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Demographic Population Model for American Shad: Will Access to Additional Habitat Upstream of Dams Increase Population Sizes?

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Abstract
American shad *Alosa sapidissima* are in decline in their native range, and modeling possible management scenarios could help guide their restoration. 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 on sonic-tagged adult American shad and oxytetracycline-marked American shad fry both above and below dams on the Roanoke River with information from other systems to estimate a starting population size and vital rates. We modeled the adult female population over 30 years under plausible scenarios of adult transport, effective fecundity (egg production), and survival of adults (i.e., to return to spawn the next year) and juveniles (from spawned egg to age 1). We also evaluated the potential effects of increased survival for adults and juveniles. The adult female population size in the Roanoke River was estimated to be 5,224. With no transport, the model predicted a slow population increase 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 effective fecundity and juvenile survival could be achieved. Currently, transported adults and young are less likely to successfully out-migrate than individuals below the dams, and the estimated adult population size is much smaller than either of two assumed values of carrying capacity for the lower river; therefore, transport is not predicted to help restore the stock under present conditions. Research on survival rates, density-dependent processes, and the impacts of structures to increase out-migration success would improve evaluation of the potential benefits of access to additional spawning habitat for American shad.

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

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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). Spawning habitat in rivers has been generally characterized by shallow depth (<5 m), moderate current velocity (0.3–0.9 m/s), adequate dissolved oxygen (>5 mg/L), and substrates lacking silt (Stier and Crance 1985; Ross et al. 1993; Beasley and Hightower 2000; Bilkovic et al. 2002; Hightower and Sparks 2003). Studies suggest that individuals return to 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 further 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 the stocking of fry appears to have improved populations (Cooke and Leach 2003; St. Pierre 2003; Weaver et al. 2003). However, Leggett et al. (2004) suggested that access to upstream habitats may negatively affect populations with a high proportion of repeat spawners due to increased mortality associated with a longer upstream migration and downstream passage through dams. Habitat above dams may also be highly altered, and fish must sometimes migrate through large reservoirs; thus, the quantity and quality of and likelihood of reaching suitable spawning habitat at upstream sites may be lower than it was prior to dam construction. For an iteroparous population, mortality due to downstream passage through dam turbines could cause population reductions, whereas access to additional spawning habitat could lead to higher production, which would lead to population increases. The balance between these negative and positive factors is likely to be system specific and determines 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 plausible levels of survival and effective fecundity (egg production) and to compare such outcomes with those of increasing survival rates of adults (i.e., to return to spawn the next year) or juveniles (from spawned egg to age 1). The Roanoke River appears to be ideal for examining the opportunities for transport to upper-basin habitats because the population is depressed; upstream habitat has been evaluated as suitable for spawning (Read 2004); 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 American shad in the Roanoke River, but after modification of some vital rates it could be useful for evaluating the effects of transport in other regulated rivers.

METHODS

American shad in the Roanoke River.— Water flow in the Roanoke River is regulated by six dams, with the most downstream one located in Roanoke Rapids, North Carolina, at river kilometer (rkm) 221 (Rulifson and Manooch 1990; Walsh et al. 2005; Figure 1). Other dams on the river's main stem include Gaston Dam at rkm 233 and Kerr Dam at rkm 288 (Figure 1). Historically, adult American shad were reported to migrate as far upstream as Salem, Virginia (McDonald 1884), to approximately rkm 579 (Gannett 1901); however, the current series of dams provide no fish passage, so spawning is presently restricted to the lower 221 rkm.

Our primary estimate of the carrying capacity of adult American shad in the Roanoke River was based on the "50 shad per acre" (124 per hectare) rule of thumb developed by St. Pierre (1979). St. Pierre's (1979) equation was developed from historic stock data on the Connecticut River, but it has been used to estimate the carrying capacity of other rivers (Hightower and Wong 1997; Weaver et al. 2003). This calculation includes all riverine habitats, not just areas considered spawning sites, and makes the assumption that some areas will have higher densities of adult American shad than others, with 124/ha being a good estimate for the entire accessible portion of the river. Assuming 124/ha as the density for carrying capacity and a river length of 221 km with an average width of roughly 100 m, the lower Roanoke River would be expected to support about 273,100 spawning adult American shad annually. However, carrying capacity is likely river specific and dependent on the quality and quantity of spawning habitat available in the system; thus, we also evaluated the model using a different density calculation (49/ha) to produce an alternative estimate of carrying capacity for the Roanoke River (109,200 spawning adults). This alternative calculation was developed from more current estimates of population size in the Connecticut River (T. Savoy and V. Crecco, 1994 memorandum to E. Beck, State of Connecticut, Department of Environmental Protection, Bureau of Natural Resources and Marine Fisheries, on Thames River goals). The carrying capacity of the lower Roanoke River is presently unknown; however, we speculate that it would fall between these

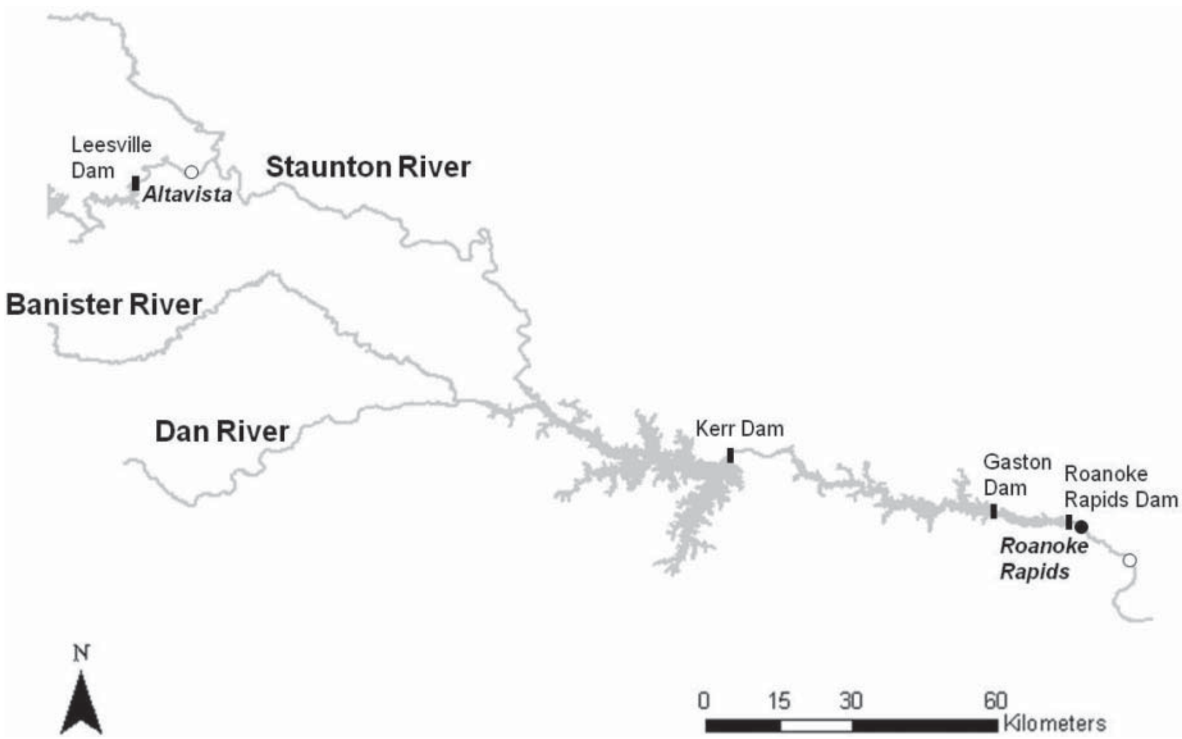

FIGURE 1. Locations of upper Roanoke River basin rivers, dams, fry release sites (open circles), and the current main spawning site for American shad at Roanoke Rapids (filled circle).

two estimates, so using both should give us a good understanding of the range of potential outcomes.

