North American Journal of Fisheries Management

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/ujfm20>

Movement Patterns of American Shad Transported Upstream of Dams on the Roanoke River, North Carolina and Virginia

Julianne E. Harris^a & Joseph E. Hightower^b

^a North Carolina Cooperative Fish and Wildlife Research Unit, Department of Biology, North Carolina State University, 127 David Clark Labs, Campus Box 7617, Raleigh, North Carolina, 27695-7617, USA

^b U.S. Geological Survey, North Carolina Cooperative Fish and Wildlife Research Unit, Department of Biology, North Carolina State University, 127 David Clark Labs, Campus Box 7617, Raleigh, North Carolina, 27695-7617, USA

Available online: 25 Jun 2011

To cite this article: Julianne E. Harris & Joseph E. Hightower (2011): Movement Patterns of American Shad Transported Upstream of Dams on the Roanoke River, North Carolina and Virginia, North American Journal of Fisheries Management, 31:2, 240-256

To link to this article: <http://dx.doi.org/10.1080/02755947.2011.572806>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan, sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

ARTICLE

Movement Patterns of American Shad Transported Upstream of Dams on the Roanoke River, North Carolina and Virginia

Julianne E. Harris*

North Carolina Cooperative Fish and Wildlife Research Unit, Department of Biology,
North Carolina State University, 127 David Clark Labs, Campus Box 7617, Raleigh,
North Carolina 27695-7617, USA

Joseph E. Hightower

U.S. Geological Survey, North Carolina Cooperative Fish and Wildlife Research Unit,
Department of Biology, North Carolina State University, 127 David Clark Labs, Campus Box 7617,
Raleigh, North Carolina 27695-7617, USA

Abstract

American shad *Alosa sapidissima* are in decline throughout much of their native range as a result of overfishing, pollution, and habitat alteration in coastal rivers where they spawn. One approach to restoration in regulated rivers is to provide access to historical spawning habitat above dams through a trap-and-transport program. We examined the initial survival, movement patterns, spawning, and downstream passage of sonic-tagged adult American shad transported to reservoir and riverine habitats upstream of hydroelectric dams on the Roanoke River, North Carolina and Virginia, during 2007–2009. Average survival to release in 2007–2008 was 85%, but survival decreased with increasing water temperature. Some tagged fish 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) than a larger (20,234-ha) reservoir, suggesting that the 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. No American shad eggs were collected during weekly plankton sampling in upper basin rivers. The estimated initial survival of sonic-tagged American shad after downstream passage through each dam was 71–100%; however, only 1% of the detected fish migrated downstream through all three dams and many were relocated just upstream of a dam late in the season. Although adult American shad were successfully transported to upstream habitats in the Roanoke River basin, under present conditions transported individuals may have reduced effective fecundity and postspawning survival compared with nontransported fish that spawn in the lower Roanoke River.

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). Recreational and commercial fisheries for the species still exist, 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 habitat (Pringle et al. 2000; Trush et al. 2000; Freeman

*Corresponding author: jeharris@ncsu.edu

Received August 8, 2010; accepted December 30, 2010

Published online April 21, 2011

FIGURE 1. Map of the Roanoke River basin in North Carolina and Virginia, including sampling sites, tributary rivers, and dams. Filled circles accompanied by letters denote release sites (a = Summit, b = Stonehouse, c = County Line, d = Island Creek, and e = Staunton River), open circles with numbers denote stationary receivers (3–10, 13, and 14 were used in all years and 1, 2, 11, and 12 were used in 2008 and 2009). Plankton sampling for American shad eggs was completed near receivers 11, 12, 13, and 14 and at sites denoted by stars. Impounded lakes are located above the dams with the same names. The collection site for American shad at Roanoke Rapids is just downstream of the Roanoke Rapids Dam.

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 decrease the degree of iteroparity in an American shad population, since individuals in upstream habitats may suffer increased mortality associated with downstream passage through dams as well as higher energetic demands associated with the longer migration and any delays at migratory barriers (Leggett et al. 2004; Castro-Santos and Letcher 2010).

This study was completed to evaluate movement patterns and habitat use of adult American shad transported upstream of dams on the Roanoke River, North Carolina and Virginia. The most downstream dam in the system 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 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).

Upstream of Kerr Lake in the Roanoke River basin, there are approximately 400 rkm of accessible riverine habitat (Read 2004). Using field data on habitat features and environmental data from five main-channel and tributary rivers above Kerr Lake and habitat suitability models for American shad, Read (2004) estimated that there would be at least 62 rkm of suitable spawning habitat in the upper Roanoke River basin in May. 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 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 during 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 and direction. 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. Therefore, 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 for 5 d in holding tanks. On 4 April 2007, we collected 22 adult American shad by boat electrofishing at Roanoke Rapids, in the area between 1 and 2 rkm below the Roanoke Rapids Dam (Figure 1). Fish were held on board in a tank with flow-through water during processing. All fish were measured for total length (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 weight in air, had a battery life of 70 d, a delay period of 10–30 s, and used a single frequency of 69 kHz (V9–1 L, Vemco Division/AMIRIX Systems, Inc., 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 net into a 2,271-L circular hauling tank with circulating current. 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). Oxygen was also added to the tank through oxygen-fed air stones. Typical hauling densities for American shad are two to three fish per 100 L (Hendricks 2003), so a hauling tank of this size should successfully (low mortality) transport 45–68 adult American shad per trip. The hauling tank was driven for over an hour to simulate transport to the upper basin and at the hour's end delivered 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 1). Each afternoon for 4 d, we recorded dissolved oxygen (DO) and temperature via a Yellow Springs Instrument (YSI85, Yellow Springs, Ohio) and examined each tank for any dead individuals. On 9 April 2007, we sacrificed all fish to collect the tags. Only 1 of the 22 fish (4.5%) died during this experiment. In this one female, the tag was slightly posterior in the stomach than it was for other fish, although no trauma was apparent, and the fish showed no obvious reasons for its death. Overall, our collecting, transporting, and tagging procedures resulted in a low level of mortality.

Trap and transport.—In 2007 and 2008, American shad were collected, sonic-tagged, transported, and released by personnel

from North Carolina State University and Aquatic Ecosystem Management Inc. Personnel from North Carolina State University subsequently detected the tagged American shad via manual tracking and stationary receivers throughout reservoir and riverine habitats in the upper Roanoke River basin (Figure 1). In 2009, fish were collected, tagged, and released by Aquatic Ecosystem Management Inc. and were only detected by stationary receivers. Depending on the analysis, some or all data from 2009 were excluded because of errors in data recording (Harris and Hightower 2010). On each sampling date, approximately 50–60 American shad were collected by boat electrofishing at Roanoke Rapids. During 2007, we released approximately half of the fish from each of two locations per sampling date within one reservoir, either Lake Gaston or Kerr Lake (Figure 1). Movement patterns for fish released at the two different sites within a reservoir appeared similar; thus in 2008 and 2009, we released all fish from one location per day (i.e., Stonehouse in Lake Gaston and Island Creek in Kerr Lake). In 2008, we added a release site in the lower Staunton River to evaluate movement patterns for fish released in riverine habitat. In 2009, tagged fish were only released in Kerr Lake and the Staunton River. On each release date, 8–18 fish were each implanted with a sonic tag. In 2007, most American shad were tagged at the release site, since all fish were transported in the same tank and it was otherwise impossible to ensure that equal numbers of tagged individuals would be released at each of the two sites in the reservoir. In 2008 and 2009, all fish were tagged on the electrofishing boat before being placed in the haul tank because there was only one release site per day. 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 haul tank to the release site, as described above.

