the addition of downstream passage structures, we also assumed that those in the upper basin would have the same survival as those in the lower river.

Starting values for population size.—The population size of American shad in the Roanoke River is unknown, but appears small compared to historical levels (Burgess et al. 2007). We used data from the NCWRC fry stocking program to estimate the number of adult female American shad in the Roanoke River from 2002 to 2008. Assuming equal catchability, behavior, and survival of wild and hatchery fry released below Roanoke Rapids Dam, we used the ratio of wild to OTC-marked juveniles collected by NCWRC in the fall as the ratio of wild to hatchery fry at age in the system and thus estimated the number of wild fry at age. For example, if 1 million OTC-marked fry were stocked and fall samples showed a 10:1 ratio of wild to OTC-marked juveniles, then it would be assumed that there were 10 million wild fry in the river at the age of stocking. We did not account for any added

predation mortality that is sometimes associated with stocking procedures; only a small amount (variable, but usually < 2%) of predation mortality was estimated for American shad fry stocked at similar densities in the Susquehanna River (Johnson and Ringer 1995, 1998). The number of females to spawn in a given year ($N(t)$) was estimated as a function of the estimated number of wild fry at age produced that year ($W_x(t)$), female fecundity (F_{Al}), and the survival rate of eggs from spawn to the age of the OTC-marked fry at release (S_{W_x}):

$$N(t) = \frac{W_x(t)}{(F_{Al} * S_{W_x})}$$

Marked fry were released at 4 to 10 days old in the lower Roanoke River between 2002 and 2008; therefore, S_{W_x} varied annually depending on the age of fry at release.

To obtain an estimate of precision for our annual adult female population estimates, we used a parametric bootstrap technique (Efron and Tibsirani 1993). Our bootstrap estimate included: the proportion of OTC-marked juveniles collected, female fecundity, time to hatch, survival rate to hatch, and survival rate to 4-10 days in age. We did not include egg ripening or fertilization rates, since we do not have estimates of variability for those rates (i.e. only averages were presented). For fecundity and time to hatch, we assumed a normal distribution and used standard error estimates from the data (Holland and Yelverton 1973; data in Chapter 2 and 4). For OTC-marked juveniles, we assumed a binomial model and used annual estimates of sample size and proportion with OTC marks. Although survival rates can be described by a binomial model (i.e alive or dead), the estimates used in this study were obtained from catch-curve analysis (or unknown methods) and appropriate sample sizes

for the binomial model were unknown; thus, we generated random values within the ranges observed in the studies (Crecco and Savoy 1987; Crecco et al. 2007). We produced 1,000 bootstrap samples and assigned our lower and upper error bars as the 2.5% and 97.5% values, respectively.

For our matrix model calculations, we used the average $N(t)$ from 2002 to 2008 as a starting value for adult females in the population. If a constant environment and density-independent growth are assumed, the distribution of individuals in each stage will stabilize after some number of time steps. This distribution can be determined from the right eigenvector of the projection matrix (Caswell 2001). We used values determined by the stable stage distribution of the model, when run assuming no density-dependence and no transport, as starting values for the number of female yearlings and sub-adults in all model runs. To examine if the production of juveniles over the seven years appeared relatively stable, we compared the estimated number of fry stocked below Roanoke Rapids (standardized to 18 days in age), with the proportion of juveniles collected with OTC marks, using linear regression. If the number of fry released was significantly correlated with the proportion of juveniles collected with OTC marks, then the number of wild fry produced annually was reasonably similar over the years. We standardized the fry to a common age at release, since they were released at different ages in different years, which could affect their survival rate to capture.

Analyses.—The primary purpose of this modeling exercise was to evaluate if and under what conditions transporting adult American shad above dams on the Roanoke River

might increase the population size. In studies employing matrix models, population growth over time and under different management options is often evaluated with eigenvalues and eigenvectors; however, in a density-dependent model, vital rate(s) are a function of population size and thus the eigenvalues and eigenvectors of the population matrix change with population size. Thus, we evaluated the utility of each suggested management scenario by the total number of adult females estimated after 30 time steps (30 years). We ran the transport model assuming a carrying capacity of either 136,526 (124/ha) or 54,610 (49/ha) adult females, under each survival scenario (two fecundity rates for adults, three survival rates for adults, and two survival rates for young) assuming that 10% to 50% (by 10%) of adults were transported to upstream habitats. The lowest values examined were those expected under current environmental and transport conditions. Increased values for fecundity and survival would be expected under optimal environmental conditions or with the establishment of facilities to improve downstream passage. We then ran the basic model (no transport) at each assumed carrying capacity, but either increased adult survival 5% to 25% (by 5%) or increased yearling survival 5% to 25% (by 5%), to predict if management options to improve survival (e.g. reducing harvest in Albemarle Sound to increase adult survival) would be more or less beneficial than transport. Finally, the transport model was run under both estimates of carrying capacity assuming that the population included 20,000 adults (10,000 females assuming a 1:1 sex ratio) to evaluate the effects of transport at the population size specified in the FERC license for Roanoke Rapids Dam. Many vital rates used in this study were not calculated from data on American shad in the Roanoke River;

therefore, there is likely error associated with the specific population projections. However, assuming the rates used were reasonable, the model should be useful for comparing between different management options. Thus, comparisons between scenarios, rather than the specific numbers generated, should be considered the focus of this modeling exercise.

Model evaluation.—We evaluated the fit of the matrix model using a few techniques. First, using our model estimates for the stable stage distribution, the annual survival rate for adults, and the annual rate to transition to adulthood, we estimated the percent of adults expected to be repeat spawners and compared that to the actual percent of repeat spawners in the population. Second, using estimates of survival and maturity, we estimated the expected proportion of American shad to be collected by age and spawning history and compared that to the actual age and spawning histories of fish collected. Third, we used our model to estimate the number of OTC-marked fry released below the Roanoke Rapids Dam expected to return annually as spawning adults between 2005 and 2008. The numbers of adult American shad from the spawning grounds (2005 to 2008) that were examined for OTC marks (n = 400) and found with single OTC marks (n = 7) were small; thus, we included results from both male and female American shad. Males in the Roanoke River may mature earlier than females (Burgess et al. 2007), possibly influencing results. We compared the predicted proportion to return (number expected per year divided by the average number of adults predicted on the spawning grounds) to the proportion that actually returned (number with an OTC mark divided by total number sampled for OTC marks) between 2005 and 2008. We assumed that the population had a 1:1 sex ratio (i.e. we doubled our female

population estimate to get the total population estimate and we did not half the number of yearlings produced by females to include yearlings that were both male and female). We similarly completed a bootstrap analysis assuming a binomial distribution for the proportion of returning adults with an OTC mark, to assign precision to our estimates (2.5% and 97.5% values were again used for error bars). In addition, we estimated the number of 18-day-old female fry required to produce one spawning female and compared that value to the 320 ~18 day old fry to produce one adult estimate for the Susquehanna River (Johnson and Ringler 1995, 1998; Sadinzki and Hendricks 2007).

Results

Population parameters

The estimated number of adult female American shad in the Roanoke River, North Carolina, between 2002 and 2008, ranged from 1,965 in 2006 to 8,449 in 2004 with an average of 5,224 individuals (Figure 5.2). This estimate puts the population at 4% of the assumed carrying capacity (124/ha) for the lower Roanoke River system. No pattern in the number of adult females over the period from 2002 to 2008 was evident (Figure 5.2). Bootstrap analyses illustrated the lower precision in estimates from earlier years, when fewer OTC-marked fry were released and fewer juveniles were examined for OTC marks (Table 5.3). The proportion of OTC-marked juveniles collected in the lower Roanoke River was significantly related to the number of OTC-marked fry released earlier that year in the lower Roanoke River ($R^2 = 0.907$, $p < 0.001$; Figure 5.3), suggesting that the production of juveniles was of similar magnitude in all years between 2002 and 2008.

The modified Maki et al. (2002) likelihood model estimated the adult annual survival rate at 0.2516, which corresponds to an instantaneous mortality rate (Z) of 1.3799 for spawning adult females. Instantaneous natural mortality rates (M_j) for sub-adults (Table 5.4) from the Lorenzen (1996) model were much lower than the estimated Z for adults, suggesting that survival declined as a result of the spawning migration and commercial harvest. In fact, the average ratio of adult to sub-adult survival (R value in Maki et al. 2002) would be 0.4380. As constrained in the likelihood model, females matured between ages 3 and 8 and the proportion that matured at age either increased or stayed the same with increasing age (Table 5.4). Most females were predicted to mature at age 4 (Table 5.4) and over 85% between ages 4 and 6. Over 95% of American shad females were predicted to mature by 7 years of age (Table 5.4).

Model runs

Vital rates used in the basic model and those assuming transport upstream of dams are presented in Table 5.5. The matrix model for American shad in the Roanoke River was first run without the density-dependent function for yearling survival and assuming no transport to obtain starting population sizes for yearlings and sub-adults. The density-independent model had a λ value of 1.0771, suggesting a slightly increasing population. Assuming 5,224 adults, the stable stage distribution from the density-independent model suggested starting values for yearlings and sub-adults below the Roanoke Rapids Dam of 49,299 and 31,967, respectively.

The model predicted that transport of small percentages of American shad would result in an increasing population; however, increases would generally be slower than

expected without transport (Figures 5.4 and 5.5). The basic model with density-dependence, assuming a carrying capacity of 136,526 adult females, predicted that the adult female population would reach 22,300 after 30 years under conditions of no transport. Therefore, the model predicted that the population would more than quadruple to reach approximately 16% of carrying capacity (124/ha) for the lower Roanoke River, under current conditions. We examined possible results of transporting 10% to 50% (by 10%) of the population above all three dams under different scenarios (two fecundity rates, three survival rates for adults and two survival rates for yearlings, see Table 5.5). The only scenario that resulted in more than 22,300 females after 30 time steps occurred when all vital rates were at their highest (Figure 5.4L). Similar results were obtained when the assumed carrying capacity was lower (Figure 5.5). If carrying capacity was 54,610 adult females, the population would only be expected to reach 12,400 adult females after 30 years. Under current conditions, the population would thus be expected to reach almost 23% of carrying capacity (49/ha). The population would similarly only be expected to benefit from transport under high levels of adult fecundity and survival of young (Figure 5.5 K and L).