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 Commission (FERC) license for the Roanoke Rapids and Gaston dams specifies that Dominion/North Carolina Power must further evaluate and potentially prepare to move American shad upstream of dams once the population has been estimated to reach 20,000 adults in two years (not necessarily two consecutive years). The intent of the fish passage program was to provide access to habitat above Kerr Dam, the third dam in the Roanoke River system. Upstream of Kerr Lake, there is approximately 400 rkm of riverine habitat (Read 2004). To evaluate the possible outcomes of access to this habitat, various studies have been completed. Read (2004) examined environmental parameters (i.e., temperature, velocity, dissolved oxygen, pH, and substrate) in main-channel and tributary sections of rivers in the upper basin to evaluate their suitability for spawning by 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 egg development and survival. We recently characterized migration, spawning, and survival downstream past dams for sonic-tagged adult American shad released into upstream habitats (Harris and Hightower 2011). In addition, data on the out-migration of oxytetracycline (OTC)-marked American shad fry released in the main river upstream of Kerr Dam are presently being collected (North Carolina Wildlife Resources Commission [NCWRC] study).

The Roanoke River population of American shad is subjected to commercial harvest in the Albemarle Sound. This harvest averaged approximately 58,000 kg per year between 1972 and 2005 and 75,000 kg 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), this harvest would represent approximately 38,000 individuals per year between 1972 and 2005. Because Albemarle Sound includes American shad from both the Roanoke and Chowan river basins, it is unknown what proportion of this harvest is from the Roanoke River.

Matrix model development.—Our model includes five stages and uses data evaluated in the form of a prebreeding 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 prebreeding census (i.e., data collected just prior to the onset of spawning) with an annual time step, appeared appropriate. The five stages included are as follows: juveniles (age 1) produced below Roanoke Rapids Dam (*JUVl*); juveniles (age 1) produced

TABLE 1. Structure of the stage-based matrix model for female American shad. Variables are as follows: S_2 = the probability of surviving from age 1 to age 2, $S_{[stage]}$ = the probability of surviving in a particular stage (see below), S_t = the probability of surviving the transition to adulthood, $F_{[stage]}$ = the fecundity of an individual in a particular stage, K = the carrying capacity of the lower Roanoke River, D = the proportion of subadults that become mature, and $p(T)$ = the proportion transported above dams on the Roanoke River. The five stages are as follows: (1) juveniles produced by adults below Roanoke Rapids Dam (*JUVl*); (2) juveniles produced by adults passed above dams (*JUVu*); (3) subadults (*SUB*); (4) adults spawning below Roanoke Rapids Dam (*Al*); and (5) adults spawning above dams (*Au*).

Stage	1	2	3	4	5
1	0	0	0	$F_{Al}S_{JUVl}(\frac{K-Al}{K})$	0
2	0	0	0	0	$F_{Au}\,S_{JUVu}$
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	$DS_t\,p(T)$	$S_{Al}\,p(T)$	$S_{Au}\,p(T)$

in riverine habitat above Kerr Dam (*JUVu*); subadults (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 1; Figure 2). The model was run under a variety of 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 1), and $N(t+1)$ is the number of American shad in each stage in the next time step (Caswell 2001).

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 data from the

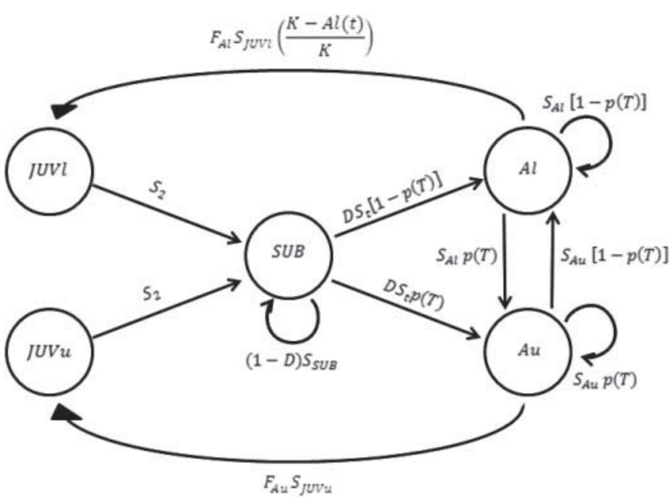

FIGURE 2. Prebreeding census life cycle diagram for American shad in the Roanoke River, including the opportunity for transport above dams. The five stages are as follows: (1) juveniles produced by adults below Roanoke Rapids Dam (*JUVl*); (2) juveniles produced by adults passed above dams (*JUVu*); (3) subadults (*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 1. See text for additional details.

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. We assumed a 1:1 sex ratio, as observed by fishery-independent monitoring for adult American shad in Albemarle Sound just prior to spawning (Burgess et al. 2007). 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).

Density dependence.—Both density-dependent (i.e., predation and starvation) and density-independent (i.e., water temperature and water discharge rate) processes have been suggested to impact the survival of American shad during the first year of life (Leggett 1977; Crecco and Savoy 1984, 1985; Savoy and Crecco 1988). We incorporated density dependence into the production of juveniles in our model to account for the potentially limiting amount of habitat below Roanoke Rapids Dam. Density dependence can be incorporated into matrix models in a variety of ways; however, it is often done with an estimate of carrying capacity through the use of the logistic equation (Jensen 1995; Caswell 2001; Miller et al. 2002; Rintala and Tiainen 2008). To incorporate density dependence into this model, we modified the production of juveniles below Roanoke Rapids Dam by the number of spawning females there, as it related to an estimate of the carrying capacity for the lower Roanoke River. The resulting equation was

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

where $JUVl(t+1)$ is the number of female juveniles produced below the Roanoke Rapids Dam in year $t+1$, F_{Al} is the adult fecundity below Roanoke Rapids Dam, S_{JUVl} is the survival rate to become a juvenile when produced below the Roanoke Rapids Dam, K is the carrying capacity below Roanoke Rapids Dam, and $Al(t)$ is the number of adult females below the Roanoke Rapids Dam in year t. Juveniles produced upstream of the dams were assumed not to be affected by density dependence, as habitat is not expected to limit their population growth at current stock sizes.

Fecundity.—Data in Holland and Yelverton (1973) suggest that the average adult female American shad in the Albemarle Sound produces approximately 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 adult female are required (Olney et al. 2001). As for most stocks, these values are unknown for the Roanoke River population; therefore, the average value from Holland and Yelverton (1973) was used.

Survival to become a juvenile.—To estimate the juvenile survival rate (i.e., the survival rate 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:

$$\log_e(EDT) = 8.9 - 2.484 \cdot \log_e(T),$$

where EDT is egg development time in days and T is temperature in °C (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 (Harris and Hightower 2010) 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 d) 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 d old, from 10 to 18 d old, and from 19 to 35 d old from Crecco and Savoy (1987), as also used by Limburg (1996). Once hatched, 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 d to age 150 d, American shad were in Albemarle Sound and used the average of the two survival estimates developed by Tuomikoski et al. (2008) for American shad in the sound. We have no estimates of survival for subadult American shad in the ocean. Therefore, to estimate survival for American shad age 150–365 d, 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 the 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 d in age appeared to be around 100 mm (From Figure 4 in Limburg 2001). We used a length–weight equation developed by Hoffman and Olney (2005) for American shad of approximately this age 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), namely,

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

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

Survival to become a subadult.—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. We assigned instantaneous natural mortality rates, by age, using the Lorenzen (1996) equation. We assumed no harvest on these fish in the ocean and again estimated annual survival rates through the following equation:

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

where S_x is the 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 juveniles move into the subadult stage after one annual time step, as they approach 2 years of age. The annual survival rate to become a subadult (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 (i.e., become adults) 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 subadult females that survive to mature annually as well as the average annual survival rate for subadults (i.e., the survival rate to remain in the subadult stage) and adults (i.e., to return to spawn the next year) 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 subadults remain in the ocean and 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 could be different for adults and subadults 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, each 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). For each year of life, either an annulus or a spawning mark (but not both) will be produced on the scale. 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 methodology, the scale itself, or both resulted in inaccurate age estimates for American shad, at least in that specific river. However, aging by scale marks using Cating's (1953) method is still commonly done 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 2). We used scale data from adult females 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 became an adult, she would spawn each year until she perished. The assumption that spawning occurs each spring after reaching maturity is suggested by scales, since they appear to lack annuli between spawning marks to suggest that the fish had skipped a spring spawning event (Maki et al. 2001). To determine a maturity schedule and annual survival rate for adults, 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:

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

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 the spawning histories of all age-*i* fish. The model accounts for the differential survival of adults and subadults by including the ratio of adult survival to subadult survival in the 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). We used Lorenzen's (1996) equation to estimate the ratio of adult survival to age-specific subadult survival. As an example, the likelihood of collecting an age-5 American shad (Λ_5) during the spawning migration was

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

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

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

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

where S_{Al} is the annual survival rate for adults and S_x is the annual survival rate for subadults 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 4–8. All conditional maturation rates and S_{Al} values were constrained to fall 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 ($\wedge$), which is the product of all individual likelihoods:

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

TABLE 2. Spawning histories for adult female American shad collected in the Albemarle Sound from 2000 to 2005. The table entries are from data in Burgess et al. (2007) for fish collected by commercial fishers and the NCDMF independent gill-net 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

Transition and survival rates for subadults.—Subadults transition to adulthood if they survive to maturity. The proportion of subadults that transition at each time step is the sum of the individual proportions of subadults 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 subadult 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 subadults that will mature at age 5. The total proportion (D) of subadults that will mature at each time step is the sum of all (similarly calculated) individual proportions, that is,

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

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

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

where S_t is the proportion that survive from the subadult to adult stage.

The proportion of fish in the subadult stage that remain there is equal to $1 - D$. The rate to survive and stay as a subadult in the next time step is the product of the proportion of fish that remain ($1 - D$) and the average survival rate of a remaining subadult fish. To calculate the average survival rate for remaining subadults, the proportion of fish remaining subadults at each age must be estimated. As an example, for an age-5 fish, the proportion to survive and remain as a subadult would be

$$(1 - \pi_3)(1 - \pi_4)(1 - \pi_5) * S_3 * S_4 * S_5.$$

To estimate the average survival rate of a subadult (S_{SUB}), we summed the product of each age-specific proportion to remain a subadult [$(1 - D)_j$] and its age-specific survival rate (S_j) and divided by the sum of the proportions to remain:

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

Thus, the proportion to survive and remain a subadult is the product of the proportion ($1 - D$) to remain a subadult and the average survival rate (S_{SUB}) of remaining subadults.

Vital rates for transported American shad.—To estimate vital rates for American shad transported to the upper Roanoke River basin, we used data on tagged adults in both upstream and downstream habitats of the Roanoke River (Sparks 1998; Harris and Hightower 2011), OTC-marked American shad fry released by the NCWRC in riverine habitats just below the spawning grounds at Weldon, North Carolina, and upstream of Kerr Reservoir at Altavista, Virginia (NCDMF and NCWRC 2007; Kevin Dockendorf, North Carolina Wildlife Resources Commission, personal communication; Figure 1), and literature on other American shad populations (Bell and Kynard 1985; Sadzinski and Hendricks 2007).

The behavior of adult American shad in habitats below Roanoke Rapids Dam and above Kerr Dam suggests differential effective fecundity (i.e., egg production) and postspawning survival in the two areas. The results suggest that many radio-tagged American shad adults were on the spawning grounds at Roanoke Rapids for 3 times as long as most sonic-tagged adults transported to upstream areas were in riverine habitat (Sparks 1998; Harris and Hightower 2011). The reduced time in riverine habitat by fish transported 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 procedures, and may vary annually with environmental and transport conditions (Harris and Hightower 2011). 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 d (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 adult American shad were only able to spawn 1/3 as many eggs as those left in the lower Roanoke River and that they had the same fecundity (i.e., same potential number of eggs to spawn).

We also used data on out-migration 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 adult females. First, we examined predictions assuming no survival of transported adult fish. Only 1% of the sonic-tagged individuals (2 of 146) transported to upstream habitats successfully out-migrated through all three dams to reach the lower Roanoke River (Harris and Hightower 2011). Assuming that adults not migrating through the dams 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 adult females located near the dam were able to out-migrate. We observed that some individuals were located near the upstream sides of dams near the end of season, possibly indicating that they were unable to pass downstream through the turbines but were available to out-migrate. 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; Harris and Hightower 2011). The third rate examined would be considered optimal; it assumed that all adults out-migrated but that the survival rate was that for adults 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 at Altavista, Virginia, and below Roanoke Rapids Dam at Weldon, North Carolina (Figure 1). The ages at marking varied annually (3–9 d); 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 American shad hatched earlier that year in the lower Roanoke River and examines a proportion of these emigrating individuals for the presence and number of OTC marks (Table 3). Assuming that all of these OTC-marked juveniles 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):

$$N_{LOC} = R_{LOC} \cdot S_{LOC} \cdot C.$$

Using age-specific survival rates for fry released below Roanoke Rapids Dam (stated above) we estimated catchability, and from that we estimated the survival rate for fry released above Kerr Dam. With this, we estimated the survival rate to become a juvenile for fry stocked in the upper basin (S_{JUVu}). Recent catches of OTC-marked American shad over 1 year in age in Lakes Gaston and Roanoke Rapids indicate that some OTC-marked individuals did not emigrate during their first fall (Kevin Dockendorf, personal communication). Downstream passage structures might induce and aid in out-migration for more individuals. To evaluate possible outcomes with the addition of downstream passage structures, we also assumed that juveniles in the upper basin would have the same survival as juveniles in the lower river.

Starting values for population size.—The adult population size of American shad in the Roanoke River is unknown, but appears small relative 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 single-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 at Weldon (Figure 1) and fall samples of American shad hatched earlier that year showed a 10:1 ratio of wild to OTC-marked fish, 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 Ringler 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 spawning to the age of the OTC-marked fry at release (S_{W_x}), that is,

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

TABLE 3. Number of American shad fry released with a single OTC-mark at Weldon (lower river release) and a double OTC-mark at Altavista (upper river release; See Figure 1) and the number juveniles sampled in the fall in the lower Roanoke River with no OTC mark, a single OTC mark, and a double OTC, 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

Marked fry were released at 4–10 d old (one day after marking) in the lower Roanoke River between 2002 and 2008; therefore, S_{Wx} varied annually depending on the age of the fry at release.

To obtain an estimate of the precision of our annual adult female population estimates, we used a parametric bootstrap technique (Efron and Tibshirani 1993). Our bootstrap estimate included the proportion of OTC-marked juveniles collected in fall samples by NCWRC, adult female fecundity, time to hatch, survival rate to hatch, and survival rate to 4–10 d 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 Harris and Hightower 2010). For OTC-marked juveniles collected during fall sampling, 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 from a uniform distribution between 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 juveniles and subadults in all model runs. To examine how stable production was over the 7 years, we regressed the estimated number of fry stocked below Roanoke Rapids (standardized to 18 d in age) with the proportion of OTC-marked juveniles collected during fall sampling that had originated from that release below Roanoke Rapids. 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 whether and under what conditions transporting adult American shad upstream of 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, the vital rate(s) are a function of population size and thus the eigenvalues and eigenvectors of the population matrix change with population size. Therefore, 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 lower-river carrying capacity of either 136,526 (124/ha) or 54,610 (49/ha) adult females under each survival scenario (two effective fecundity rates for adults, three survival rates for adults, and two survival rates for juveniles) assuming that 10% to 50% (by 10% increments) of adults were transported to upstream habitats. The lowest values examined were those expected under current environmental and transport conditions. Increased values for effective 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% increments) or increased juvenile survival 5% to 25% (by 5% increments) to predict whether management options to improve survival (e.g., reducing harvest in the Albemarle Sound to increase adult survival) could 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 of the vital rates used in this study were not calculated from data on American shad in the Roanoke River; therefore, there is probably error associated with the specific population projections. However, assuming the rates used were reasonable, the model should be useful for comparing 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 model by using several techniques. First, using our model estimates for the stable stage distribution, the annual survival rate for adults, and the annual rate of transition to adulthood, we estimated the percent of adult females expected to be repeat spawners and compared that with the actual percent of repeat-spawning females in fishery-dependent and fishery-independent samples (Burgess et al. 2007). Second, using estimates of survival and maturity, we estimated the expected proportion of female American shad to be collected by age and spawning history and compared that with the actual age and spawning histories of females collected in fishery-dependent and fishery-independent sampling (Burgess et al. 2007). Third, we used our model to estimate the number of OTC-marked fry released below 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 the results from both male and female American shad. Males in the Roanoke River appear to mature earlier than females (Burgess et al. 2007), possibly influencing the 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 halve the number of juveniles produced by females to include juveniles 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-d-old female fry required to produce one spawning female and compared that value with the 320 fry that were approximately 18 d old to produce one adult estimate for the Susquehanna River (Johnson and Ringler 1995, 1998; Sadzinski and Hendricks 2007). Comparing model predictions with actual data can facilitate evaluation of the model's fit and utility and can help identify future research needs, which can be very valuable.