Once at the release site in 2007 and 2008, 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. In 2009, fish were placed in pens overnight on some dates and were released directly into the river on other dates. Water temperature was recorded using a YSI85 m in the river at the time of fish collection, in the haul

tank during transport, and at the site when fish were placed in a net pen.

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 haul tank, water temperature difference between the haul tank and the release site, fish length, and fish sex) during 2007 and 2008. Logistic models were blocked by collection date because fish collected on a given date were subjected to the same conditions. All combinations of conditions were examined ($N = 31$ models), and the most parsimonious model was selected using Akaike's information criterion corrected for small sample sizes (AIC_c ; Burnham and Anderson 2002). Akaike's information criterion (AIC) is an information theoretic approach used to rank multiple candidate models based on parsimony, which balances bias and variance (Burnham and Anderson 2002). The small-sample correction, AIC_c , is preferred when the sample size is small compared with the number of parameters in the global model ($N/K < 40$), which was the case for our data. We also calculated the likelihood of each model given the data, to estimate Akaike weights, which help evaluate the evidence for each candidate model compared with all others in the set (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 with stationary receivers (VR2; 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 all years (Figure 1). Another receiver was placed in Roanoke Rapids Lake to assess fallback or out-migration through Gaston Dam (Figure 1). We put one receiver at the entrance to the Dan River, another at the entrance of the Staunton River, and others (two in 2007 and four in 2008 and 2009) farther upstream in the Dan and Staunton rivers (Figure 1). In 2008 and 2009, we placed two receivers at Roanoke Rapids to obtain information about downstream movements of transported American shad (Figure 1). We checked stationary receivers for detections of tagged American shad at least monthly from mid-April to late June or July. In 2009, receiver 7 was missing from the buoy to which it was attached in Kerr Lake before data were downloaded; thus, no information from this receiver was obtained. In 2007 and 2008, we manually tracked tagged American shad, when possible, with a VEMCO model VR100 manual receiver, to examine specific movement patterns in reservoir and riverine habitats and to evaluate survival and passage downstream through dams.

To estimate the proportion of time tagged American shad spent in habitat suitable for spawning, we calculated the amount of time that the tagged fish spent in all upper basin habitats and the amount of time that they 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 fixed receiver 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 receiver 9 or 10 to enter a river) and river exit (when the fish passed receiver 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 in 2008 using analysis of variance (ANOVA). Using a t -test, we also examined for differences in the total length of tagged American shad from Kerr Lake in 2009 between those that entered a river and those that were only detected in the reservoir. This test was completed to evaluate whether size potentially affected the extent of upstream migration. Similar tests were not completed for American shad released in Kerr Lake in 2008 because few individuals migrated into riverine habitat.

We estimated the distances moved by tagged American shad to evaluate differences in movement patterns between fish released in different habitats and during different years and the general consequences of transporting fish upstream of dams. The minimum total distance moved was calculated as the total linear distance between fixed receivers 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. Using a conical equidistant projection, we estimated the linear distances between release locations and fixed receivers in ArcMap (ESRI, Redlands, California) from the U.S. Geological Survey's National Hydrography Dataset (<http://nhd.usgs.gov/>) maps for the upper Roanoke River Basin. All tagged American shad not found by at least one method outside of their general site of release were eliminated from all analyses, as they may have died or regurgitated 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). We considered fallback to be any fish 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 tagging, 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 6 individuals. All fish were put in the hauling tank, driven around for over 1 h, held overnight in net pens set at Roanoke Rapids, and released the next morning, which was similar to fish transported to upstream habitats. We placed stationary receivers near the collection site and about 2.7 rkm downstream (Figure 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 and releases through spill gates did not occur at either Gaston or Kerr dams during these years, so downstream passage would occur 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 but not within the same 24 h, 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 because ranges for stationary receivers are affected by depth and bathymetry. However, the environmental conditions at receiver locations 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. We estimated the survival rate for downstream passage at each dam as the percentage of sonic-tagged fish that survived out of the total number of sonic-tagged fish that moved downstream past that dam. We calculated 95% confidence intervals (CIs) for these survival rates using an exact method for binomial data (survived or died) described by Clopper and Pearson (1934). We only used data from 2007 and 2008 to estimate mortality because manual tracking was not done in 2009; however, we did include the numbers of 2009 fish detected at receivers downstream from dams to obtain information about out-migration. Because manual tracking was not conducted in 2009, tagged fish in a tailrace that died as a result of downstream passage but did not reach the first downstream receiver would not have been detected, so out-migration rates during this year may be biased downwards compared with 2007 and 2008. To determine whether any tagged

American shad made it past the series of dams to migrate back to the ocean, we examined receiver detections in 2008 and 2009 at Roanoke Rapids. From 9.2–19.1 m³/s is released through spill gates at Roanoke Rapids Dam, so downstream passage could occur through turbines or surface releases at this dam.

Sampling for American shad eggs.—Following an approach used in previous studies (Bilkovic et al. 2002; Hightower and Sparks 2003; Burdick and Hightower 2006), we used plankton tows to document spawning in upper rivers in 2007 and 2008. From mid May to late June in 2007, we conducted a 15-min oblique plankton tow (bongo frame with two 0.3-m diameter plankton nets, 6:1 tail to mouth ratios, and 500- μ m mesh) weekly at each of three stationary locations near receivers 10, 13, and 14 in the Staunton River (Figure 1). In 2008, four additional plankton stations were sampled from mid April to late June, one in the Staunton River near receiver 12 and three in the Dan River (Figure 1). To determine the timing and temperature range when spawning occurred, 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 1; Hightower and Sparks 2003). At each plankton tow site, water temperature and DO were recorded (YSI85 m) at approximately 0.5 m below the water surface. A standard General Oceanics Environmental flowmeter (General Oceanics, Miami, Florida) 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 1,161 American shad (313 in 2007, 425 in 2008, and 423 in 2009) were transported and released in lakes Gaston (294) and Kerr (522) and the lower Staunton River (345). Water temperature at Roanoke Rapids when American shad were collected for transport ranged from 12.0°C to 18.8°C (average = 14.6, SE = 0.433). Water temperatures at upper basin release sites were generally slightly warmer than those at Roanoke Rapids, ranging from 12.2°C to 23.0°C (average = 16.6, SE = 0.601). American shad spent between 2.8 and 7.6 h in the haul tank before release into an upstream habitat. Females ranged in total length (TL) from 422 to 667 mm (average = 491 mm) and males ranged from 331 to 526 mm TL (average = 434 mm). Of the 1,161 American shad released into upstream habitats, 300 received sonic tags. A total of 227 sonic-tagged American shad were used in analyses, including 55 released in Lake Gaston, 110 released in Kerr Lake, and 62 released in the Staunton River (Table 1). The majority of collected (about 80%) and tagged (about 72%) American shad were males. To see more specifics on tagged and untagged American shad transported to upstream areas see Harris and Hightower (2010).