The number of adult females in the Roanoke River increased under all conditions of elevated survival of adults or young (Figure 5.6). Increasing yearling survival appears more influential than increasing survival of adults. For example, the model predicted that after 30 time steps with a 25% increase in adult survival, the population would reach just over 33,300 individuals (24% of carrying capacity at 124/ha), whereas if yearling survival was increased by 25%, the model predicted that after 30 time steps the population would reach just over

51,500 individuals (38% of carrying capacity at 124/ha). The assumed value of carrying capacity greatly influenced the predicted population-level effects of changes in survival for adults and young—improvements in survival were predicted to be much more profound under the higher level of assumed carrying capacity (Figure 5.6).

The effects of transport were also examined assuming that the population first reached 10,000 females; i.e., the FERC-mandated trigger for fish passage (Figures 5.7 and 5.8). Assuming carrying capacity values of 136,526 adult females (124/ha), the basic model predicted that the population would reach 29,100 females after 30 years. While the population increased at some levels of transport, the population was predicted to surpass 29,100 adult females after transport only when adult fecundity and survival of young were high and there was some survival of transported adults (Figure 5.7 K and L). When the lower estimate of carrying capacity (49/ha) was used in model runs, the model predicted that the population would only reach 13,650 adult females after 30 years. Under these conditions, the effects of density dependence on population growth were evident and the model predicted that transport of any percent of the population would benefit the stock, even with no survival of adults, under conditions of optimal survival of young and adult fecundity (Figure 5.8 J, K, and L).

Model evaluation

To evaluate the fit of our model's vital rates, we compared a few predictions to actual data. The stable stage distribution from this model predicted 23% repeat spawners annually, which is lower than the average percentage (43%) of repeat spawners observed in 2000-

2005; however, it is within the range annually observed (19-60%) in the data used (from Burgess et al. 2007). Although the model reasonably estimated the proportion of American shad at age expected in the catch, it predicted that the highest proportion would be age 4 and that there would be a larger proportion of age-8 and age-9 fish, as compared to the actual catch, which had a greater proportion of age-5 and age-6 fish (Figure 5.9). The model predicted that 1,406 18-day old fry would produce one adult; thus, the model would predict that few hatchery released fry would return as adults (Table 5.6). The actual proportion of adults with OTC marks collected on the spawning grounds was higher than that predicted by the model in most years (Figure 5.10).

Discussion

Our model predicts that the American shad population in the Roanoke River is increasing slowly under present conditions. Only under optimal conditions of effective fecundity and survival would transport of American shad above dams on the Roanoke River be predicted to lead to a higher rate of increase at the current stock size. Information regarding behavior and outmigration success of adult American shad released in upstream habitats suggests that transported individuals would have both lower reproductive output and lower survival than those remaining in the lower river, since most individuals spent less time in suitable spawning habitat and no individuals were documented to outmigrate past all three dams (Chapter 4). In addition, outmigration success of OTC-marked American shad fry released in the upper river was lower than that for marked fry released in the lower river. Present collections of these OTC-marked American shad in upper basin habitats suggest that

outmigration may be delayed, rather than reduced. However, only one double-marked adult American shad has returned to the spawning grounds (Kevin Dockendorf, NCWRC, personal communication), and considering that only slightly smaller numbers (see Table 5.3) of slightly older individuals (7-10 days in age, rather than 4-10 days in age) were released at the upstream site, we would expect fairly similar numbers from each release location to return as adults, if survival and outmigration rates were equal. Since the estimated adult population size appears much smaller than either assumed estimate for carrying capacity in the lower Roanoke River and survival to outmigratation from the upper river appears lower under current conditions than that in the lower river, it follows that transport would not be expected to benefit the population in its present state. However, one must question whether our estimates of adult stock size and carrying capacity accurately represent the population and available spawning habitat in the lower Roanoke River system.

The model predicted that the American shad population in the Roanoke River was fairly stable between 2002 and 2008 and was composed of approximately 5,200 adult females. Our estimate of the adult female stock size should be evaluated with caution for a few reasons. First, our population estimate was calculated using natural mortality rates for young American shad from multiple rivers. Estimating natural mortality for fish at any age is difficult and research suggests that survival of young American shad is highly variable (Crecco et al. 1983; Crecco and Savoy 1987; Savoy and Crecco 1988; Limburg 2001; Hoffman and Olney 2005; Crecco et al. 2007), making accurate estimation of production problematic. Second, we assumed that survival rates experienced by wild fry were the same

as those for stocked fry. Research on the Susquehanna River suggested that added predation on stocked American shad larvae was generally low, but appear related to time of day, fry age, and most especially, fry density, at stocking (Johnson and Ringer 1995, 1998). The numbers of fry stocked per day (< 700,000, Jeff Evans, North Carolina Wildlife Resources Commission) in the Roanoke River were generally associated with low levels of added mortality in the Susquehanna River (< 2%; Johnson and Ringer 1995, 1998); however, differences in environmental conditions, as well as predator composition and abundance, could result in differences between the Susquehanna and Roanoke rivers in term of added predation mortally for stocked fry. Third, fecundity of American shad may be highly variable and not well represented by the number of eggs developed prior to spawning (Olney et al. 2001; Olney and McBride 2003; Hyle 2004). American shad are batch spawners and may have indeterminate fecundity; therefore, average estimates of batch size and the number of batches spawned are required to reasonably estimate annual fecundity (Olney et al. 2001). Hyle (2004) suggested that previous fecundity estimates for York River American shad might be much lower than actual values. More research on the reproductive ecology of American shad in the Roanoke River and other systems would improve estimates of fecundity; however, if the estimates we used were similarly low, than our population estimate would be too high. Despite these uncertainties, the adult population estimate we used (2 * 5,200) is similar to those found by completely independent methods. Hydroacoustic studies completed annually from 2004 to 2007 suggest that the spawning American shad population

in the Roanoke River is between 5,000 and 35,500 individuals (Mitchell 2006; Magowan 2008).

The significant positive relationship that we observed between the number of OTC-marked fry released and the proportion of OTC-marked juveniles collected later that year in the lower Roanoke River might suggests that wild production was relatively similar in all years. Crecco and Savoy (1988) suggest that egg and prolarval survival of American shad is strongly affected by both density-dependent and density-independent factors. However, the authors also suggest that density-dependent regulation would most likely be important when the adult population was large enough to be crowded on the spawning grounds or as a function of predation rates (Crecco and Savoy 1988). Considering that the American shad population in the Roanoke River appears far below either assumed value for carrying capacity in the lower Roanoke River, it seems more likely that female abundance is low, but relatively stable, leading to a small, but stable production of young.

Our assumed estimates of carrying capacity were calculated from two very different equations developed from information on present and historic American shad stock sizes in the Connecticut River (St. Pierre 1979; Hightower and Wong 1997; Savoy and Creeco 1994; Weaver et al. 2003). Although these calculations (especially 124/ha) have been used to estimate potential habitat above dams for a variety of rivers, their accuracies are unknown (Hightower and Wong 1997). Both assumed values were developed for another system and were based on total area only; thus, neither accounts for the quantity or quality of spawning habitat or any other physical or environmental factors that could affect the population size

(Hightower and Wong 1997). In fact, differences between the two carrying capacity estimates developed for the Connecticut River (124/ha from historic data and 49/ha from more current data) may be a result of habitat change within the river basin over time. Telemetry suggests that American shad in the Roanoke River spawn mostly in a small area between Roanoke Rapids (rkm 218) and Weldon (rkm 209; Sparks 1998; Hightower and Sparks 2003); however, plankton sampling to estimate spawning intensity river-wide could help identify any other spawning sites in the Roanoke River. In addition, habitat surveys combined with habitat suitability models could be used to identify other potential spawning sites, since spawning may be concentrated in the best habitats, rather than in all suitable habitats, if the population is far from carrying capacity. Regardless of their differences, both estimates suggest that the American shad population is presently far below carrying capacity and could still increase below the dams. Closer examination of estimates of carrying capacity in a variety of systems would help verify calculation methods, which would allow for better evaluation of the effects of transport on American shad.

Reproductive potential of adults and survival to age one (yearlings) appear to influence the population projection more than the survival of adults. It has been suggested that American shad populations with high percentages of repeat spawners may not benefit from transport to upstream habitats because adults may have lower survival as a result of the longer distance migration and downstream passage through dams (Leggett et al. 2004). Our model suggests, however, that the population projection is more affected by the survival of young American shad, than that of returning adults. There is often high variability in growth

and survival within the first year of life, but even small differences can cause large changes in year class strength, which can be important for population growth (Houde 1987; Bailey and Houde 1989). The quality and accessibility of upstream habitat for the production, growth, and survival of young and the ability of juvenile fish to outmigrate may be more important for successful transport, than the survival rate of transported adults returning to the ocean. The percentage of young American shad prevented or delayed in outmigration from the upper Roanoke River basin is unknown and, as a result, their actual survival and growth in upstream reservoir and riverine habitats is also unknown. It is possible that survival above the dams is higher than it is in the lower river, but that outmigration delays, especially combined with turbine mortality, are resulting in an apparent reduction in survival. Aunins and Olney (2009) suggest that survival of young American shad above Bosher's Dam in the James River, Virginia, appears much higher than that below the Dam. Hatchery released OTC-marked American shad over one year in age have been collected in upper Roanoke River basin reservoirs, which suggests that some young survive despite not reaching the ocean. However, whether these fish would reach maturity in freshwater is unknown. For some anadromous alosines, entirely freshwater individuals and populations have become established (Limburg et al. 2001; Bagliniere et al. 2003; McDowall 2003); however, despite considerable stocking efforts, only one landlocked population of American shad has been observed; it is located in a reservoir on the San Joaquin River, California (Lambert et al. 1980; Limburg et al. 2003). Structures to increase outmigration would likely increase juvenile survival and the overall benefits of transport.