RESULTS

Population Parameters

The estimated number of adult female American shad in the Roanoke River between 2002 and 2008 ranged from 1,965 in 2006 to 8,449 in 2004, with an average of 5,224 individuals (Figure 3). This estimate puts the adult population at 4% of the assumed carrying capacity (124/ha) for the lower Roanoke River. No pattern in the number of adult females over the period from 2002 to 2008 was evident (Figure 3). Bootstrap analyses illustrated the lower precision in estimates from earlier years, when fewer OTC-marked fry were released at Weldon and fewer juveniles were collected during fall sampling and examined for OTC marks (Table 3). The proportion of OTC-marked juveniles collected in the fall by NCWRC was significantly related to the number of OTC-marked fry released earlier that year in the lower Roanoke River ($R^2 = 0.907$, $P < 0.001$), suggesting that the production of wild fish was of similar magnitude in all years between 2002 and 2008.

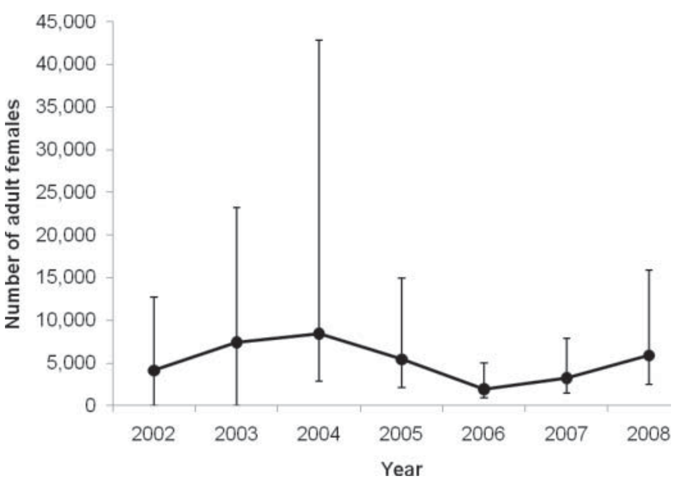

FIGURE 3. Estimated total number of adult female American shad spawning in the Roanoke River from 2002 to 2008, by year. The error bars represent the 2.5–97.5% values from 1,000 parametric bootstrap samples.

TABLE 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

The modified Maki et al. (2002) likelihood model estimated the adult female annual survival rate at 0.25, which corresponds to an instantaneous mortality rate (Z) of 1.38 for spawning adult females. Instantaneous natural mortality rates (M_j) 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 survival to subadult survival (R value in Maki et al. 2002) is 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 remained constant with increasing age (Table 4). Approximately 45 percent of American shad females were predicted to mature at age 4, with over 95% predicted to mature by age 7 (Table 4).

Model Runs

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

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

TABLE 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 1 and Figure 2 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; Harris and Hightower 2011)
S_{JUVl}	Survival to become a juvenile (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_{JUVu}	Survival to become a juvenile (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; Harris and Hightower 2011)
D	Proportion of sub-adults to mature	0.3048	Maki et al. (2002); Burgess et al. (2007)
S_t	Survival to transition to adulthood	0.4424	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	Hightower and Wong (1997); Weaver et al. (2003), (1/2) the value for females only; Savoy and Crecco (memorandum)

without transport (Figures 4, 5). The basic model with density dependence, assuming a carrying capacity of 136,526 adult females (124/ha), 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 the carrying capacity for the lower Roanoke River under current conditions. We examined the possible results of transporting 10% to 50% (by 10% increments) of the population above all three dams under different scenarios (two effective fecundity rates, three survival rates for adults, and two survival rates for juveniles; see Table 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 4L). Similar results were obtained when the assumed carrying capacity was lower (Figure 5). If the carrying capacity was 54,610 adult females (49/ha), 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. The population would similarly only be expected to benefit from transport under high levels of effective fecundity for adult females and survival of juveniles (Figure 5K, L).

The number of adult females in the Roanoke River increased under all conditions of elevated survival of adults or juveniles (Figure 6). Increasing the survival of juveniles appears to be more influential than increasing the 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 adult females (24% of carrying capacity at 124/ha), whereas if juvenile survival was increased by 25% the model predicted that after 30 time steps the population would reach just over 51,500 adult females (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 juveniles—improvements in survival were predicted to be much more profound under the higher level of assumed carrying capacity (Figure 6).

The effects of transport were also examined assuming that the population first reached 10,000 females, that is, the FERC-mandated trigger for further consideration of fish passage (Figures 7, 8). Assuming a carrying capacity 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, it was predicted to