TABLE 1. Numbers of sonic-tagged American shad and relevant water temperatures for fish collected at Roanoke Rapids and released at three upriver sites. The date for one fish transported to Kerr Lake in 2009 is unknown.

Date	Release site	Number of tagged American shad	Temperature, Roanoke Rapids (°C)	Temperature, release site (°C)
2007				
Apr 10	Lake Gaston	5	13.0	15.5
Apr 17	Lake Gaston	10	13.4	13.6
Apr 19	Kerr Lake	7	14.1	14.3
Apr 24	Lake Gaston	4	15.2	16.1
Apr 26	Kerr Lake	5	16.0	18.5
May 1	Lake Gaston	8	18.3	23.0
May 2	Kerr Lake	6	18.8	20.8
May 8	Kerr Lake	8	17.2	18.3
2008				
Apr 9	Kerr Lake	11	13.3	15.5
Apr 11	Lake Gaston	8	13.8	16.5
Apr 14	Staunton River	11	13.1	14.9
Apr 16	Kerr Lake	9	12.9	15.4
Apr 18	Lake Gaston	11	14.1	19.8
Apr 21	Staunton River	10	16.1	17.3
Apr 23	Kerr Lake	8	16.4	19.8
Apr 25	Lake Gaston	9	16.7	19.6
Apr 29	Staunton River	10	17.7	18.4
2009				
Apr 7	Kerr Lake	18	13.3	12.2
Apr 9	Staunton River	17	12	12.6
Apr 14	Staunton River	14	12.2	13.3
Apr 16	Kerr Lake	16	12.5	16.3
Apr 21	Kerr Lake	7	14.2	16.9

Survival of transported American shad was generally high for tagged and untagged fish in 2007 and 2008. The only exception was on 24 April 2007, when the net pen at Summit (Figure 1) was moved into an area of low water during the night, 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 because the outcome was a result of human interference, rather than transport procedures. Excluding that date, the average rate of survival to release during 2007 and 2008 was 85% (81% for females, 86% for males). We could not compare survival of tagged and untagged fish in 2007 because 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 mainly influenced by river water temperature but was also affected by total length (Table 2). American shad survival during transport generally decreased with increasing river water temperature (Figure 2). Survival was also lower, in general, for larger individuals. The most parsimonious model according to AIC_c included both temperature and total length as covariates

(Table 2). In combination, the two most parsimonious models according to AIC_c (one including both river water temperature and total length and the other with just water temperature as a covariate), accounted for almost 50% of the Akaike weight (Table 2). Also, all candidate models with any Akaike weight contained temperature as a covariate.

Telemetry

The movement patterns of sonic-tagged American shad differed by release site. Tagged American shad were released in Lake Gaston during 2007 ($N = 27$) and 2008 ($N = 28$) and movements were highly variable (Figure 3). Of all tagged fish released in Lake Gaston, 80% were detected at least once by receiver 4 in the middle of the reservoir (Figure 1). Approximately 31% of all tagged fish were detected at receiver 5 in the tailrace of Kerr Dam (Figure 1), most detections being from late April to early July. The distance between receivers 4 and 5 is almost 29 km, and 15% of tagged fish released in Lake Gaston moved repeatedly between the two receivers, two fish completing this migration four times (Figure 3B). Some tagged fish in Lake Gaston moved as far upstream as was possible (the

TABLE 2. Candidate models for logistic regression of the probability of survival for transported American shad, including the number of parameters in the model, the deviance ($-2 \cdot \log$ likelihood), the Akaike information criterion (AIC_c), ΔAIC_c , the likelihood of the model given the data ($L(g_i | x)$), and the Akaike weight (W_i). Covariates are defined as follows: temperature = the temperature in the river at the time of collection, time in tank = the time spent in transport (min), and difference = the difference in water temperature between the tank and the release location. The models were produced from data collected during 2007 and 2008.

Model	Number of parameters	Deviance	AIC_c	ΔAIC_c	$L(g_i x)$	W_i
Temperature, TL	3	638.6	646.3	0.0	1.0000	0.2900
Temperature	2	642.4	647.2	1.0	0.6196	0.1797
Temperature, TL, time in tank	4	637.5	648.6	2.4	0.3084	0.0894
Temperature, time in tank	3	641.0	648.7	2.4	0.2953	0.0856
Temperature, TL, sex	4	637.9	649.0	2.7	0.2576	0.0747
Temperature, TL, temperature difference	4	638.1	649.2	2.9	0.2322	0.0673
Temperature, temperature difference	3	641.8	649.5	3.2	0.2008	0.0582
Temperature, sex	3	641.8	649.5	3.3	0.1962	0.0569
Temperature, time in tank, sex	4	640.5	651.6	5.3	0.0702	0.0204
Temperature, TL, time in tank, sex	5	636.9	651.9	5.6	0.0600	0.0174
Temperature, time in tank, temperature difference	4	641.0	652.1	5.8	0.0550	0.0159
Temperature, sex, temperature difference	4	641.2	652.3	6.0	0.0501	0.0145
Temperature, TL, sex, temperature difference	5	637.5	652.5	6.2	0.0441	0.0128
Temperature, TL, time in tank, temperature difference	5	637.5	652.5	6.3	0.0434	0.0126
Temperature, time in tank, sex, temperature difference	5	640.5	655.5	9.2	0.0099	0.0029
Temperature, TL, time in tank, sex, temperature difference	6	636.9	656.5	10.3	0.0059	0.0017
TL, time in tank, temperature difference	4	706.6	717.7	71.4	0.0000	0.0000
TL, time in tank	3	711.4	719.2	72.9	0.0000	0.0000
Time in tank, temperature difference	3	712.2	720.0	73.7	0.0000	0.0000
TL, time in tank, sex, temperature difference	5	705.7	720.7	74.4	0.0000	0.0000
TL	2	716.9	721.7	75.4	0.0000	0.0000
Time in tank	2	717.1	721.9	75.6	0.0000	0.0000
TL, time in tank, sex	4	710.9	722.0	75.7	0.0000	0.0000
Time in tank, sex, temperature difference	4	711.4	722.5	76.2	0.0000	0.0000
Time in tank, sex	3	715.9	723.6	77.4	0.0000	0.0000
TL, temperature difference	3	716.0	723.7	77.5	0.0000	0.0000
TL, sex	3	716.4	724.2	77.9	0.0000	0.0000
Sex	2	721.7	726.5	80.2	0.0000	0.0000
TL, sex, temperature difference	4	715.5	726.6	80.3	0.0000	0.0000
Temperature difference	2	722.5	727.3	81.0	0.0000	0.0000
Sex, temperature difference	3	721.1	728.8	82.5	0.0000	0.0000

tailrace of Kerr Dam); however, most did not migrate that far, but moved smaller distances within the reservoir (Table 3). Of the tagged American shad released in Lake Gaston, 49% passed downstream through Gaston Dam and entered Roanoke Rapids Lake (Figure 3C). Of those that passed downstream, 59% first made upstream migrations, some to receiver 5. Downstream passage occurred from late April to late May in both 2007 and 2008. Also, 32% of the tagged fish released in Lake Gaston 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 tagged 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). Tagged

fish were released in Kerr Lake in 2007 ($N = 26$), 2008 (28), and 2009 (56). During 2007 and 2008, 96% of the tagged fish that actively migrated, were detected in the middle of Kerr Lake by either receiver 6 or 7 or, more commonly (81%), by both of those receivers (Figure 4). In fact, many tagged fish moved back and forth (up to four times) between receivers 6 and 7 without passing another receiver (Figure 4B). In general, tagged fish released in Kerr Lake in 2007 and 2008 did not move great distances upstream, but did move around within the reservoir (Table 3). In 2009, receiver 7 was lost, so movements in the middle of Kerr Lake were not as frequently detected, perhaps negatively biasing the total distances moved compared with 2007 and 2008. Still, tagged American shad moved greater distances overall and greater distances upstream in 2009 than in 2007 or 2008

FIGURE 2. Percent survival of American shad during transport around dams on the Roanoke River in 2007 and 2008 in relation to river water temperature at collection.