Although adult fecundity and the survival of young appeared to contribute most to population growth in a trap-and-transport operation, repeat spawners may be more important than predicted by our model. Although we cannot validate our model, we did evaluate how well it fit the data used to parameterize it and how closely it predicted some field observations. Compared to the NCDMF data on age and spawning history of American shad in the Albemarle Sound, the model predicted fewer repeat spawners than were actually observed in samples from Albemarle Sound. Studies suggest that larger females may produce and spawn more eggs (Holland and Yelverton 1973; Olney and McBride 2003; Hyle 2004). Although there is no clear pattern between repeat spawning and egg batch size (Hyle 2004), it is not known if repeat spawners put more energy toward reproduction and less toward survival, by spawning more times during a season, for example. If repeat spawners are more fecund than virgins, then their impact on the population projection would be greater than predicted by our model. More research on reproductive ecology of American shad, especially in relation to age and spawning history, could help determine the importance of repeat spawners to populations.

The model predicted that a lower proportion of adults collected from 2005 to 2008 would have OTC marks, than was observed in collections. As expected, the observed proportion of OTC-marked adults was small and generally increased over the three year period, as the number of fish with OTC marks matured. The difference in expected and actual returnees may simply be a result of small sample sizes, as predicted values appeared within reasonable ranges of actual values. Also, males are collected at younger ages than

females (Burgess et al. 2007), and thus the inclusion of males may have inflated the number of returnees slightly, especially in 2005 when OTC marked fry would have been age three and younger. Less than 100% OTC–mark retention rates may have caused fewer returnees to be detected, although tests suggest that retention was very high (≥ 95%) for fish with single marks (Dockendorf 2004). Alternatively, the model may predict too few returnees either because the population estimate is too large or the estimated survival rate is too low. The estimated number of 18-day old fry predicted to produce one spawning adult in the Roanoke River (1,400) was much higher than that for the Susquehanna River (320; Sadzinski and Hendricks 2007). Differences in these predicted rates, however, may be at least in part a function of actual differences between the two populations. Harvest of American shad in the Albemarle Sound is very high compared to the estimated population size in the Roanoke River; however, it is unknown what proportion of commercial catch is from the Roanoke River population, compared to that in the Chowan River. In 2007 and 2008, NCDMF collected some American shad in the Albemarle Sound for identification of OTC marks. The proportion of individuals with single OTC marks in the Albemarle Sound during those two years (4 of 208) was similar to that on the Roanoke River spawning grounds (4 of 223; Kevin Dockendorf NCWRC, personal communication). Although these sample sizes are small and may not adequately represent harvest within the entire Albemarle Sound, the similarity could suggest that the Roanoke River population is well represented in the commercial catch. In contrast, commercial and recreational harvest of American shad in the Susquehanna River have been closed since 1980 and harvest from the Susquehanna flats has been fairly low

since the early 1980s (Sadzinski and Hendricks 2007). Thus, adult survival in the Roanoke River may be much lower than that observed in the Susquehanna River. In addition, the yearling survival rate that we used was developed from populations already experiencing some level of density dependence in the wild; thus, our addition of a density-dependent parameter may have reduced survival too much during this life stage. Further examination of survival rates for this and other American shad populations, especially for sub-adult fish in the ocean and for adults before and after spawning, would help better parameterize this model, which might correct for this difference between the expected and actual proportions of OTC-marked adults. Although our model predicted a lower number of OTC-marked individuals to return, it appears to generally describe the population status and survival rates for American shad in the Roanoke River fairly well. If our total survival rate was low, we would expect the population to be increasing even more than predicted. Alternatively, if our adult population estimate was high, we would expect less of an effect of density dependence below the dams, than was predicted. Either or both of these changes to the model would likely reduce the benefits of transport at the present stock sizes, at least in the short term, making interpretation of our model results similar.

Increasing survival rates for either young or adult American shad in the lower Roanoke River was predicted to result in more rapid increases in the population. We examined increases in survival of 5 to 25%, but it is not known if such improvements would be feasible. If harvest in the Albemarle Sound is substantial, then increases in adult survival could be achieved by reducing commercial catch rates. More extensive collections of OTC-

marked juveniles throughout the Albemarle Sound and the Roanoke River could help establish the proportion of the commercial catch that is from the Roanoke River, as opposed to the Chowan River. An estimate of the number of Roanoke River American shad harvested annually would clarify the overall effects of commercial harvest on the population. Increased predation on adult American shad by native and introduced finfish predators, such as striped bass *Morone saxatilis* and flathead catfish *Pylodictus olivaris,* has been suggested as an important source of mortality in some systems (Savoy and Crecco 2004; Brown et al. 2005); however, increased predation may not be occurring, or may not be influencing population sizes, in all rivers (Kahnle and Hattala 2007). Improvements in survival for young American shad could increase the population size in the lower Roanoke River, but may be less feasible. Survival rates of young American shad may be affected by biotic conditions, such as predation rates, and abiotic conditions such as flow releases from the Roanoke Rapids Dam, but the relationships between these factors and young-of-year survival are not always clear or easy to quantify (Crecco and Savoy 1984; Crecco and Savoy 1985; Tuomikoski et al. 2008; Pine et al. 2007).

In summary, we constructed a matrix model to predict possible population-level effects of transporting American shad to habitats above dams on the Roanoke River, North Carolina and Virginia. To our knowledge, no such model has previously been developed for American shad in any river system. Our model predicts that transport would only benefit the current American shad population if effective fecundity and survival rates were optimal. These results are system-specific, and benefits of transport in other systems would depend on

population size, the quantity and quality of upstream habitat, and ability of young and adults to outmigrate to the ocean. Models like this are useful not only to guide management, but also to identify future research needs, such as to suggest studies on reproductive ecology and natural mortality rates. While some of our model inputs were specific to the Roanoke River American shad population, vital rates used in this model could be modified to evaluate the effects of transport on American shad populations in other river systems.

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Tables

Table 5.1. Structure of the stage-based matrix model for female American shad. S_2 is the probability of surviving from age 1 to age 2, (S_{stage}) is the probability of surviving to stay in the same stage, (S_t) is the probability of surviving to transition to adulthood, F_{Stage} is the fecundity of an individual in that stage, K is the carrying capacity of the lower Roanoke River, D is the proportion of sub-adults that become mature, and $p(T)$ is the proportion transported above dams on the Roanoke River. The five stages are: (1) yearlings produced by adults below Roanoke Rapids Dam (Yl); (2) yearlings produced by adults passed above dams (Yu); (3) sub-adults (SUB); (4) adults spawning below Roanoke Rapids Dam (Al); and (5) adults spawning above dams (Au).

	1	2	3	4	5
1	0	0	0	$F_{Al}S_{Yl}\left(\frac{K-Al}{K}\right)$	0
2	0	0	0	0	$F_{Au}S_{Yu}$
3	S_2	S_2	$(1-D)S_{SUB}$	0	0
4	0	0	$DS_t[1-p(T)]$	$S_{Al}\ [1-p(T)]$	$S_{Au}\ [1-p(T)]$
5	0	0	$DS_t p(T)$	$S_{Al}\ p(T)$	$S_{Au}\ p(T)$

Table 5.2. Spawning histories for female American shad collected in the Albemarle Sound from 2000 to 2005. Table entries are from data in Burgess et al. (2007) for fish collected by commercial fishers and the NCDMF independent gillnet survey.

	Age at maturity					
Age at capture	3	4	5	6	7	8
3	46					
4	3	181				
5	0	83	216			
6	0	22	72	163		
7	0	1	27	49	47	
8	0	0	0	11	16	13

Table 5.3. Number of American shad juveniles in the lower Roanoke River with no OTC mark, a single OTC mark (lower river release), and a double OTC (upper river release), by year. These data were collected by the NCWRC (Kevin Dockendorf, personal communication). NA = no double OTC marks could be collected, since none were released.

Year	Number of fry released with single mark	Number of fry released with double mark	Number of juveniles without OTC mark	Number of juveniles with single OTC mark	Number of juveniles with double OTC mark
2002	820,000	0	131	2	NA
2003	1,204,340	1,081,289	160	2	4
2004	1,197,822	1,132,000	217	5	5
2005	1,346,834	1,226,000	383	29	9
2006	1,429,936	991,000	222	13	1
2007	2,200,000	2,100,000	273	33	0
2008	4,300,000	3,900,000	226	59	5

Table 5.4. Estimated values for instantaneous natural mortality (M_x), annual survival (S_x), conditional maturity (π_j), cumulative percent mature (% mature), and proportion to transfer to adulthood (D_j), by age, for American shad in the Roanoke River, North Carolina. NA = age-2 fish could not transfer in the next time step, since they had not yet become sub-adults.

Age	M_x	S_x	π_j	% mature	D_j
2	0.8224	0.4394	0	0	NA
3	0.6081	0.5444	0.01	0.0328	0.01
4	0.5127	0.5989	0.2379	0.4535	0.1282
5	0.4322	0.6491	0.3598	0.7439	0.0885
6	0.3918	0.6758	0.4592	0.8979	0.0469
7	0.3704	0.6905	0.4592	0.9542	0.0172
8	0.3586	0.6987	1	1	0.0139

Table 5.5. Names, verbal descriptions, and ranges of vital rates. Citations and sources of data used to determine the vital rates were also included. See Table 5.1 and Figure 5.1 for model structure, matrix and symbol descriptions.