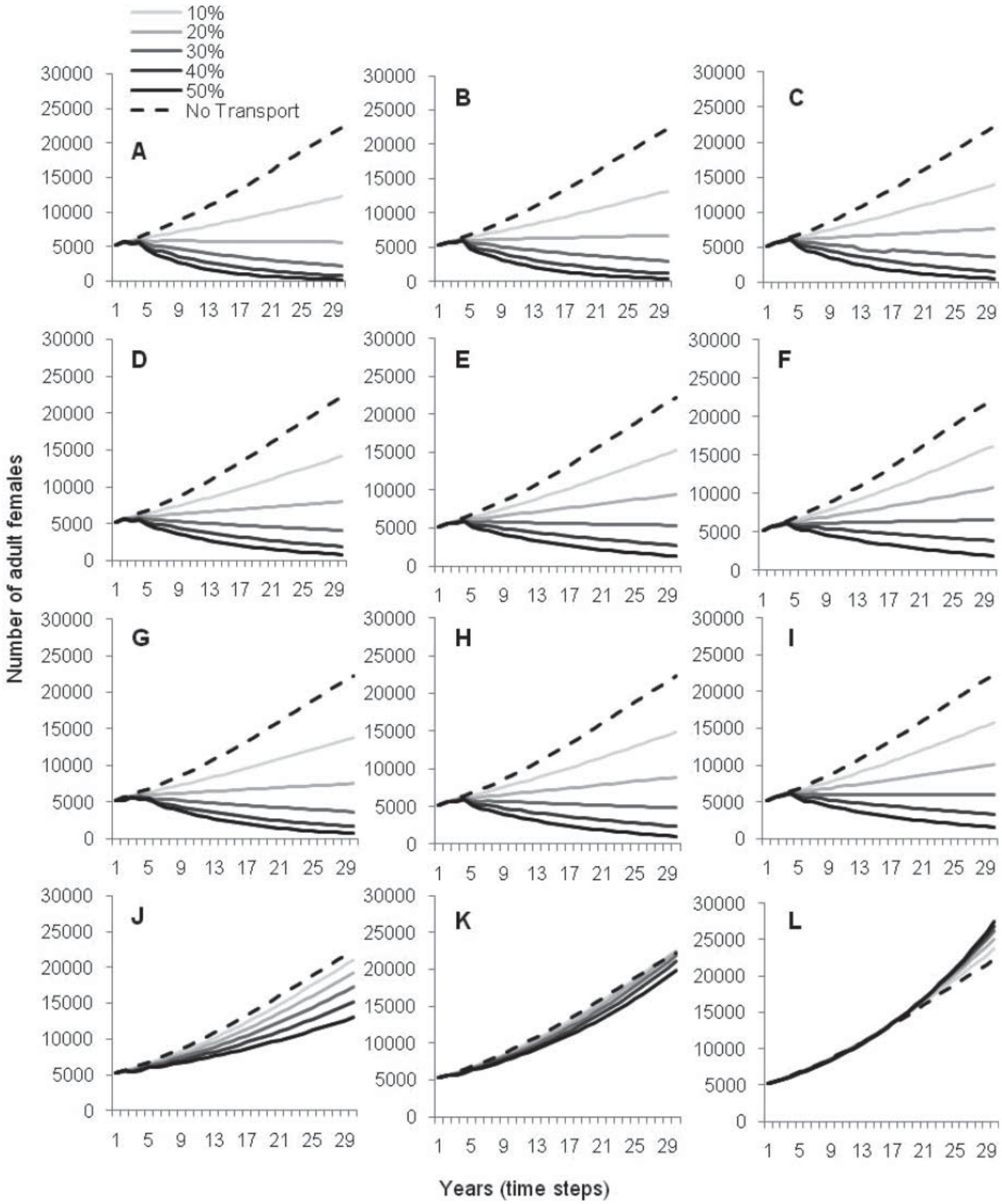

FIGURE 4. Projected number of adult American shad females under different transport scenarios when the assumed carrying capacity was 136,526 adult females. The different lines indicate the different percentages of the adult population to be transported. Columns indicate adult survival from none on the left to high on the right. The individual panels are for the following conditions: **(A)–(C)** low effective fecundity and low juvenile survival, **(D)–(F)** low effective fecundity and high juvenile survival, **(G)–(I)** high effective fecundity and low juvenile survival, and **(J)–(L)** high effective fecundity and high juvenile survival. For survival rates, see Table 5.

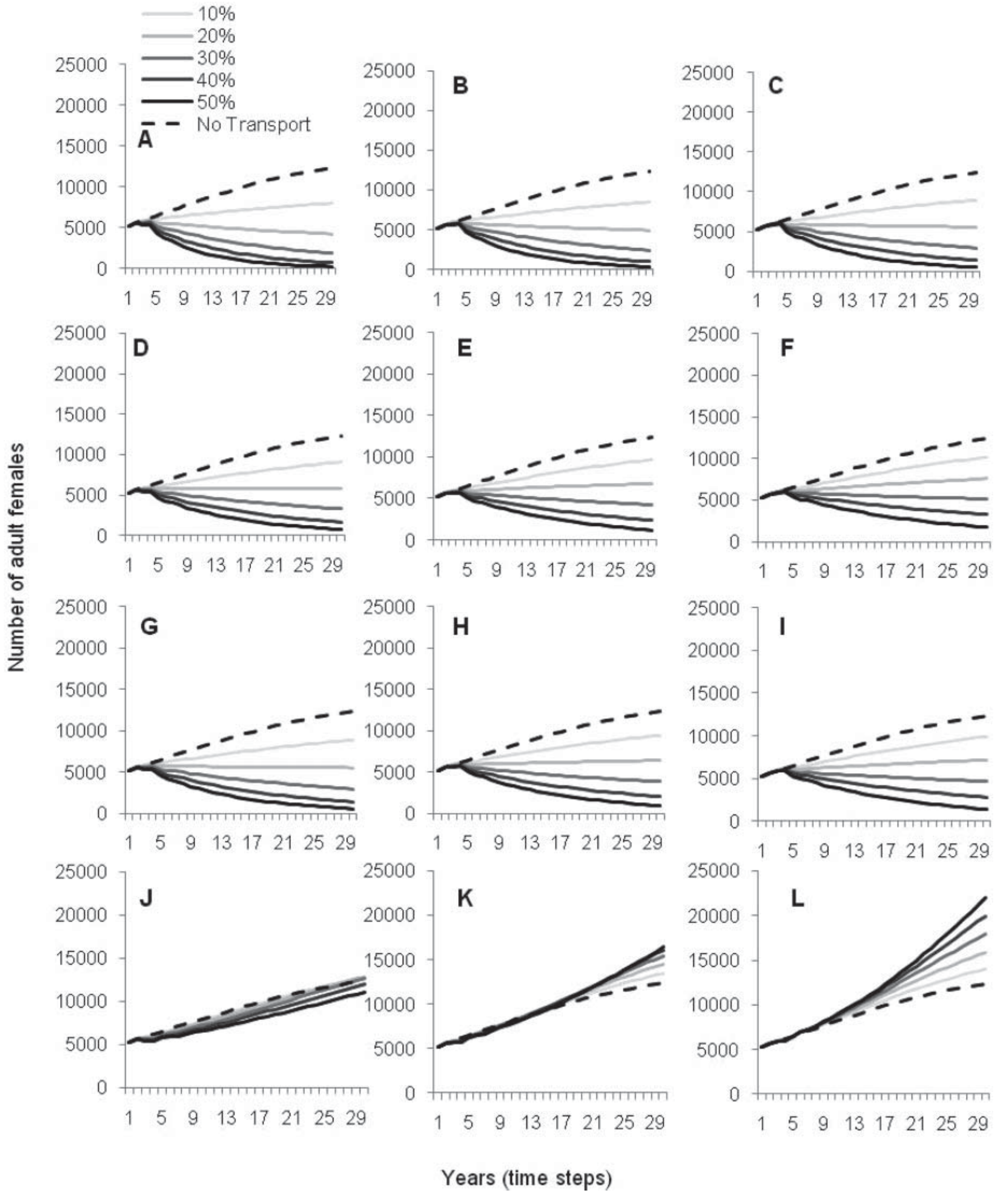

FIGURE 5. Projected number of adult American shad females under different transport scenarios when assumed the carrying capacity was 54,610 adult females. See Figure 4 for additional details.

surpass 29,100 adult females after transport only when adult fecundity and the survival of juveniles were high and there was some survival of transported adults (Figure 7K, 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 percentage of the population would benefit the stock, even with no survival of adults, under the conditions of optimal survival