(Table 3). Less than 35% of tagged fish released in Kerr Lake in any year migrated into either the Staunton or Dan rivers; however, more tagged American shad moved into the Staunton and Dan rivers in 2009 (34%) than in 2007 (12%) or 2008 (7%; Table 4). Additionally, in 2009 one tagged fish was detected at the most upstream receiver in the Staunton River (receiver 14) and seven individuals were detected at the most upstream receiver in the Dan River (receiver 11); these fish may have made greater upstream migrations into the upper basin rivers than we detected that year.

Although the tagged individuals from Kerr Lake in 2009 that migrated into riverine habitat (average = 455.4, SE = 6.550) were slightly larger than those that were detected only in the reservoir (average = 447.2, SE = 5.07), the difference was not statistically significant ($t = 0.98$, $P = 0.330$). While most tagged American shad only made brief forays into upper basin rivers (Figure 4A), three fish spent considerable time (≥ 10 d) in

riverine habitat (Figure 4C). Tagged fish released in Kerr Lake were detected in the Staunton and Dan rivers from mid-April to mid-May. These fish entered riverine habitat after spending between 2.0 and 35.2 d in Kerr Lake, for an average of 13.8 d (SE = 1.8) spent in reservoir habitat before reaching a river. Tagged American shad from Kerr Lake detected in upper basin rivers spent less than 1 h to almost 30 d in the riverine habitat of the upper basin (average = 4.9 d). For 2007–2009 combined, only seven tagged fish (6%) released in Kerr Lake migrated downstream through Kerr Dam. These individuals were first detected in Lake Gaston from late April to mid-June. Two of these individuals (both in 2009) were later detected to pass receiver 3 and 2, indicating that they had migrated downstream into the lower Roanoke River, and one fish migrated past receiver 1. In 2007 and 2008, 27% of the tagged fish that did not pass downstream through Kerr Dam were last relocated by manual tracking just upstream of the dam in June.

TABLE 3. Minimum total and minimum upstream migration distances (km) for tagged American shad released in Lake Gaston, Kerr Lake, and the Staunton River, by year. Distances are minima because they were calculated from the linear distances between stationary receivers or points of manual relocation and do not include non-straight-line movements between receivers. The value n is the number of American shad that were detected during the season and that could be used for distance calculations.

Year	n	Total range	Total average (SE)	Upstream range	Upstream average (SE)
Lake Gaston					
2007	27	5.7–113.6	27.1 (5.4)	0–44.3	11.1 (2.7)
2008	28	6.9–311.0	86.2 (17.6)	0–35.5	17.2 (2.9)
Kerr Lake					
2007	26	6.0–155.5	43.2 (7.7)	0–47.3	10.9 (2.8)
2008	28	6.0–276.3	38.2 (10.0)	0–44.6	5.1 (2.1)
2009	56	13.5–316.6	61.3 (7.9)	0–103.6	18.2 (2.7)
Staunton River					
2008	31	21.2–212.3	77.1 (9.5)	0–57.5	4.1 (2.1)
2009	31	1.5–511.5	162.3 (26.5)	0–57.5	9.3 (2.7)

FIGURE 3. Three examples from 2007–2008 representing the different movement patterns of individual sonic-tagged American shad released in Lake Gaston, as determined by detections (black dots) at stationary receivers 1–5 (see Figure 1 for the locations): (A) fish spent time in the middle of Lake Gaston but migrated once to the tailrace of Kerr Dam; (B) fish migrated multiple times to the tailrace of Kerr Dam; and (C) fish was detected in the middle of Lake Gaston and then out-migrated to the lower Roanoke River.

TABLE 4. Number (*n*) and percentage of tagged American shad that were detected in the Staunton or Dan rivers and the total duration and percent of time that these fish were found in riverine habitat, by year and release site (Kerr Lake or the Staunton River). All fish released in the Staunton River were first detected in riverine habitat, so the percentage is 100.

Year	<i>n</i> (%)	Duration (d), range	Duration (d), average (SE)	Percent of time, range	Percent of time, average (SE)
Kerr Lake					
2007	3 (12%)	1.9–2.4	2.1 (0.1)	4.3–11.7	9.1 (2.4)
2008	2 (7%)	<0.1–29.9	15.0 (14.9)	0.1–50.8	25.4 (25.3)
2009	19 (34%)	<0.1–29.9	4.3 (1.6)	<0.1–64.5	11.3 (3.8)
Staunton River					
2008	31 (100%)	0.2–23.2	3.5 (1.0)	0.6–100	27.8 (6.0)
2009	31 (100%)	0.4–58.7	9.7 (2.0)	3.7–100	31.2 (5.3)

FIGURE 4. Three examples from 2007–2009 representing the different movement patterns of individual sonic-tagged American shad released in Kerr Lake, as determined by detections (black dots = Kerr Lake, gray squares = Staunton River, and white squares = Dan River) at stationary receivers 1–14 (see Figure 1 for locations): (A) fish completed a foray into the Staunton River; (B) fish was detected multiple times by receivers 6 and 7 in Kerr Lake, sometimes moving from one to the other in less than 3 h; and (C) fish migrated into the Dan River and remained upstream of receiver 11 for almost 30 d.

Tagged American shad released in the Staunton River behaved differently from those released in either reservoir (Figure 5). Ninety-four percent (29) of the 31 tagged American shad released in 2008 initially fell back, and 2 moved upstream; all 31 tagged fish released in 2009 initially fell back (Figure 5). Of the fish that fell back, 92% moved downstream at least to receiver 10 in the lower Staunton River, a distance 16.7 rkm below the release site. Of the tagged fish that fell back in the river, 65% later moved upstream within or back into riverine habitat in the Staunton or Dan rivers (later passing upstream receivers 9 or 10). Except in the fallback period, most tagged American shad released in the Staunton River in both years were found in the Staunton and Dan rivers from mid-April to mid-May, similar to tagged fish released in Kerr Lake. Tagged fish released in the Staunton River generally appeared to migrate as far or farther

than fish released in reservoir habitats; however, they made the shortest migrations directed upstream (Table 3). Fish released in the Staunton River remained longer in riverine habitat than did the tagged fish released in Kerr Lake that migrated into an upstream river (Table 4). In 2008, there was not a significant difference in riverine duration for males and females ($t = 0.85$, $P = 0.400$). Tagged American shad released earlier in 2008 appeared to spend more time in riverine habitat than those released later in the season, although differences were not quite significant ($F = 3.02$, $P = 0.065$; Figure 6). Tagged fish released in the Staunton River in 2009 migrated longer distances upstream and remained in riverine habitat longer than fish released there in 2008 (Tables 3, 4). Twenty-one percent of tagged fish released in the Staunton River spent at least 10 d in riverine habitat: 10% released in 2008 and 32% released in 2009. Only two