Name	Description	Value range	Citations/data
F_{Al}	Adult fecundity in the lower river	272,710	Holland and Yelverton (1973)
F_{Au}	Adult fecundity in the upper river	90,903 and 272,710	Estimated 1/3 reduction in fecundity due to reduced time spent in riverine habitat (Sparks 1998; Chapter 4)
S_{1_l}	Survival to become a yearling (lower River)	0.0000373	Crecco and Savoy 1987; Limburg (1996); Lorenzen (1996); Tuomikoski (2004); Hoffman and Olney (2005); Crecco et al. (2007); Sadzinski and Hendricks (2007); Tuomikoski et al. (2008)
S_{1_u}	Survival to become a yearling (upper River)	0.0000109 and 0.0000373	Estimated from fry released by NCWRC, with and without downstream passage
S_2	Survival to become a sub-adult	0.4394	Estimated for a 1-2 year old oceanic American shad (Lorenzen 1996; Hattala et al. 2007)
S_{SUB}	Sub-adult survival	0.5744	Maki et al. (2002); Burgess et al. (2007)
S_{Al}	Non-transported adult survival	0.2516	Maki et al. (2002); Burgess et al. (2007)
S_{Au}	Transported adult survival	0.0000, 0.1038 and 0.1834	Assuming 0 to 0.5660 proportion downstream passage (Bell and Kynard 1985; Sadzinski and Hendricks 2007; Chapter 4)
D	Proportion of sub-adults to mature	0.3048	Maki et al. (2002); Burgess et al. (2007)
S_t	Transfer to adulthood	0.4428	Maki et al. (2002); Burgess et al. (2007)
$p(T)$	Proportion of adults transported	0.0-0.5	
K	Carrying capacity	136,526 and 54,610	Savoy and Crecco (1996); Hightower and Wong (1997); Weaver et al. (2003), (1/2) the value for females only

Table 5.6. The number and proportion of OTC-marked American shad expected to return to the Roanoke River as spawning adults between 2005 and 2008 and the actual number and proportion of OTC-marked individuals collected on the spawning grounds during those years.

Year	Predicted number with an OTC mark	Predicted proportion with an OTC mark	Number sampled for OTC marks	Number of females with an OTC mark	Number of males with an OTC mark	Actual proportion with an OTC mark
2005	2	0.0002	62	0	1	0.0161
2006	34	0.0033	115	0	2	0.0174
2007	82	0.0079	141	1	0	0.0071
2008	172	0.0165	82	2	1	0.0366

Figures

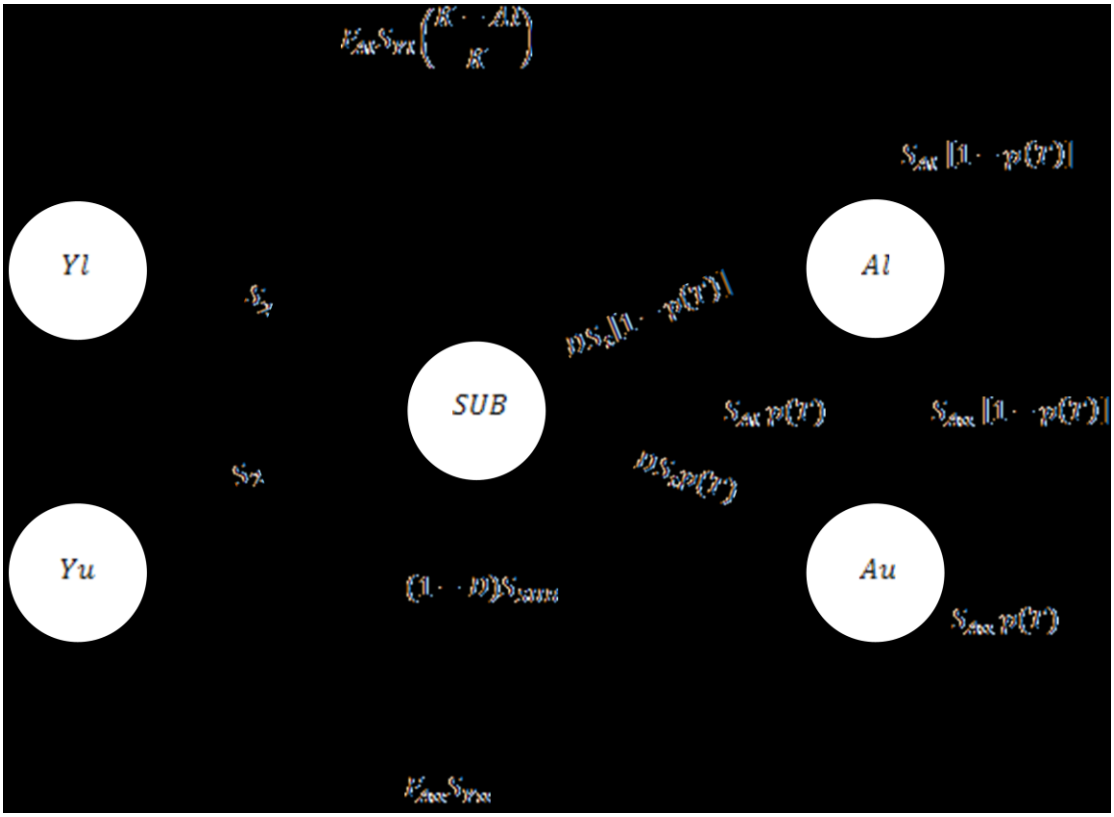


Figure 5.1. Pre-breeding census life cycle diagram for American shad in the Roanoke River, including the opportunity for transport above dams. The five stages are: (1) yearlings produced by adults below Roanoke Rapids Dam (Yl); (2) yearlings produced by adults passed above dams (Yu); (3) sub-adults (SUB); (4) adults spawning below Roanoke Rapids Dam (Al); and (5) adults spawning above dams (Au). The corresponding population projection matrix is illustrated in Table 5.1.

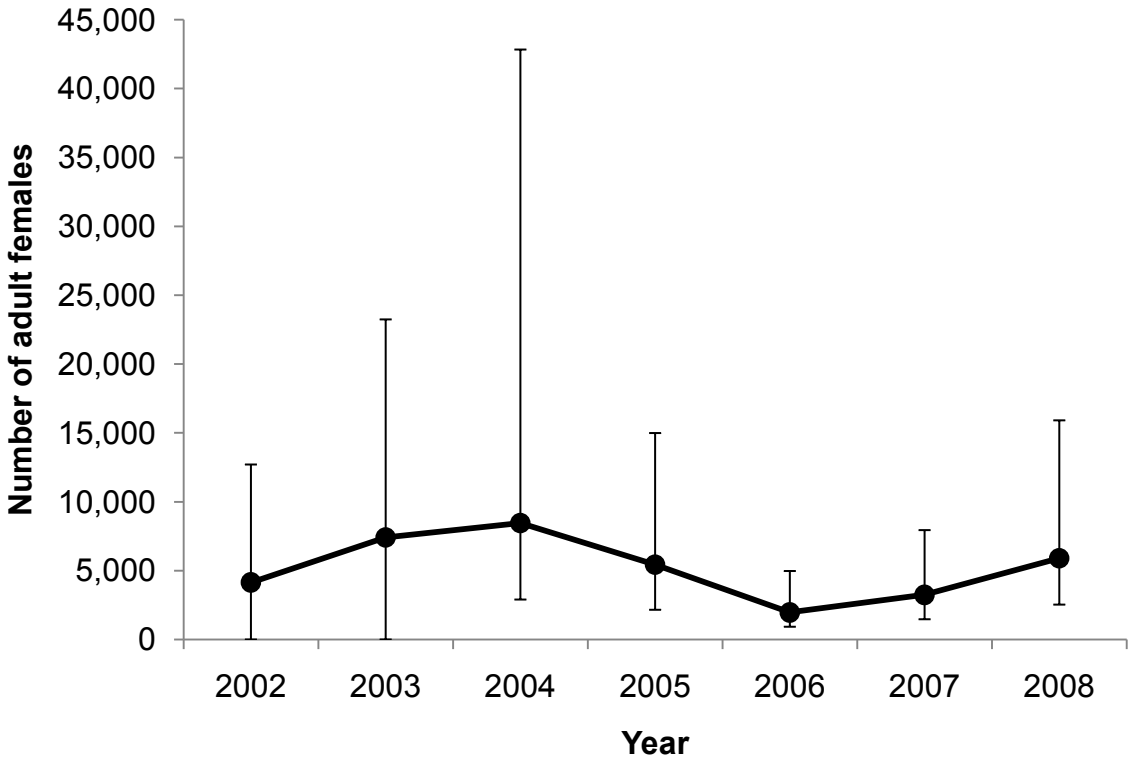


Figure 5.2. Estimated total number of adult female American shad spawning in the Roanoke River, by year, from 2002 to 2008. Error bars represent the 2.5% and 97.5% values from 1,000 parametric bootstrap samples.

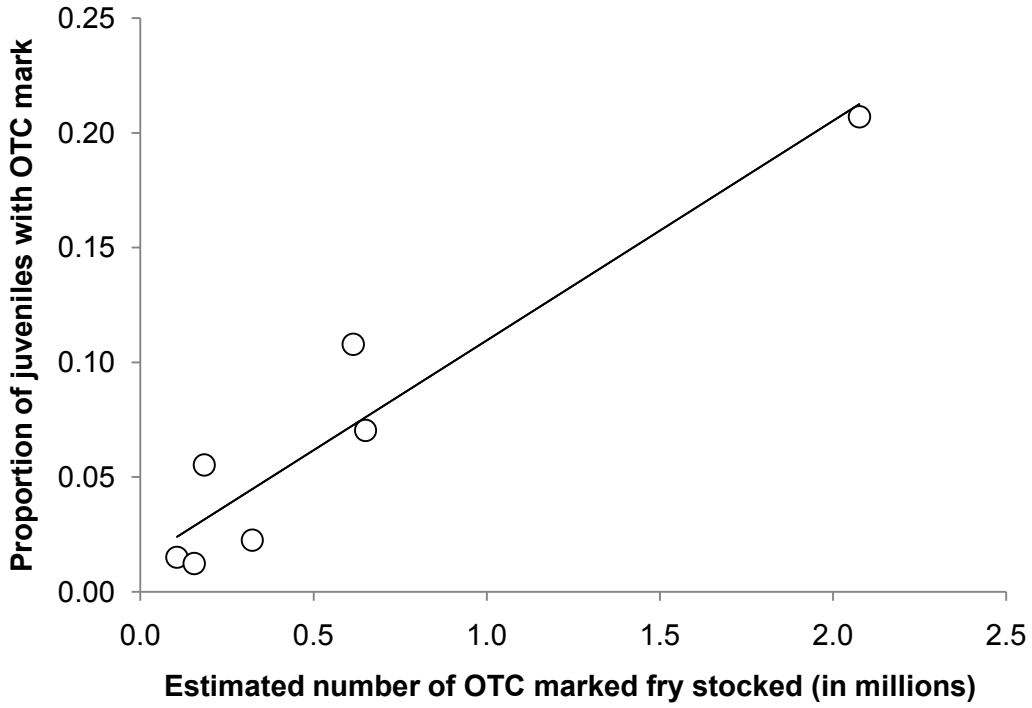


Figure 5.3. Estimated number of oxytetracycline (OTC) marked fry stocked below the Roanoke Rapids Dam during a year and the corresponding proportion of juveniles with a OTC mark signaling that they were released earlier that year below the Roanoke Rapids Dam. Age at stocking varied annually, so stocked fry numbers were adjusted for mortality to a common day of release (day 18). Each open dot represents a year and the line represents the best fit linear regression line.