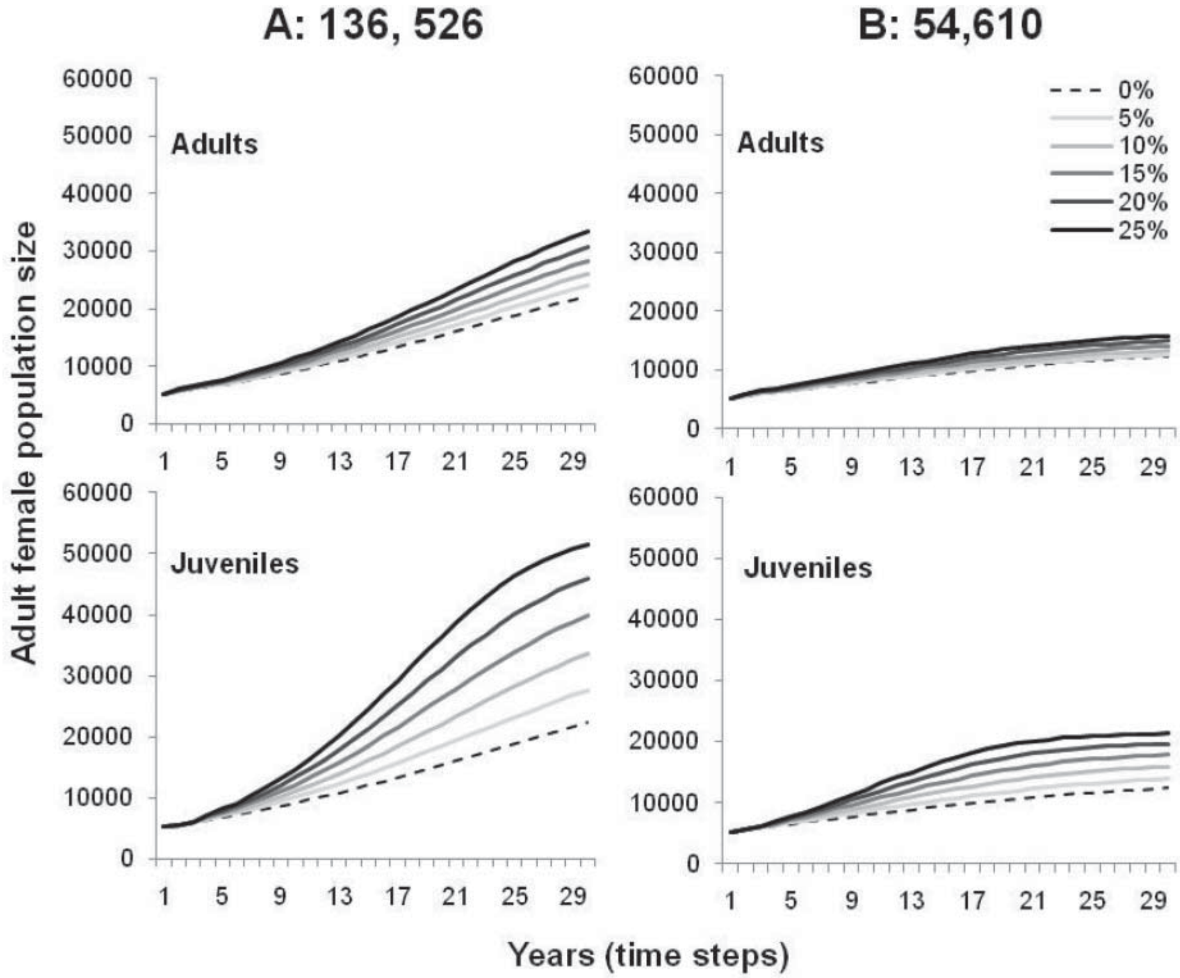

FIGURE 6. Projected number of adult American shad females with no transport but under conditions of increased survival for adults and juveniles assuming a carrying capacity of (**A**) 136,526 adult females or (**B**) 54,610 adult females. The individual lines indicate the increased survival percentages.

of juveniles and optimal effective fecundity for adult females (Figure 8J, K, L).

Model Evaluation

To evaluate the fit of our model's vital rates, we compared a few predictions with 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 (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 larger proportions of age-8 and age-9 fish, as compared with the actual catch, which had greater proportions of age-5 and age-6 fish (Figure 9). The model predicted that 1,406 18-d-old fry would produce one adult; thus, the model would predict that few hatchery-released fry would have already returned as spawning adults (Table 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, although values were within the 95% bootstrap confidence intervals (Figure 10).

DISCUSSION

Our model predicts that the American shad population in the Roanoke River is increasing slowly under present conditions of no transport to upstream habitats. Only under optimal conditions of effective fecundity and survival would the transport of American shad upstream of dams on the Roanoke River be predicted to lead to a higher rate of increase at the current stock size. Information regarding the behavior and out-migration 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 only 1% of individuals were documented to successfully out-migrate past all three dams to

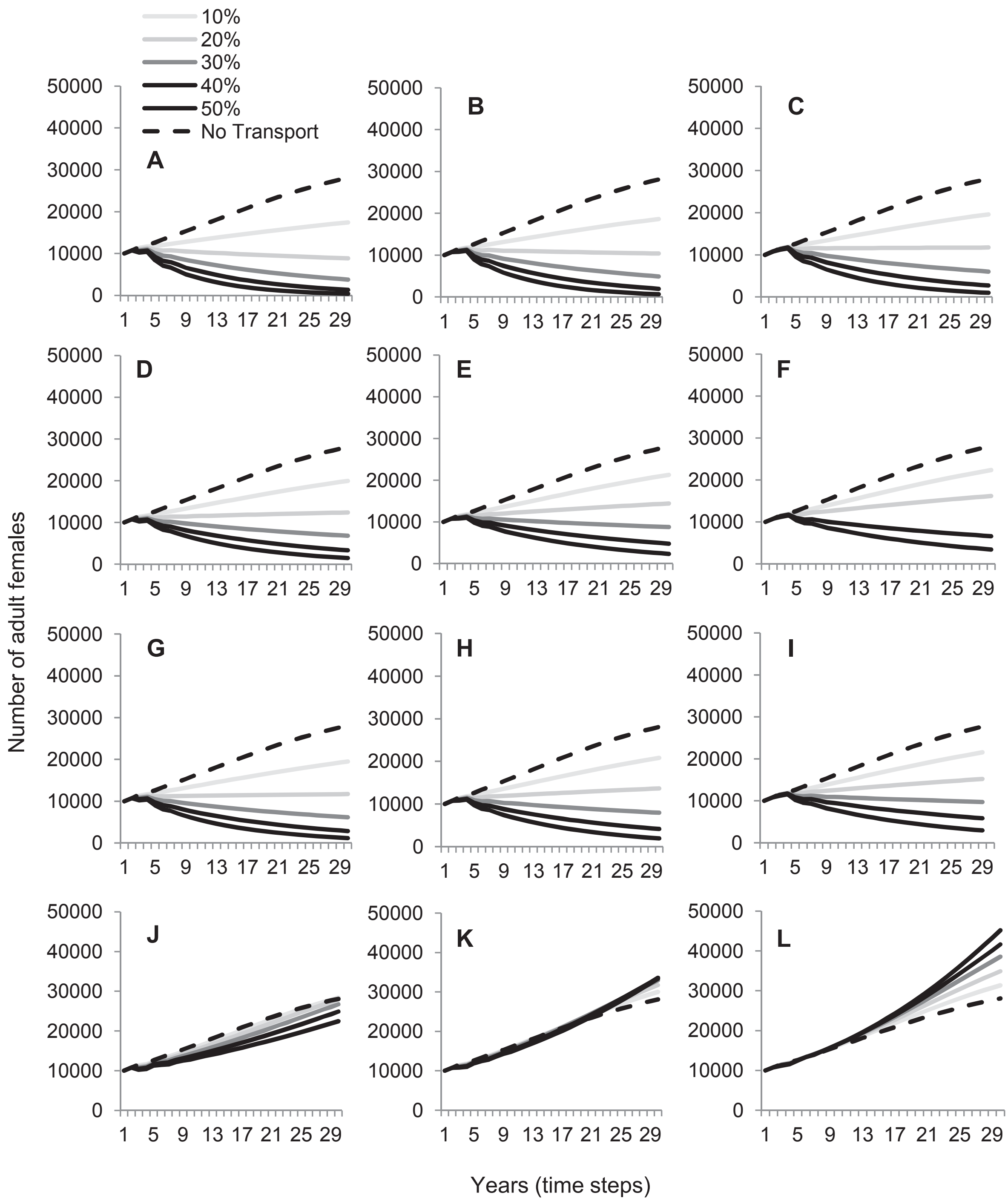

FIGURE 7. Projected number of adult American shad females under different transport scenarios when the assumed carrying capacity was 136,526 adult females and the starting female population size was 10,000. See Figure 4 for additional details.

potentially spawn in future years (Harris and Hightower 2011). In addition, the out-migration success of OTC-marked American shad fry released in the upper river was lower than that for marked fry released in the lower river. Recent collection of some of these OTC-marked American shad in upper basin habitats suggests that out-migration may be delayed rather than reduced. However, only one double-marked (upper basin release) adult American shad has been collected on the spawning grounds during sampling (Kevin Dockendorf, personal communication), and considering that only slightly smaller numbers (see Table 3) of slightly older individuals (7–10 d in age, rather than 4–10 d in age) were released at the upstream site,