FIGURE 5. Three examples from 2008–2009 representing the different movement patterns of individual sonic-tagged American shad released in the lower Staunton River, as determined by detections (black dots = Kerr Lake, gray squares = Staunton River, and white squares = Dan River) at stationary receivers 1–14 (see Figure 1 for locations): (A) fish first made an upstream migration to receiver 13 but spent most of its time in Kerr Lake; (B) fish fell back and spent most of its time in Kerr Lake; and (C) fish fell back but then migrated within the Staunton River, Dan River, and Kerr Lake between late April and mid-May before remaining in Kerr Lake.

individuals (3%), both released in 2009, were detected out-migrating through Kerr Dam and entered Lake Gaston. Neither of these individuals was detected in either Roanoke Rapids Lake or the lower Roanoke River. In 2008, 13% of tagged fish released in the Staunton River were last found by manual tracking just above Kerr Dam in June. Only one tagged fish was located repeatedly at the same location in the lower Staunton River during regular manual tracking (about once/week in May and June in 2008), suggesting that it died or regurgitated its tag in the river.

Assessment of Fallback

Of the 12 tagged American shad released at Roanoke Rapids in 2008, 4 (33%) fell back past receiver 1, approximately 2.7

rkm below the release site. One of the four was in the net pen overnight, and the other three were released immediately after tagging. Fallback to receiver 1 occurred from 3 h to 2 d after release (average = 1 d, SE = 0.38). Of the four fish that fell back, three returned to the main spawning area and the fourth was not detected again. Four tagged fish later out-migrated past receiver 1, whereas three others remained on the spawning grounds at the end of June, over 50 d after tagging.

Downstream Passage and Survival

In 2007 and 2008, passage rates downstream through a dam and the estimated immediate survival associated with that downstream passage varied by dam. Three tagged fish (3.5%) passed downstream through Kerr Dam, two in 2007 and one in 2008,

FIGURE 6. Average number of days spent in riverine habitat by sonic-tagged American shad released in the lower Staunton River in 2008, by release date. The error bars denote SEs.

and all appeared to survive (95% CI: 0.292–1.000). All three American shad were detected by receiver 5 on a few separated occasions; two of the individuals passed receiver 4 in the middle of Lake Gaston, and one was detected in Roanoke Rapids Lake. Thus, one of the three fish that migrated downstream past Kerr Dam also passed downstream through Gaston Dam (Figure 1). During 2008, no tagged fish out-migrated past all three dams to reach the lower Roanoke River. For tagged fish in Lake Gaston, including those released in Lake Gaston ($N = 55$) and those that out-migrated past Kerr Dam into Lake Gaston ($N = 3$), 48% passed downstream through Gaston Dam into Roanoke Rapids Lake. Of the 28 that passed downstream, approximately 71% appeared to survive (95% CI: 0.513–0.868), about 21% had unknown fates, and approximately 7% (2 fish) died (95% CI: 0.009–0.235). The two fish categorized as definite turbine mortalities (one in 2007 and the other in 2008) were found in the same location 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; they 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, fixed receivers were placed in the river at Roanoke Rapids to identify downstream passage from Roanoke Rapids Lake to the lower Roanoke River. Between 55% and 67% of the tagged American shad that previously completed and survived downstream passage through Gaston Dam to enter Roanoke Rapids Lake in 2008 (6 of the 9 to 11 surviving individuals), later passed downstream through Roanoke Rapids Dam into the lower Roanoke River. The apparent survival of these tagged fish after passing downstream through Roanoke Rapids Dam was 83% (95% CI: 0.359–0.996); 17% had unknown fates, and there were no apparent mortalities (95% CI: 0.000–0.459).

FIGURE 7. Temperatures when plankton tows were completed and collections of American shad eggs, by date, for (A) Roanoke Rapids in 2007, (B) the Staunton River in 2007, and (C) the Staunton and Dan rivers in 2008 (see Figure 1). No American shad eggs were collected from plankton tows in the Staunton or Dan rivers in 2007 or 2008 (panels B and C).

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°C to 25.5°C (Figure 7A). The greatest number of eggs/m³ occurred on 7 June 2007, when the water temperature was 24.3°C. No American shad eggs were collected from any plankton samples in the Staunton or Dan rivers. Temperatures between 18°C and 25°C, when spawning would be expected, generally occurred in the upper Staunton and Dan rivers during late April, May, and sometimes early June (Figure 7). Temperatures appeared generally more variable in upper river areas than at Roanoke Rapids (Figure 7), although this may be a function of the times when sampling was completed; samples were collected between 2000 and 2200 hours eastern standard time at Roanoke Rapids but throughout the day at upper river sites.

Synopsis of Results

Many sonic-tagged American shad released in upper basin habitats moved back and forth between stationary receivers, often within a reservoir. Almost all tagged fish released in the lower Staunton River fell back; however, 65% of those that fell back later moved upstream to riverine habitat. The amount of time spent in riverine habitat was affected by release location and year, but also showed high individual variability. American shad released directly into the Staunton River spent a longer average amount of time in riverine habitat than did those released in Kerr Lake. Tagged fish released in the Staunton River spent an average of 4 d in riverine habitat in 2008 and an average of 10 d in 2009. Lower percentages of tagged fish released in Kerr Lake entered an upstream river in 2007 (12%) and 2008 (7%) than in 2009 (34%). American shad were detected in upper basin rivers mainly from mid-April to mid-May in all years. No American shad eggs were collected to document spawning in the Staunton or Dan rivers. There were only two documented turbine mortalities, but the downstream passage rate was not high at any dam (all <67%). More specifically, the downstream passage rate at Kerr Dam including all years was only 5% (9 of 172 individuals). Only 1% of all sonic-tagged American shad detected in 2008 and 2009 above Kerr Dam (2 of 146 individuals) moved downstream through all three dams and both of those fish out-migrated during 2009. Some tagged individuals were located by manual tracking just above dams in June in 2007 and 2008.

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 in 2007 and 2008 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 probably accounts for much of the same effect because females were generally larger than males. Given that (1) mortality was lowest early in the season, (2) fish released early appeared to spend comparably more time in riverine habitat, and (3) most detections in rivers occurred during April and early May, we suggest that it would be best to transport a high proportion of American shad as early as possible during the spawning season. We collected American shad on their spawning grounds at Roanoke Rapids, 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, most 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°C and 24°C) and dissolved oxygen (generally >5 mg/L), moderate water velocity (generally 0.3–0.9 m/s), and substrates free from silt (Stier and Crance 1985; Ross et al. 1993; Beasley and Hightower 2000; Hightower and Sparks 2003). The riverine habitat upstream of Kerr Lake met these conditions. However, most transported American shad, including many individuals released in the Staunton River, spent much of their time in Kerr Lake, which is a large (22,234 ha), deep (average around 9 m) reservoir that lacks adequate flow to provide suitable spawning habitat for American shad.