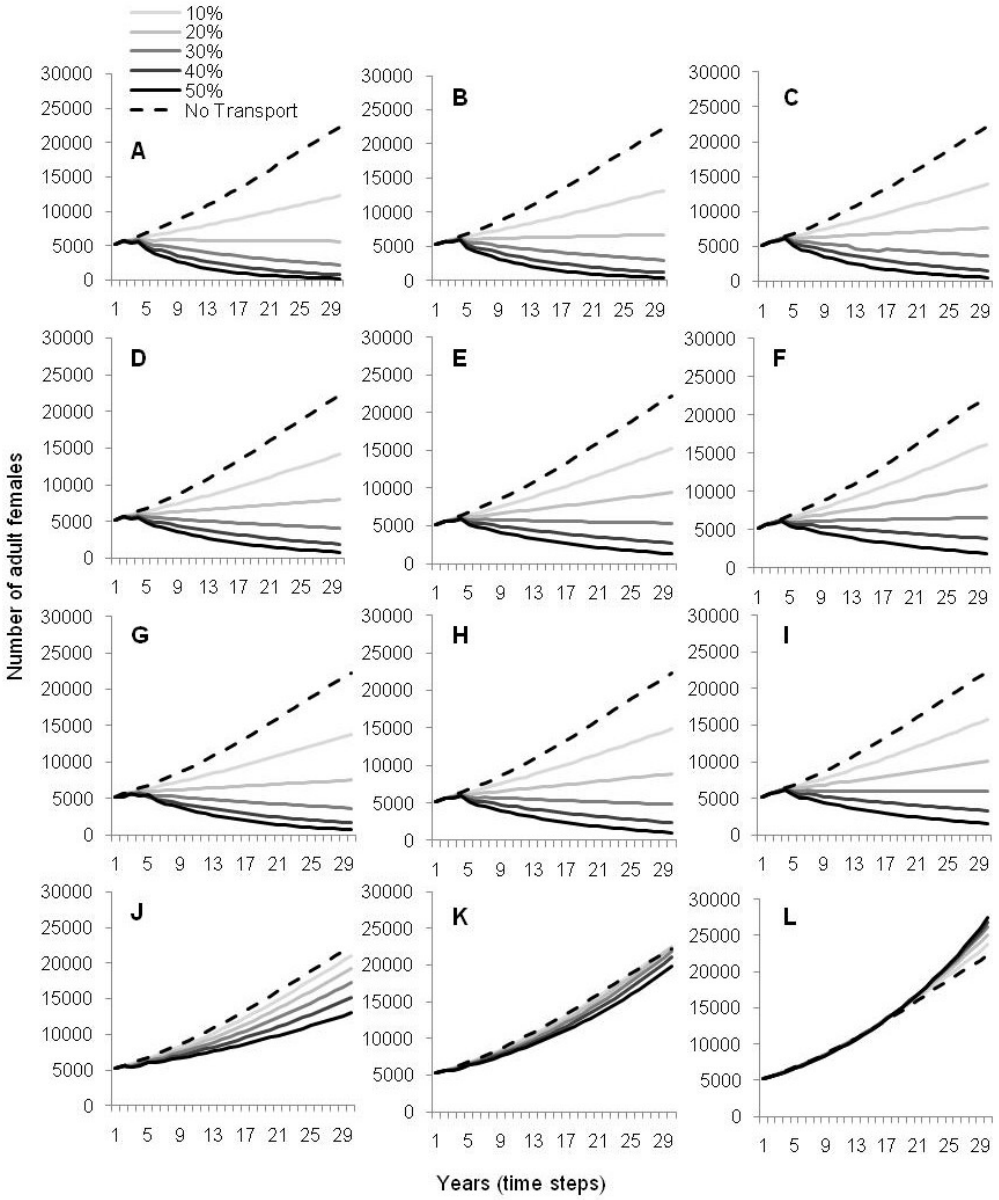


Figure 5.4. Projected number of adult American shad females under different transport scenarios when assumed carrying capacity was 136,526 adult females. The different lines indicate the different percentages of the adult population to be transported. Columns indicate adult survival from none on the left to high on the right. Specific panels are: (**A-C**) low fecundity and low yearling survival, **(D-F)** low fecundity and high yearling survival, **(G-I)** high fecundity and low yearling survival, and **(J-L)** high fecundity and high yearling survival. For survival rates, see Table 5.5.

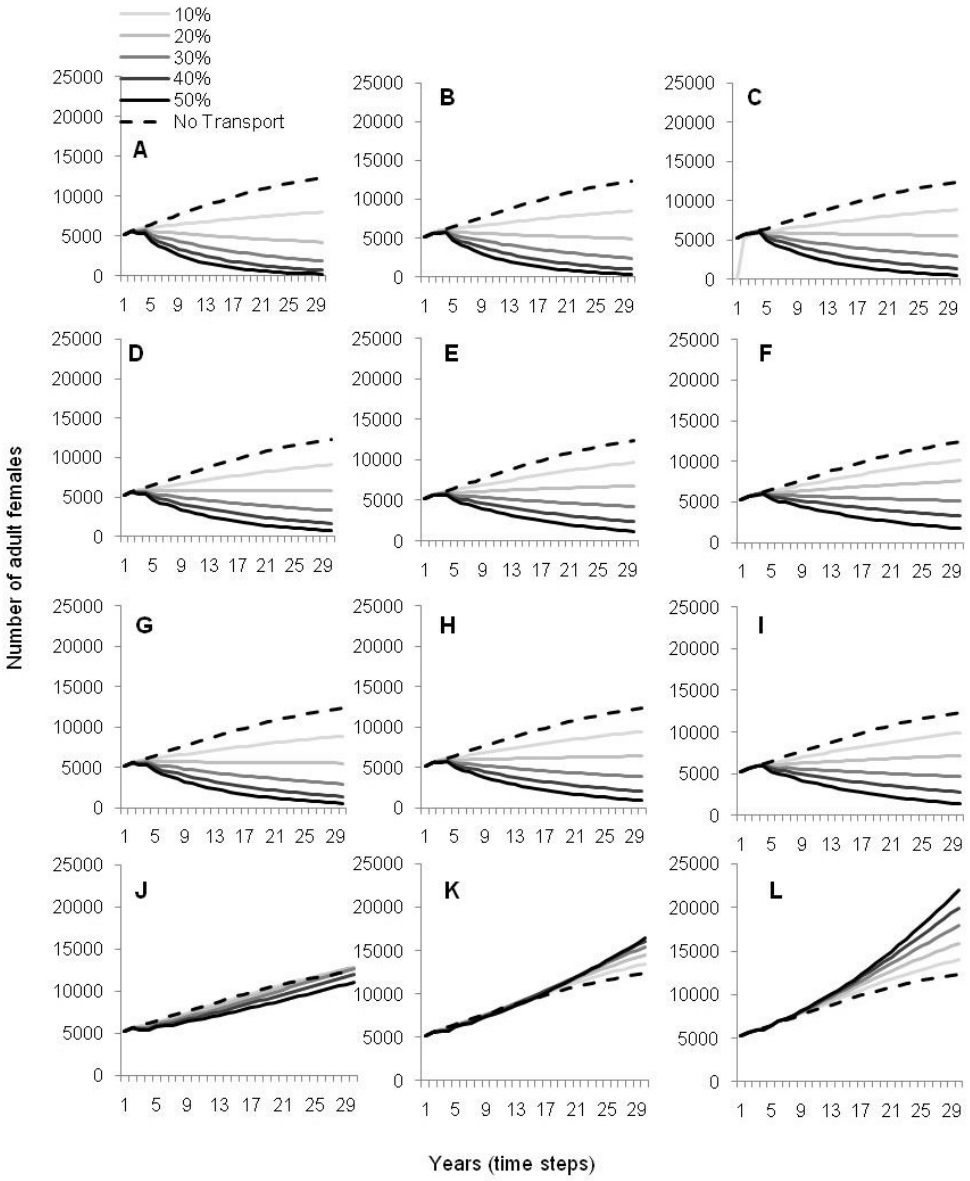


Figure 5.5. Projected number of adult American shad females under different transport scenarios when assumed carrying capacity was 54,610 adult females. The different lines indicate the different percentages of the adult population to be transported. Columns indicate adult survival from none on the left to high on the right. Specific panels are: (**A-C)** low fecundity and low yearling survival, **(D-F)** low fecundity and high yearling survival, **(G-I)** high fecundity and low yearling survival, and **(J-L)** high fecundity and high yearling survival. For survival rates, see Table 5.5.