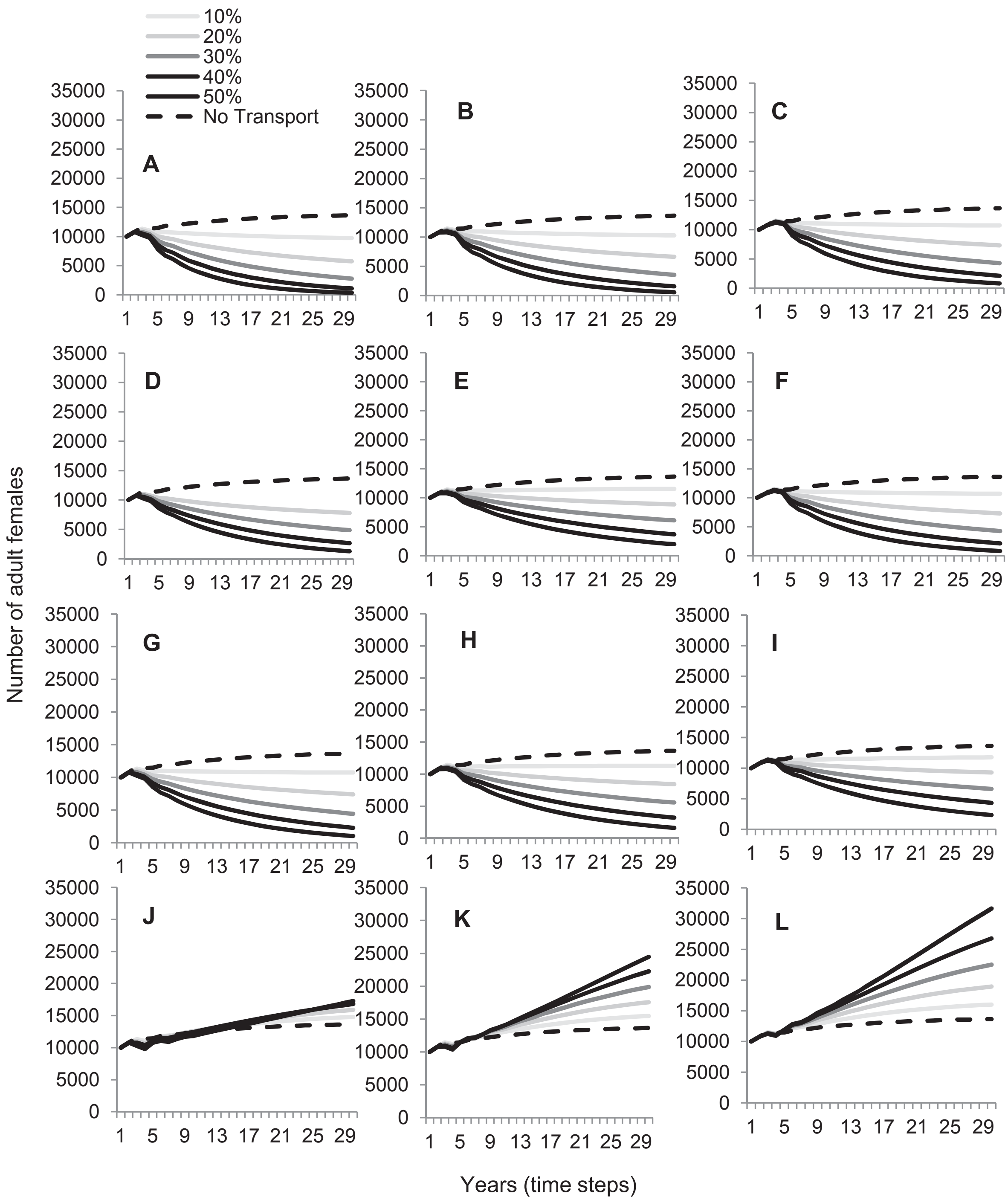

FIGURE 8. Projected number of adult American shad females under different transport scenarios when the assumed carrying capacity was 54,610 adult females and the starting female population size was 10,000. See Figure 4 for additional details.

we would expect fairly similar numbers from each release location to return as adults if survival and out-migration rates were equal. Since the estimated adult population size appears much smaller than either estimate for carrying capacity in the lower Roanoke River and survival to out-migration 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 under current conditions. 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.

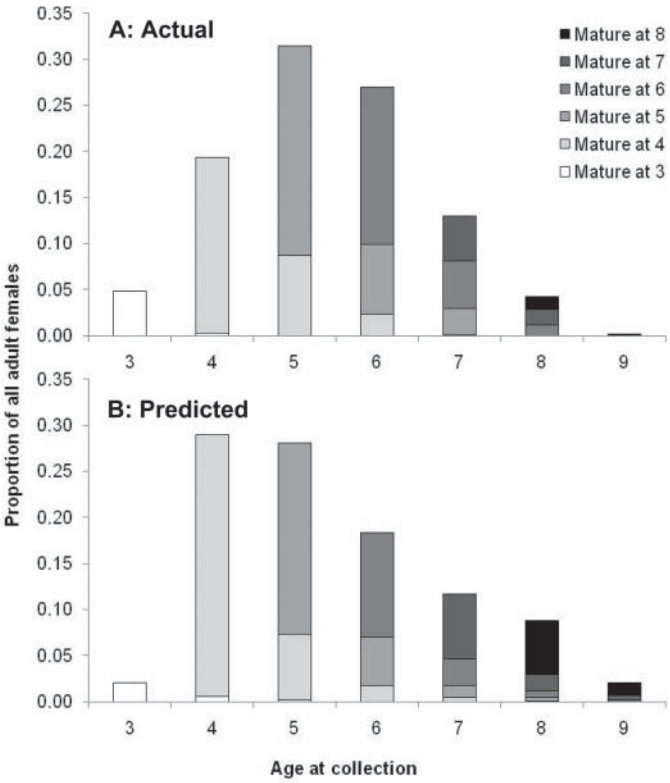

FIGURE 9. (**A**) Actual and (**B**) predicted proportions of adult American shad females in the Roanoke River by age at collection and age at maturity.

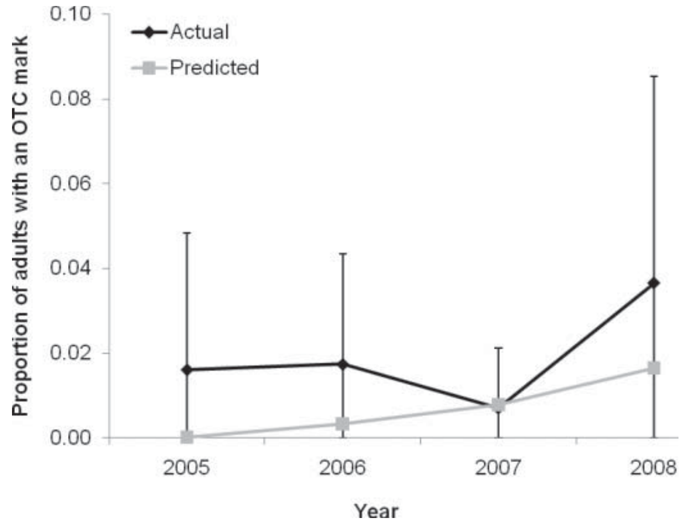

FIGURE 10. Actual and predicted proportions of adult American shad with one OTC mark to return to the spawning grounds in the Roanoke River between 2005 and 2008. The error bars represent the 2.5–97.5% values from a bootstrap analysis.

Modeling 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 American shad less than 1 year in age from multiple rivers. Estimating natural mortality for fish at any age is difficult, and research suggests that the survival of American shad during the first year of life is highly variable (Crecco et al. 1983, 2007; Crecco and Savoy 1987; Savoy and Crecco 1988; Limburg 2001; Hoffman and Olney 2005), making accurate estimation of production problematic. Second, we assumed that the survival rates experienced by wild fry were the same as those for stocked fry. Research on the Susquehanna River suggests that added predation on stocked American shad fry is generally low but related to the time of day, fry age, and, most especially, fry density at stocking (Johnson and Ringler 1995, 1998). The numbers of fry stocked per day (<700,000; Jeff Evans, North Carolina Wildlife Resources Commission, personal communication) in the Roanoke River were generally associated with low levels of added mortality in the Susquehanna River (<2%; Johnson and Ringler 1995, 1998); however, differences in environmental conditions, as well as in predator composition and abundance, could result in differences between the Susquehanna and Roanoke rivers in terms of added predation mortality for stocked fry. Third, the annual 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

TABLE 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

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 would improve estimates of fecundity. If the fecundity estimates we used were similarly low, then our population estimate would be too high. If the true population size is lower than we estimated, the value of transporting adults upstream would be reduced because the population below the dam would be less constrained by density dependence. Despite these uncertainties, the adult population estimate we used ($2 \times 5{,}200$) 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 development of similar estimates by two independent methods improves confidence in our understanding of the adult female population size in the Roanoke River.