Historically, American shad in the Roanoke River and other rivers completed long distance migrations upstream to spawning habitats (Limburg et al. 2003), so the relatively short distances between release sites and riverine habitat should not impede their reaching that habitat. Some tagged American shad moved considerable distances after transport; however, much of the movement was back-and-forth within a reservoir (Table 3; Figures 3–5) rather than a directed movement upstream. Also, our estimates of total movement were lower than actual values because they were calculated mainly from detections on stationary receivers (some over 30 km apart) and do not take into account smaller-scale movements between receivers. Therefore, the relatively small amount of time spent in upstream riverine habitats by tagged American shad released in Kerr Lake was probably not related 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 the fallback response (Barry and Kynard 1986; Beasley and Hightower 2000; Moser et al. 2000; Hightower and Sparks 2003). 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). To reduce handling time during tagging, Sprinkle (2005) collected no information on an individual's size or sex and fallback was observed for only 10% of the tagged fish. Frank et al. (2009) examined chemical levels in blood plasma associated with stress (cortisol, glucose, and chloride ions) in alewives *A. pseudoharengus* under conditions of handling and tagging. Their data suggest that handling or handling combined with tagging resulted in similarly elevated stress levels not observed in unhandled fish (Frank et al. 2009). They also observed that alewives transported for 2 h experienced even greater changes in chemical levels, suggesting more

highly elevated stress levels associated with transport. Evaluation of stress levels for American shad 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 with 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 better 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, we observed that a lower proportion of American shad tagged, transported, and 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 the spawning grounds may have suffered lower fallback rates because other American shad were present to form schools. We transported 50–60 American shad at a time, 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.

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 2004), and studies from populations in Virginia suggest that there is high individual variability, but that females generally spawn every 2–4 d, and individuals spend about a month in riverine spawning habitats (Olney et al. 2001; Hyle 2004; Olney et al. 2006; Aunins and Olney 2009). Using manual tracking, Sparks (1998) found that after tagged American shad reached the spawning grounds at Roanoke Rapids, they remained within a 1-km² area, often for about 20 d. In addition, such concentrations of tagged American shad and American shad spawning activity over a season have been observed in other studies (Bowman 2001; Bailey et al. 2004). Using this information, it seems very unlikely that many of our tagged American shad could have spawned multiple batches of eggs during their forays into 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 because our sample sizes were small relative to the size of the system. We also 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 potentially have a lower probability of repeat spawning than do fish below the Roanoke Rapids Dam. Only 5% of the fish released in either Kerr Lake or the Staunton River during the 3 years passed downstream through Kerr Dam. In addition, including fish released in 2008 and 2009, only 1% completed the entire migration back to the lower

Roanoke River. It is possible that some tagged American shad passed downstream after the study ended, the tag's battery life ended, or after regurgitating the tag, causing their outmigration to be undetected. Tagged fish located just above dams late in the season suggest that some individuals were attempting to out-migrate, but were unable to pass downstream through the turbines. In the River Gudbrandsdalslagen, a regulated river in Norway, postspawning brown trout *Salmo trutta* 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 out-migrated 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 (Leim 1924; Chittenden 1976; Walter and Olney 2003; Harris and McBride 2009); therefore, the combination of longer migration distances, delayed or ceased out-migration, and turbine mortality (Chittenden 1976; Kynard and Buerkett 1997; Limburg et al. 2003; Leggett et al. 2004) could cause increased mortality and reduce the numbers of repeat spawners. Although highly variable, the estimated percentage of repeat spawners in the Roanoke River averages 55% and some individuals spawn in more than 2 years (Burgess et al. 2007). Thus, fish transported upstream of Kerr Lake would presently appear to have a reduced chance of repeat spawning compared with fish in the lower Roanoke River. Structures or surface releases to aid in downstream passage at Kerr Dam could potentially improve the percentage of American shad that successfully out-migrate.

In contrast to the low downstream passage rates at Kerr Dam, almost 50% of fish passed downstream through Gaston Dam and just over 50% passed Roanoke Rapids Dam. 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 hp, 20.7-m head, 128.6 rotations/min) and Gaston Dam has one adjustable-blade and three fixed-blade Kaplan turbines (70,000 hp, 20.4-m head, 100 rotations/min). 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 American shad spawning season. In contrast, Kerr Dam has nine vertical-shaft Francis turbines (six with 45,000 hp, 27.4-m head, 85.7 rotations/min; one with 17,000 hp, 27.4-m head, 138.5 rotations/min; and two with 1,600 hp, 27.4-m head, 450.0 rotations/min) that pull water from the hypolimnion, which is poorly oxygenated. The slightly higher percentage of American shad out-migrating past Roanoke Rapids Dam, than past Gaston Dam might be due to the combination of turbine and surface releases at Roanoke Rapids Dam, whereas Gaston Dam has only turbine releases. Alternatively, this observed difference may be the result of small sample sizes. Overall, our results suggest that, like other systems, downstream passage through dam turbines can result in low initial mortality for American shad, but rates may vary with the dam's configuration and power output (Bell and Kynard 1985; St. Pierre 2003; Sadzinski and Hendricks 2007; Heisey et al. 2008). Delayed mortality potentially

associated with downstream passage at hydroelectric facilities, as suggested for out-migrating juvenile Pacific salmon smolts (Budy et al. 2002), was not examined or quantified, but could result in higher mortality rates for out-migrating American shad. Downstream passage structures or spilling water could potentially increase downstream passage of transported fish, which would reduce the negative effects of transport on the proportion of repeat spawners in the population.

Environmental conditions may affect the annual results of a trap-and-transport program. Compared with 2007 and 2008, a higher percentage of the 2009 sonic-tagged fish released in Kerr Lake migrated into one of the upper basin rivers and tagged fish released in the lower Staunton River spent a longer amount of time in riverine habitat. Average discharge rates in both the Dan and Staunton rivers in April were similar during the 3 years, although higher flows were observed in 2009 in May and especially in June. The additional rainfall in 2009 could have maintained cooler water temperatures during the spring, thus attracting fish into the upper basin rivers. Also, more tagged American shad out-migrated in 2009 than in 2007 and 2008, and two fish past downstream through all three dams to the lower Roanoke River in 2009. Larger amounts of water passing through dam turbines during periods of higher water flow may have increased downstream passage, especially for fish above Kerr Dam. To determine when and how to best transport American shad upstream of dams, continued research should evaluate how movement patterns in upstream habitats are affected by water flow and water temperature.

The overall success of a trap-and-transport program in a river system is affected by release site and upper basin characteristics. American shad released directly into the Staunton River 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; they 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 similar difficulty locating flow in large reservoirs, such as Kerr Lake. 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 upstream 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. An example of such a system could be the Susquehanna River of Maryland and Pennsylvania. The most downstream dam on the Susquehanna River is at rkm 16 (Conowingo Dam). Stocking and access to habitat upstream of dams have improved the stock status of American shad in the Susquehanna River, although it has been suggested that improved upstream passage rates at some dams and reductions in downstream mortality rates would improve the results of restoration efforts (Sadzinski and Hendricks 2007).

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 introduced into reservoirs that are later located in riverine habitat, and the relatively little time 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, our study was small and experimental, and American shad might perform better in a program characterized by less handling, no tagging, and large-scale transport. Other potential concerns associated with transport programs are out-migration delays at dams and passage mortality; both might be reduced by structures to aid downstream migration. The effectiveness of trap and transport depend, in part, on upper basin characteristics. Overall, a transport program would 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.