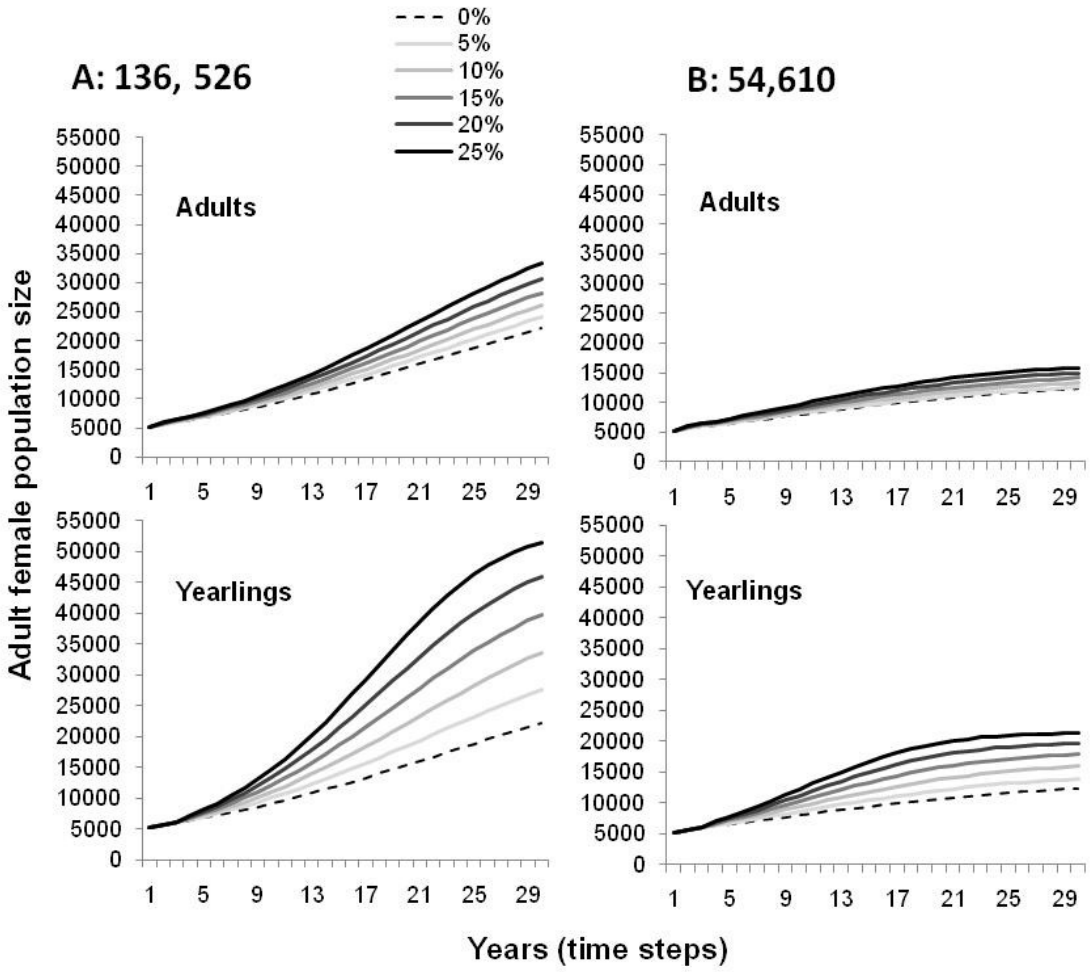


Figure 5.6. Projected number of adult American shad females with no transport, but under conditions of increased survival for adults and yearlings assuming a carrying capacity of (**A**) 136,526 adult females or (**B**) 54,610 adult females. Lines indicate the increased survival percent.

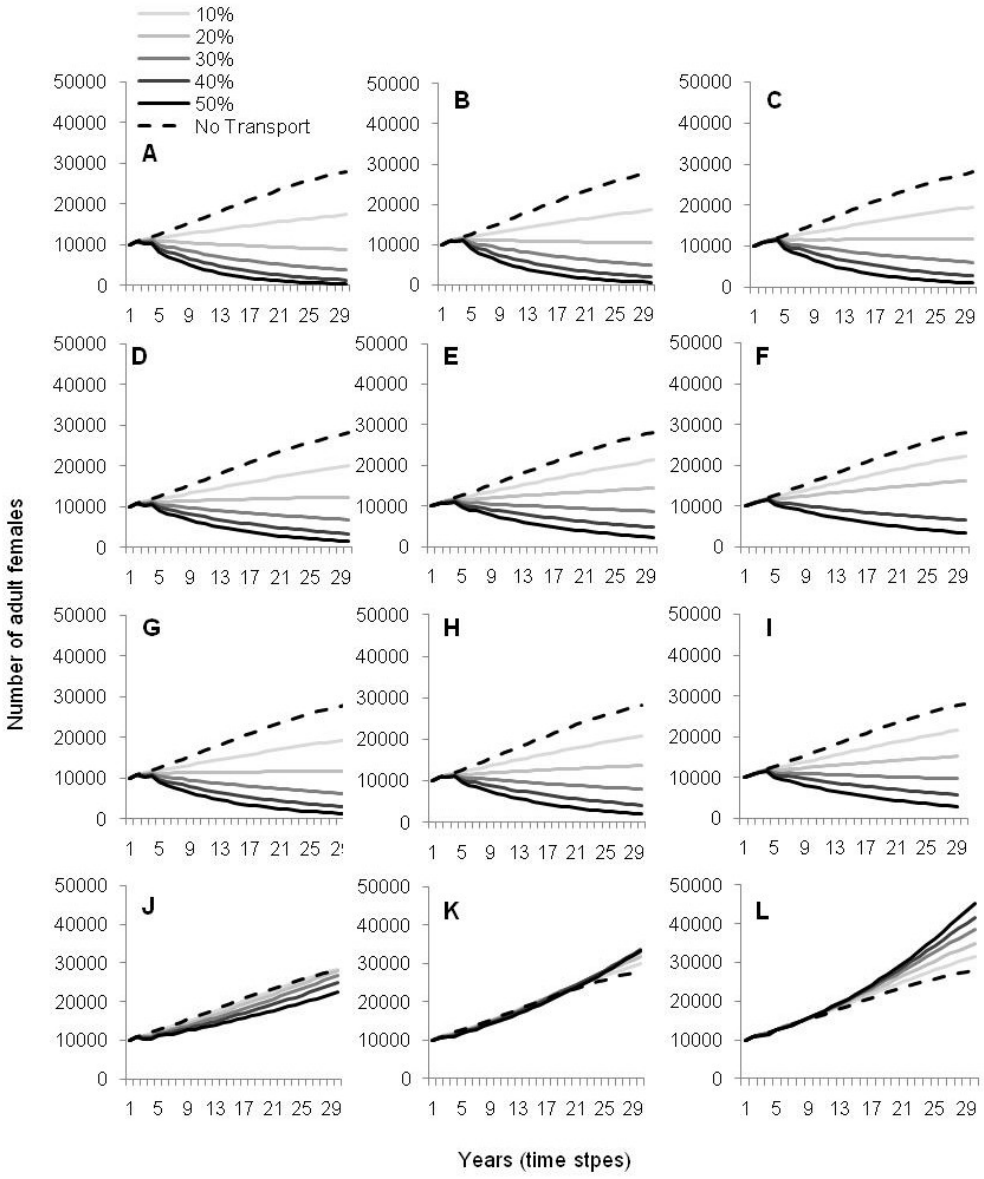


Figure 5.7. Projected number of adult American shad females under different transport scenarios when the assumed carrying capacity was 136,526 adult females and the starting female population size was 10,000. The different lines indicate the different percentages of the adult population to be transported. Columns indicate adult survival from none on the left to high on the right. Specific panels are: (**A-C)** low fecundity and low yearling survival, **(D-F)** low fecundity and high yearling survival, **(G-I)** high fecundity and low yearling survival, and **(J-L)** high fecundity and high yearling survival. For survival rates, see Table 5.5.