The positive relationship detected 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 suggest that wild production was relatively similar in all years. Savoy and Crecco (1988) suggested that the survival of eggs and recently hatched American shad is strongly affected by both density-dependent (i.e., predation and starvation) and density-independent (i.e., water temperature and flow) 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 (Savoy and Crecco 1988). Considering that the American shad population in the Roanoke River appears to be far below either of the assumed values 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 juveniles.

Our assumed estimates of carrying capacity were calculated from two equations developed from information on present and historic American shad stock sizes in the Connecticut River (St. Pierre 1979; Hightower and Wong 1997; Weaver et al. 2003; Savoy and Crecco, memorandum). Although these calculations (especially 124/ha) have been widely used to estimate the potential carrying capacity of habitat above dams for a variety of rivers, their accuracies are unknown (Hightower and Wong 1997). Both assumed values were based on an estimate of stock size and the total area of the river; 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, the differences between the two 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. Riverine habitat selected for spawning by American shad is typically characterized by shallow depth (generally <5 m, often much less), appropriate temperature and dissolved oxygen (generally 14–24°C and >5 mg/L, respectively), and moderate water velocity (generally 0.3–0.9 m/s; Stier and Crance 1985; Ross et al. 1993; Bilkovic et al. 2002). In addition, when available in a river, spawning sites are often in areas of higher gradient with large, diverse substrates, especially areas dominated by gravel (Beasley and Hightower 2000; Hightower and Sparks 2003; Bailey et al. 2004). Rivers that contain more suitable spawning habitat on a spatial and temporal scale should, at least in theory, support larger populations of American shad, regardless of their total length; however, specific relationships between the availability of suitable spawning habitat and the carrying capacity of American shad have not been developed.

Until a better understanding of the relationship between carrying capacity and riverine habitat is obtained, it is important to evaluate predictions using multiple models. Differences between the Connecticut and Roanoke rivers in terms of habitat, discharge levels, temperature, and so forth, could yield differences in their densities at carrying capacity. We evaluated the results using the most common model (124/ha) and a more conservative equation (49/ha); both suggest that the population is far below the current carrying capacity. Although we do not know which better represents carrying capacity for American shad in the Roanoke River, obtaining similar results from both models gives us confidence in our conclusions regarding the benefits of transport. 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; Figure 1); however, plankton sampling riverwide would help identify if there are any other spawning sites in the river system. Habitat surveys combined with habitat suitability models could also be used to identify other potential spawning sites riverwide, since spawning may be concentrated in the best habitats—rather than in all suitable habitats—if the population is far from the carrying capacity, as it appears to be.

The model predicted that the effective fecundity (i.e., egg production) of adults and survival of juveniles (i.e., to age 1) would influence the population projection more than the survival of adults (i.e., to return to spawn the next year). 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 rate of juvenile 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 production, growth, and survival during the first year of life and the ability of juvenile fish to out-migrate may have more of an impact on the success of a transport program than the ability of transported adults to survive out-migration to the ocean. The percentage of juvenile American shad prevented from or delayed in out-migration 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 out-migration delays, especially combined with turbine mortality, are resulting in an apparent reduction in survival. Aunins and Olney (2009) suggest that the survival of American shad hatched above Bosher's Dam in the James River, Virginia, appears to be much higher than the survival of those below the dam. Hatchery-released, OTC-marked American shad over 1 year in age have been collected in upper Roanoke River basin reservoirs, which indicates that some 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, there has been only one successful landlocked population of American shad located in a reservoir on the San Joaquin River, California (Lambert et al. 1980; Limburg et al. 2003). Structures to increase out-migration would likely increase juvenile survival and the overall benefits of transport.

Although effective adult fecundity and the survival of juveniles were predicted 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 with the NCDMF data on the age and spawning history of American shad in the Albemarle Sound, the model predicted fewer repeat spawners than were actually observed in samples from the 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 whether repeat spawners devote more energy to reproduction and less to 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. Also, adult survival had a more direct relationship with the density-dependent function in our model, since it is based on the number of adults; therefore, increasing adult survival could have a larger density-dependent impact than increasing the survival of the young. More research on the reproductive ecology of American shad, especially in relation to age and spawning history, could help determine the importance of repeat spawners to populations.

Our 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 3-year period as the number of fish with OTC marks matured. The difference between the expected and actual returnees may simply be a result of small sample sizes, as the predicted values were within reasonable ranges of the actual values. Also, males are collected at younger ages than females (Burgess et al. 2007), and the inclusion of males may have inflated the number of returnees, especially in 2005 when OTC-marked fry would have been age 3 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 ($\geq$95%) for fish with single marks (Dockendorf 2004). Alternatively, the model may predict too few returnees, either because our population estimate is too large or our survival rate from fry to adult is too low. Little is known about the behavior, survival, or habitat use of subadult American shad in oceanic environments. As a result, we used general survival rates for oceanic fish in our model, which may have been too low. Unless the rates used were vastly different from the actual values, the predicted results for transport would not change much, but the population size and the predicted number of OTC-marked individuals to return could change. In addition, the survival rates that we used were developed mostly from field studies on populations that were already experiencing some level of density dependence in the wild; thus, the density-dependent factor in the model may have reduced survival too much. Although our model predicted a lower number of OTC-marked adults to return, it appears to generally describe the population status and survival rates for American shad in the Roanoke River fairly well. If our estimate of survival was low, we would expect the population to be increasing even more than predicted. 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.

The predicted number of 18-d-old fry 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 values may be at least in part a function of differences between the two populations. The harvest of American shad in the Albemarle Sound is very high (estimated at 38,000 individuals from data in Burgess et al. 2007) relative to the estimated population size in the Roanoke River; however, it is unknown what proportion of commercial catch is from the Roanoke River population, as opposed to the Chowan River stock. In 2007 and 2008, NCDMF collected adult American shad in the Albemarle Sound (n = 208) for identification of OTC marks. The proportion of adults with single OTC marks in the Albemarle Sound during those 2 years (4 of 208) was similar to that on the Roanoke River spawning grounds (4 of 223; Kevin Dockendorf, personal communication). Although these sample sizes are small and may not adequately represent harvest throughout the Albemarle Sound, the similarity could mean 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). Therefore, the survival rate from fry to adult for an individual in the Roanoke River may actually be considerably lower than for one in the Susquehanna River.

Increasing survival rates for either juvenile or adult American shad in the lower Roanoke River were predicted to result in more rapid increases in the population. We examined increases in survival of 5–25%, but it is not known if such improvements are 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 adults throughout the Albemarle Sound and the Roanoke River could help establish the proportion of the commercial catch that is from the Roanoke River rather than 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 finfish predators, such as striped bass *Morone saxatilis*, has also been suggested as an important source of mortality in some systems (Savoy and Crecco 2004). Improvements in survival for juvenile American shad could increase the population size in the lower Roanoke River, but they may be less feasible. Survival rates of juvenile 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 survival are not always clear or easy to quantify (Crecco and Savoy 1984, 1985; Tuomikoski et al. 2008).

In summary, we constructed a matrix model to predict possible population-level effects of transporting American shad to habitats upstream of dams on the Roanoke River. To our knowledge, no such model has previously been developed for American shad in any river system. Our model predicts that transport would not benefit the American shad population in the Roanoke River under current conditions but could improve the population if effective fecundity and survival rates were optimal. The model predicts that the population will increase slowly under current conditions below the dam and that management options that would improve survival, especially within the first year of life, could increase the rate of population increase. While there is uncertainty in vital rate estimation, we evaluated the model under two very different levels of carrying capacity and obtained results that lead to similar conclusions about the population-level effects of transport for this stock. 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. Although some vital rates were estimated with data from other rivers, our results are system specific since many of the rates that allowed us to evaluate transport (i.e., out-migration survival and effective fecundity) were from the Roanoke River population and would potentially be very different in other river systems. The benefits of transport in other systems would depend on the American shad population's size, the quantity and quality of upstream habitat, and the ability of juveniles and adults to out-migrate to the ocean. However, the vital rates used in this model could be modified to evaluate the effects of transport on American shad populations in other regulated rivers.

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