ACKNOWLEDGMENTS

We thank Nicole Antaya, Jeffery Buckel, Chad Coley, Patrick Cooney, Kevin Dockendorf, Robert Graham, Thomas Kwak, Kenneth Pollock, and Kyle Ward for help with design, field work, and analysis of this study. We appreciate Fritz Rohde and Troy Tuckey for reviewing an earlier draft of this manuscript. This work was funded by Dominion/North Carolina Power and the North Carolina Wildlife Resources Commission. The North Carolina Cooperative Fish and Wildlife Research Unit is jointly supported by North Carolina State University, North Carolina Wildlife Resources Commission, U.S. Geological Survey, U.S. Fish and Wildlife Service, and Wildlife Management Institute. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. government.

REFERENCES

- Acolas, M. L., M. L. Begout Anras, V. Veron, H. Jourdan, M. R. Sabatie, and J. L. Bagliniere. 2004. An assessment of the upstream migration and reproductive behavior of allis shad (*Alosa alosa* L.) using acoustic tracking. ICES (International Council for the Exploration of the Sea) Journal of Marine Science 61:1291–1304.
- Arnekleiv, J. V., M. Kraabol, and J. Museth. 2007. Efforts to aid downstream migrating brown trout (*Salmo trutta* L.) and smolts passing a hydroelectric dam and a spillway. Hydrobiologia 582:5–15.
- ASMFC (Atlantic States Marine Fisheries Commission) 2007. American shad stock assessment. ASMFC, Stock Assessment Report 07–01, Washington, D.C.
- Aunins, A., and J. E. Olney. 2009. Migration and spawning of American shad in the James River, Virginia. Transactions of the American Fisheries Society 138:1392–1404.
- Bailey, M. M., J. J. Isely, and W. C. Bridges Jr. 2004. Movement and population size of American shad near a low-head lock and dam. Transactions of the American Fisheries Society 133:300–308.
- Barry, T., and B. Kynard. 1986. Attraction of adult American shad to fish lifts at Holyoke Dam, Connecticut River. North American Journal of Fisheries Management 6:233–241.
- Beasley, C. A., and J. E. Hightower. 2000. Effects of a low-head dam on the distribution and characteristics of spawning habitat used by striped bass and American shad. Transactions of the American Fisheries Society 129:1316–1330.
- Bell, C. E., and B. Kynard. 1985. Mortality of adult American shad passing through a 17-megawatt Kaplan turbine at a low-head hydroelectric dam. North American Journal of Fisheries Management 5:33–38.
- Bilkovic, D. M., C. H. Hershner, and J. E. Olney. 2002. Macroscale assessment of American shad spawning and nursery habitat in the Mattaponi and Pamunkey rivers, Virginia. North American Journal of Fisheries Management 22:1176–1192.
- Bowman, S. W. 2001. American shad and striped bass spawning migration and habitat selection in the Neuse River, North Carolina. Master's thesis. North Carolina State University, Raleigh.
- Budy, P., G. P. Thiede, N. Bouwes, C. E. Petrosky, and H. Schaller. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. North American Journal of Fisheries Management 22:35–51.
- Burdick, S. M. 2005. Distribution of spawning activity by migrating fishes in the Neuse River, North Carolina, after removal of a low-head dam. Master's thesis. North Carolina State University, Raleigh.
- Burdick, S. M., and J. E. Hightower. 2006. Distribution of spawning activity by anadromous fishes in an Atlantic slope drainage after removal of a low-head dam. Transactions of the American Fisheries Society 135:1290–1300.
- Burgess, C., S. Winslow, J. Harris, B. Wynne, K. Dockendorf, K. Hattala, and A. Kahnle. 2007. Status of American shad stocks in North Carolina. Pages 251–382 in American shad stock assessment. Atlantic States Marine Fisheries Commission, Stock Assessment Report 07–01(Supplement), Part VII, Section 13, Washington, D.C.
- Burnham, K. P., and D. A. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.
- Castro-Santos, T., and B. H. Letcher. 2010. Modeling migratory energetic of Connecticut River American shad (*Alosa sapidissima*): implications for the conservation of an iteroparous anadromous fish. Canadian Journal of Fisheries and Aquatic Sciences 67:806–830.
- Chittenden, M. E. 1976. Weight loss, mortality, feeding, and duration of residence of adult American shad, *Alosa sapidissima*, in fresh water. U.S. National Marine Fisheries Service Fishery Bulletin 74:151–157.
- Clopper, C. J., and E. S. Pearson. 1934. The use of confidence limits illustrated in the case of the binomial. Biometrika 26:404–413.
- Cooke, D. W., and S. D. Leach. 2003. Beneficial effects of increased river flow and upstream fish passage on anadromous alosine stocks. Pages 331–338 in K. E. Limburg and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society, Symposium 35, Bethesda, Maryland.
- Frank, H. J., M. E. Mather, J. M. Smith, R. M. Muth, J. T. Finn, and S. D. McCormick. 2009. What is "fallback"? metrics needed to assess telemetry tag effects on anadromous fish behavior. Hydrobiologia 635:237–249.
- Freeman, M. C., C. M. Pringle, E. A. Greathouse, and B. J. Freeman. 2003. Ecosystem-level consequences of migratory faunal depletion caused by dams. Pages 255–266 in K. E. Limburg and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society, Symposium 35, Bethesda, Maryland.
- Harris, J. E., and J. E. Hightower. 2010. Movement and spawning of American shad transported above dams on the Roanoke River. Final Report prepared by North Carolina Cooperative Fish and Wildlife Research Unit for Dominion North Carolina Power, Raleigh.
- Harris, J. E., and R. S. McBride. 2009. American shad feeding on spawning grounds in the St. Johns River, Florida. Transactions of the American Fisheries Society 138:888–898.
- Heisey, P. G., D. Mathur, J. L. Fulmer, and E. Kotkas. 2008. Turbine passage survival of late running adult American shad and its potential effect of population restoration. Pages 141–152 in S. V. Amaral, D. Mathur, and E. P. Taft III, editors. Advances in fisheries bioengineering. American Fisheries Society, Symposium 61, Bethesda, Maryland.
- Hendricks, M. L. 2003. Culture and transplant of alosines in North America. Pages 303–312 in K. E. Limburg and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society, Symposium 35, Bethesda, Maryland.
- Hightower, J. E., and K. L. Sparks. 2003. Migration and spawning habitat of American shad in the Roanoke River, North Carolina. Pages 193–199 in K. E. Limburg and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. Bethesda, Maryland.
- Hightower, J. E., A. M. Wicker, and K. M. Endres. 1996. Historical trends in abundance of American shad and river herring in Albemarle Sound, North Carolina. North American Journal of Fisheries Management 16:257–271.
- Hyle, A. R. 2004. Reproductive biology of American shad, *Alosa sapidissima*, in the Mattaponi River. Master's thesis. College of William and Mary, Williamsburg, Virginia.
- Jones, P. W., F. D. Martin, and J. D. Hardy Jr. 1978. Development of fishes of the mid-Atlantic bight, volume 1. University of Maryland, Chesapeake Biological Laboratory, Solomons.
- Kynard, B., and C. Buerkett. 1997. Passage and behavior of adult American shad in an experimental louver bypass system. North American Journal of Fisheries Management 17:734–742.
- Layzer, J. B. 1979. Transportation of adult American shad past dams on the Connecticut River, Massachusetts, 1973–1976. Progressive Fish-Culturist 41: 7–9.
- Leggett, W. C., T. F. Savoy, and C. A. Tomich. 2004. The impact of enhancement initiatives on the structure and dynamics of the Connecticut River population of American shad. Pages 391–405 in P. M. Jacobson, D. A. Dixon, W. C. Leggett, B. C. Marcy Jr., and R. R. Massengill, editors. The Connecticut River ecological study (1965–1973) revisited: ecology of the lower Connecticut River, 1973–2003. American Fisheries Society, Monograph 9, Bethesda, Maryland.
- Leim, A. H. 1924. The life history of shad, *Alosa sapidissima* (Wilson), with special reference to the factors limiting its abundance. Contributions to Canadian Biology (new series) II:163–284.
- Limburg, K. E., K. A. Hattala, and A. Kahnle. 2003. American shad in its native range. Pages 125–140 in K. E. Limburg and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society, Symposium 35, Bethesda, Maryland.
- Mann, D. A., D. M. Higgs, W. N. Tavolga, M. J. Souza, and A. N. Popper. 2001. Ultrasound detection by clupeiform fishes. Journal of the Acoustic Society of America 109:3048–3054.