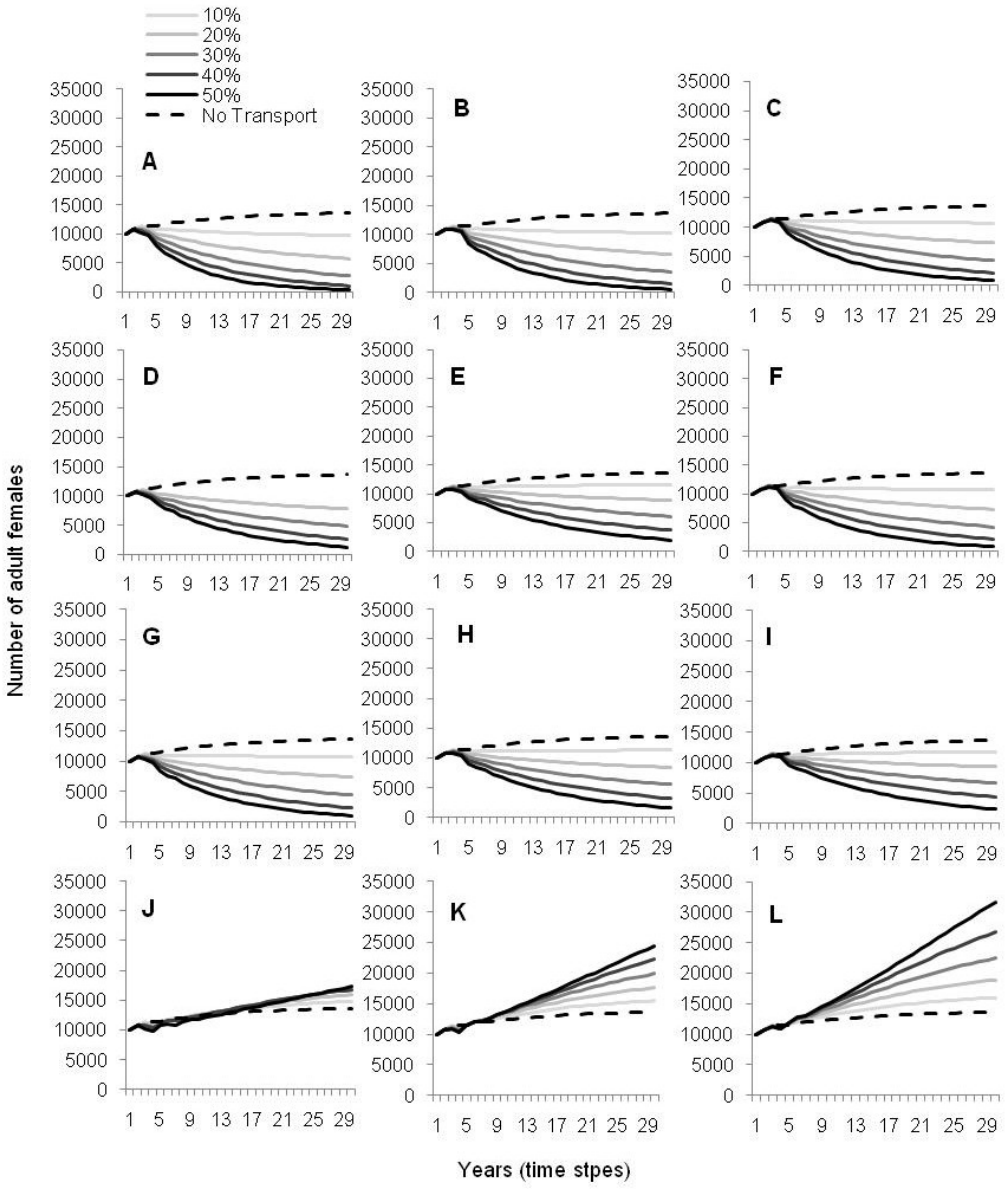


Figure 5.8. Projected number of adult American shad females under different transport scenarios when the assumed carrying capacity was 54,610 adult females and the starting female population size was 10,000. The different lines indicate the different percentages of the adult population to be transported. Columns indicate adult survival from none on the left to high on the right. Specific panels are: (**A-C)** low fecundity and low yearling survival, **(D-F)** low fecundity and high yearling survival, **(G-I)** high fecundity and low yearling survival, and **(J-L)** high fecundity and high yearling survival. For survival rates, see Table 5.5.

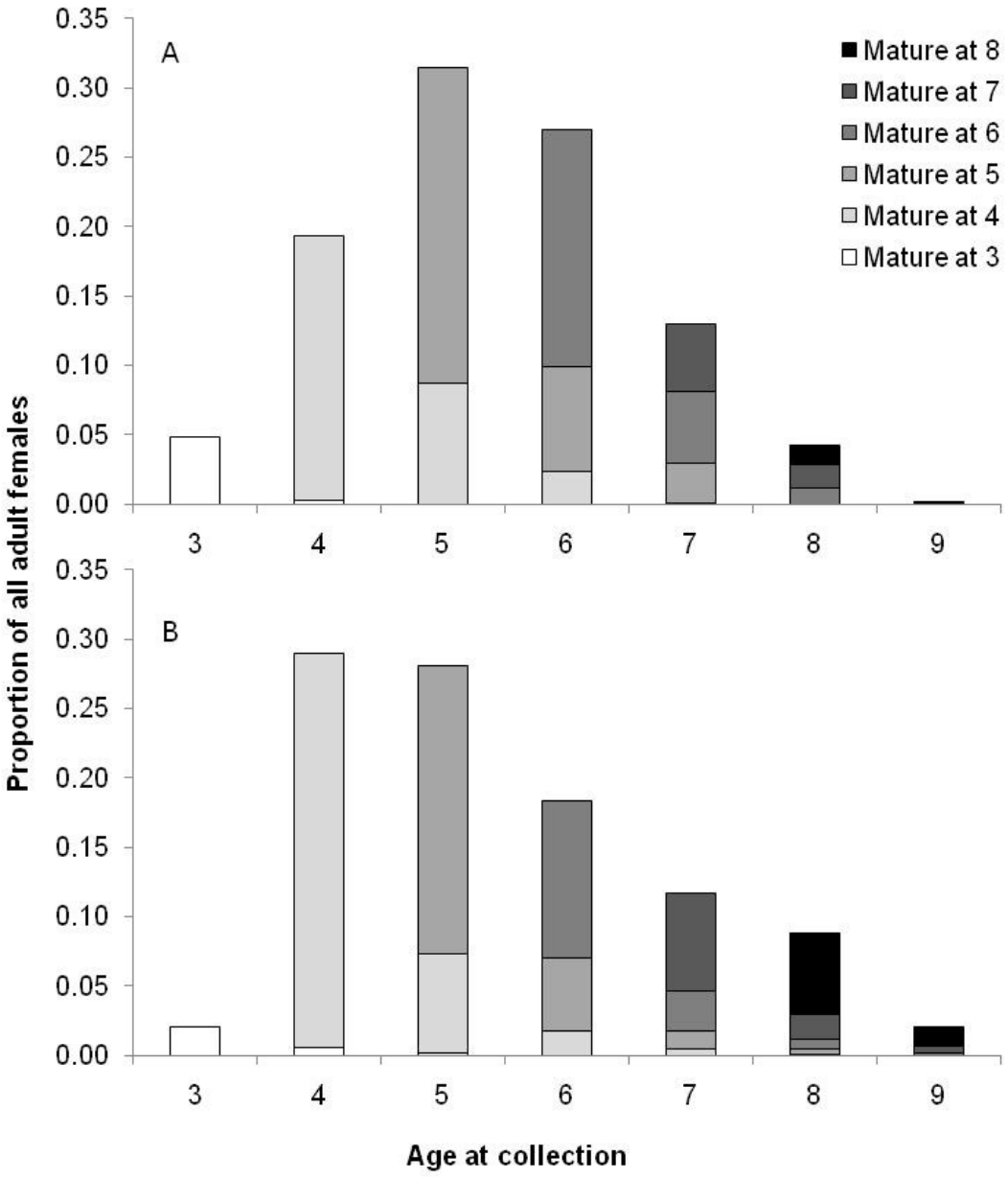


Figure 5.9. The (**A**) actual and (**B**) predicted proportions of Roanoke River adult American shad females by age at collection and age at maturity.

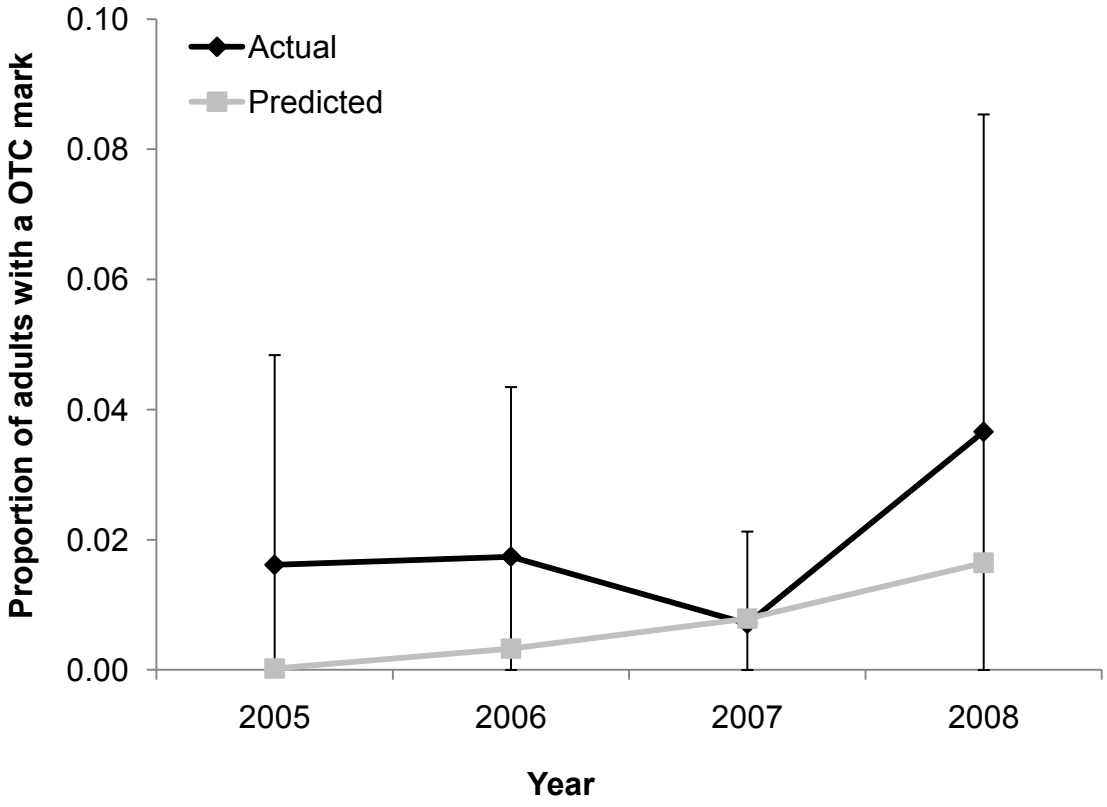


Figure 5.10. Actual and predicted proportions of adult American shad with OTC marks to return to the spawning grounds in the Roanoke River between 2005 and 2008. Error bars represent 2.5% and 97.5% values from bootstrap analysis.

CHAPTER 6. SYNTHESIS AND SUGGESTIONS FOR FUTURE RESEARCH

Synthesis—Understanding species-habitat relationships, especially spawning habitat requirements, is critical for proper management and restoration of depressed fish populations in regulated rivers (Brewer et al. 2006). Identifying, maintaining, and providing access to high quality spawning habitat for anadromous alosines may be crucial to increasing stock sizes and production since populations appear to suffer declines as a result of both fishing mortality and loss and degradation of spawning habitat in rivers (Hightower et al. 1996; Limburg et al. 2003; ASMFC 2007). A better understanding of both fish behavior and spawning habitat selectivity would improve management and restoration of anadromous fish populations in regulated river systems.

Plankton sampling for eggs appears to be the most efficient method to identify spawning sites river-wide for all alosines. Plankton sampling has been effectively employed to collect alosine eggs in a variety of river systems (Williams et al. 1975; Bilkovic et al. 2002; Burdick and Hightower 2006; Smith 2006) and could be used to evaluate spawning under different environmental and management conditions. In contrast, the most efficient method to examine spawning habitat selectivity varied by alosine. By specifying research objectives and understanding local riverine conditions, resource managers and biologists could use this information to efficiently obtain data on alosine spawning. Although habitat suitability models exist for American shad and river herring (Pardue 1983; Stier and Crance 1985), additional directed studies from more rivers or under experimental conditions, could

improve and update the included habitat parameters and their values and thus broaden the application of these models range-wide.