- Moser, M. L., A. M. Darazsdi, and J. R. Hall. 2000. Improving passage efficiency of adult American shad at low-elevation dams with navigation locks. *North American Journal of Fisheries Management* 20:376–385.
- Moser, M. L., and S. W. Ross. 1993. Distribution and movements of short-nose sturgeon (*Acipenser brevirostrum*) and other anadromous fishes in the lower Cape Fear River, North Carolina. Final Report to U.S. Army Corps of Engineers, Wilmington, North Carolina.
- Olney, J. E., S. C. Denny, and J. M. Hoenig. 2001. Criteria for determining maturity stage in female American shad, *Alosa sapidissima*, and a proposed reproductive cycle. *Bulletin Francais de la Peche et de la Pisciculture* 362/363:881–901.
- Olney, J. E., R. J. Latour, B. E. Watkins, and D. G. Clarke. 2006. Migratory behavior of American shad in the York River, Virginia, with implications for estimating in-river exploitation from tag recovery data. *Transactions of the American Fisheries Society* 135:889–896.
- Olney, J. E., and R. S. McBride. 2003. Intraspecific variation in batch fecundity of American shad: revisiting the paradigm of reciprocal latitudinal trends in reproductive traits. Pages 185–192 in K. E. Limburg and J. R. Waldman, editors. *Biodiversity, status, and conservation of the world's shads*. American Fisheries Society, Symposium 35, Bethesda, Maryland.
- Petersen, J. H., R. A. Hinrichsen, D. M. Gadomski, D. H. Feil, and D. W. Rondorf. 2003. American shad in the Columbia River. Pages 141–155 in K. E. Limburg and J. R. Waldman, editors. *Biodiversity, status, and conservation of the world's shads*. American Fisheries Society, Symposium 35, Bethesda, Maryland.
- Popper, A. N. 2003. Effects of anthropogenic sounds on fishes. *Fisheries* 28(10):24–31.
- Pringle, C. M., M. C. Freeman, and B. J. Freeman. 2000. Regional effects of hydrologic alterations on riverine macrobiota in the new world: tropical-temperate comparisons. *BioScience* 50:807–823.
- Read, A. N. 2004. Characterizing American shad spawning habitat in the upper Roanoke River basin, Virginia. Master's thesis. North Carolina State University, Raleigh.
- Ross, R. M., R. M. Bennet, and T. W. H. Backman. 1993. Habitat use by spawning adult, egg, and larval American shad in the Delaware River. *Rivers* 4:227–238.
- Rulifson, R. A., and C. S. Manooch III. 1990. Recruitment of juvenile striped bass in the Roanoke River, North Carolina, as related to reservoir discharge. *North American Journal of Fisheries Management* 10:397–407.
- Sadzinski, R., and M. Hendricks. 2007. Status of Susquehanna River and Susquehanna flats American shad stock. Pages 46–132 in American shad stock assessment. Atlantic States Marine Fisheries Commission, Stock Assessment Report 07–01 (Supplement), Part VII, Section 10, Washington, D.C.
- Schilt, C. R. 2007. Developing fish passage and protection at hydropower dams. *Applied Animal Behaviour Science* 104:295–325.
- Shuman, J. R. 1995. Environmental considerations for assessing dam removal alternatives for river restoration. *Regulated Rivers: Research and Management* 11:249–261.
- Smith, H. M. 1894. Statistics of the fisheries of the United States. U.S. Fish Commission Bulletin 13:389–417.
- Sparks, K. L. 1998. Identification of major spawning habitats used by American shad (*Alosa sapidissima*) in the Roanoke River, North Carolina. Master's thesis. North Carolina State University, Raleigh.
- Sprinkle, K. 2005. Interdam movements and passage attraction of American shad in the lower Merrimack River main stem. *North American Journal of Fisheries Management* 25:1456–1466.
- St. Pierre, R. A. 2003. A case history: American shad restoration on the Susquehanna River. Pages 315–321 in K. E. Limburg and J. R. Waldman, editors. *Biodiversity, status, and conservation of the world's shads*. American Fisheries Society, Symposium 35, Bethesda, Maryland.
- Stier, D. J., and J. H. Crance. 1985. Habitat suitability index models and in-stream flow suitability curves: American shad. U.S. Fish and Wildlife Service Biological Report 82(10.88).
- Trush, W. J., S. M. McBain, and L. B. Leopold. 2000. Attributes of an alluvial river and their relation to water policy and management. *Applied Physical Sciences* 97:11858–11863.
- Walburg, C. H. 1954. Experimental transport of live shad past Susquehanna River dams. U.S. Fish and Wildlife Service Special Scientific Report Fisheries 114.
- Walburg, C. H., and P. R. Nichols. 1967. Biology and management of the American shad and status of the fisheries, Atlantic coast of the United States, 1960. U.S. Fish and Wildlife Service Special Scientific Report Fisheries 550.
- Walter, J. F., III, and J. E. Olney. 2003. Feeding behavior of American shad during spawning migration in the York River, Virginia. Pages 201–209 in K. E. Limburg and J. R. Waldman, editors. *Biodiversity, status, and conservation of the world's shads*. American Fisheries Society, Symposium 35, Bethesda, Maryland.
- Weaver, L. A., M. T. Fisher, B. T. Boshers, M. L. Claud, and L. J. Koth. 2003. Boshers Dam vertical slot fishway: a useful tool to evaluate American shad recovery efforts in the upper James River. Pages 339–347 in K. E. Limburg and J. R. Waldman, editors. *Biodiversity, status, and conservation of the world's shads*. American Fisheries Society, Symposium 35, Bethesda, Maryland.
- Williams, R. O., and G. E. Bruger. 1972. Investigations on American shad in the St. Johns River. Florida Department of Natural Resources Marine Research Laboratory Technical Series 66.