We illustrated how field data from multiple studies and literature could be used to characterize spawning habitat selection and produce a habitat suitability model for hickory shad in both a more common format and a Bayesian belief network (BBN). Recently, BBNs have been used to model the probability of occurrence or abundance of a species in different habitat types and sometimes, under different management scenarios (Rieman et al. 2001; Borsuk et al. 2006; McNay et al. 2006 Smith et al. 2007). This framework can be employed when data are scarce or empirical data are mixed with expert opinion (McCann et al. 2006; Marcot et al. 2006; Uusitalo 2007). Hightower and Wong (1997) suggest that estimates of carrying capacity for American shad in both accessible and inaccessible riverine areas could be calculated using information on available spawning habitat. With verification, BBN habitat suitability models could be used to identify the actual probability or concentration of spawning based on available habitat types and environmental conditions. With additional knowledge of habitat and spawning river-wide, a BBN could be used to produce improved estimates of both population size and carrying capacity based on the amounts of used and available spawning habitats, respectively, throughout a system. This approach would only be beneficial for species that are well studied and in need of restoration, like American shad (Limburg et al. 2003; ASMFC 2007), since spawning habitat requirements are better understood and accurate estimates of carrying capacity are of interest to managers.

Historically, American shad was one of the most commercially valuable fishes in North America (Smith 1894; Walburg and Nichols 1967; Limburg et al. 2003). More recently, the species has been in decline throughout its native range, with harvest, anthropogenic changes to rivers, dams, water pollution, and increased predation cited as possible causes (Hightower et al. 1996; Limburg et al. 2003; Savoy and Crecco 2004; ASMFC 2007). To restore access to habitat blocked by dams, fishways have been constructed and fish have been released in upstream habitats (Hendricks 2003; St. Pierre 2003; ASMFC 2007). This research contributes to our understanding of movement patterns of American shad transported to historic spawning areas presently blocked by dams. Adult American shad can be transported with low mortality, but movement and likely effective fecundity may be affected by handling and transport, upper basin and release site characteristics, and annual environmental conditions. American shad perform best when released directly into suitable riverine habitat or relatively small reservoirs. Flow rates, water temperatures, and quality of upstream habitat for spawning, likely affect the behavior and population-level effects of transporting American shad. Transported fish can outmigrate downstream through dam turbines with low mortality, but structures to increase the percentage that outmigrate would likely increase the benefits of transport. Downstream migrating brown trout *Salmo trutta L.* kelts and smolts passed through a spillway, rather than the dam turbines, and authors suggest that surface water releases are important to aid in outmigration (Arnekleiv et al. 2007).

We developed a density-dependent stage-based population model to evaluate the population-level effects of transporting American shad above dams on the Roanoke River. To our knowledge no such model for American shad has previously been developed and after appropriate modification of vital rates, it could be used to assess management options for American shad in other regulated rivers. Model results suggest that American shad in the Roanoke River would only benefit from transport under conditions of optimal survival and outmigration of young. Presently, the survival of young American shad produced or released upstream of dams is unknown, but it is evident that they are either not surviving or not outmigrating as well as young below Roanoke Rapids Dam. If survival is high, but outmigration is low, then downstream passage structures could have a profound effect on the successful emigration of young from upstream of dams. The adult population in the Roanoke River appears small compared to our assumed values of carrying capacity (Mitchell 2006; Magowan 2008). Harvest in Albemarle Sound may be high and reductions may increase adult survival and the future population size. Increases in survival of young through improved flow releases or reductions in predator abundances might help also, if causal relationships can be defined and management options are physically and financially possible. When the adult American shad population more closely approaches downstream carrying capacity, transport to upstream habitats would likely be more beneficial than it appears currently. In addition to its use for evaluating management options, development of this model helped identify some gaps in our understanding of biology, behavior, and population dynamics of American shad.

Future research—While our American shad population model helped compare outcomes under different biological and management scenarios, the lack of data available to estimate some vital rates, especially those during the sub-adult stage, made predictions of the resulting population size after 30 years imprecise. Very little is known about the behavior, migration, or survival of sub-adult alosines in marine waters (Waldman 2003). Future advances in telemetry, especially production of smaller tags with long lasting batteries that could potentially be implanted in juvenile alosines, could help examine behavior and mortality during the sub-adult stage. Recently, small sonic tags have been used to evaluate behavior and survival of Pacific salmonid smolts (Melnychuk et al. 2007; Welch et al. 2009). Welch et al. (2009) surgically implanted 1.5-year-old hatchery produced Cultus Lake sockeye salmon *Oncorhynchus nerka* smolts with sonic tags. They tracked the smolts out of the Frazer River and along the Pacific coast on stationary arrays (Pacific Ocean Shelf Tracking Project (POST)). Their sonic tags were multiple sizes and some were programmed to be on and off at different times to better understand biology and survival to adulthood. Tagging hatchery smolts was beneficial since the specific population of sockeye salmon in the study was endangered and the hatchery smolts were larger than wild smolts and could thus sustain larger tags. Sonic tags would probably need to be even smaller to successfully implant in juvenile alosines with low mortality, which may be the case with future advances in technology. Studies of mortality and migration of sub-adult and adult alosines in coastal areas would help better manage and restore populations.

Our understanding of the reproductive ecology of anadromous shads has advanced considerably in the last decade; however, additional research to more accurately estimate annual and lifetime fecundity is needed. Alosines are batch spawners, and may have indeterminate fecundity (Olney et al. 2001; Olney and McBride 2003; Hyle 2004; Murauskas 2006; Harris et al. 2007); therefore, estimates of batch size and the total number of batches released in a season, are required to adequately estimate fecundity (Hunter et al. 1985; Olney et al. 2001). Batch size for American shad has been estimated and appears highly variable (Olney and McBride 2003). The total number of batches spawned can be calculated as the average spawning frequency multiplied by an estimate of spawning duration (Hyle 2004). The amount of time adult American shad spend on spawning grounds has been studied in some rivers (Sparks 1998; Olney et al. 2001; Olney et al. 2006; Aunins and Olney 2009) and could be used as estimates of spawning duration. However, studies in some rivers suggest that spawning occurs in more than one location (Williams et al. 1975; Burdick and Hightower 2006; Smith 2006), making it difficult to determine whether data solely from an area of concentrated spawning could be used to calculate a complete estimate of fecundity for all populations. Spawning frequency has been estimated by the presence of post ovulatory follicles (POFs) and hydrated oocytes in ovaries of American shad in the York River (Hyle 2004). Reproductive structures, such as POFs, have been aged for anchovies *Engraulis morda* in a laboratory setting (Hunter and Goldberg 1980) and similar studies would help refine estimates of spawning frequency for alosines. Studies on batch size, spawning

duration, and spawning frequency for other alosines and American shad in other rivers are needed.

Methods to obtain more accurate and precise estimates of age and spawning history of alosines would help better assess and manage stocks. Information on age and spawning history for alosines has been estimated from marks on scales (Cating 1953; Judy 1961). Ageing alosines using scale marks has benefits, most notably scales also contain information about spawning history and they can be removed non-lethally. However, more recently, it has been demonstrated that ages are not being assigned accurately, at least not for American shad in one river (McBride et al. 2005). Oxytetracycline (OTC) marked American shad fry have been and are presently being released in some rivers (ASMFC 2007), which could produce a large sample of known age fish to evaluate alternative methods for assigning age. Differences in the strontium/calcium (Sr/Ca) ratios between freshwater and marine environments have been used to identify the number of migrations individual salmonids have made between riverine and marine habitats (Brenkman et al. 2007; Riva-Rossi et al. 2007). By combining these two methodologies (OTC marks for age and otolith microchemistry for spawning history) the age and spawning history of individual alosines in various river systems could be identified more accurately. In addition, examination of these fish with known ages and known spawning histories could potentially be used to validate less invasive and costly methods. In addition, analysis of patterns in Sr/Ca ratios on brook trout *Salvelinus fontinalis* scales suggest that non-lethal methods for examining spawning history could also be possible using microchemistry techniques (Courtemanche et al. 2005).

Finally, it is unknown how our results on behavior and outmigration success from trap and transport would relate to volitional passage of American shad upstream of dams. It has been suggested that American shad suffer fallback as a result of handling and tagging (Barry and Kynard 1986; Beasley and Hightower 2000; Moser et al. 2000; Hightower and Sparks 2003; Bailey et al. 2004; Olney et al. 2006; Aunins and Olney 2009), which may negatively alter the behavior of handled fish, especially in the immediate future. Frank et al. (2009) observed that transporting alewife resulted in large changes in levels of blood chemicals associated with stress, suggesting that even without tagging, transport has negative effects. Fish passed volitionally would not be handled and would likely suffer few or none of these negative consequences and, as a result, may more successfully migrate upstream in schools. However, one benefit of transport, compared to volitional passage, is that fish can be placed directly into riverine spawning habitat, rather than being required to navigate through passage structures and large reservoirs to reach spawning habitat. In addition, water temperatures appear to warm earlier in upper Roanoke River basin rivers as compared to the lower river, where dam releases result in cooler temperatures later in the season. Volitionally passed American shad would need to migrate passed dams and through reservoirs and then find suitable spawning habitat in time to spawn during periods of adequate temperature.

Studies comparing behavior and migratory success of volitionally passed and hauled American shad could be completed on river systems with multiple dams and passage facilities already in place. Fish could be tagged with minimal handling from the most downstream passage facility and either transported directly to suitable spawning habitat

upstream, or released in place to migrate volitionally through upstream reservoirs and fishways. Behavior and passage success could be monitored at passage facilities and between using stationary receivers and manual tracking. The effects of handling and tagging on volitionally passed fish could be evaluated by comparing the percentages of tagged fish that pass dams further upstream to the percentages of untagged fish that pass the same dams. Trap and transport can allow American shad access to spawning habitat blocked by dams; however, additional research to quantify differences between transport and volitional passage would help determine their relative costs and benefits under different system-wide conditions, which could ultimately better guide managers to effectively restore alosine populations.

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