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Movement and Population Size of American Shad near a Low-Head Lock and Dam

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Abstract.—We investigated the population size and the proportion of the population of American shad *Alosa sapidissima* that passed through the New Savannah Bluff Lock and Dam, a low-head lock and dam on the Savannah River in South Carolina and Georgia. We fitted 110 American shad with radio transmitters in 2001 and 2002. All but two fish moved downstream after transmitter implantation. In 2001, a smaller proportion of American shad implanted with radio transmitters earlier in the season returned to the dam than fish released later. Of the fish that returned to the dam, over 50% in 2001 and 9% in 2002 passed through the lock and continued migrating upstream. In both years, the modal daily movement distance was less than 1 km. Movements greater than 5 km/d were generally associated with fish rapidly returning upstream after their initial downstream movement. Continuous diel monitoring indicated that movements greater than 0.1 km/h were more frequent at night than during the day. In both years, American shad were not uniformly distributed over the study area but were predominantly grouped just below the dam and in a relatively large pool approximately 6 km below the dam. We estimated the population size of American shad that reached the New Savannah Bluff Lock and Dam at 157,685 in 2001 and 217,077 in 2002.

The American shad *Alosa sapidissima* is an anadromous clupeid native to the East Coast of North America from the St. Johns River, Florida, to the St. Lawrence River, Canada (Liem 1924; Bigelow and Schroeder 1953). The timing of the spring spawning migration varies with latitude (Leggett and Whitney 1972) and is closely linked to temperature. American shad may enter their natal streams once the water temperature rises above 4°C; however, spawning activity is greatest between 14°C and 21°C (Walburg and Nichols 1967; Leggett and Whitney 1972).

Since the late 1800s, a suite of factors has caused a decline in anadromous stocks in the genus *Alosa* along the East Coast. Most markedly, the construction of dams has greatly reduced the number of spawning and nursery grounds (Rulifson 1994). Although some fishways were constructed when dams were built, most were not effective (Stevenson 1899). Navigation locks have been considered alternatives to fishways, although their effectiveness has generally not been assessed (Nichols and Louder 1970). Passage efficiency for American shad through a low-head lock varied from 15% to 50% over a 3-year period (Moser et al. 2000). Other migratory species show similar low and variable passage rates through lock systems (Chappelear and Cooke 1994; Pegg et al. 1997).

Passage may be related to retention time in the vicinity of the passage facility (Barry and Kynard 1986). Retention time of American shad has not been closely studied, but other migrating fish species have exhibited large variation in the time spent in a tailrace prior to passage or out-migration (Chappelear and Cooke 1994; Pegg et al. 1997). Nocturnal fallback—the temporary out-migration of fish encountering a barrier after sunset—has been documented (Barry and Kynard 1986). High diel variation in movement, passage, and velocity preference has also been observed (Theiss 1997; Moser et al. 2000).

The objective of this study was to examine the

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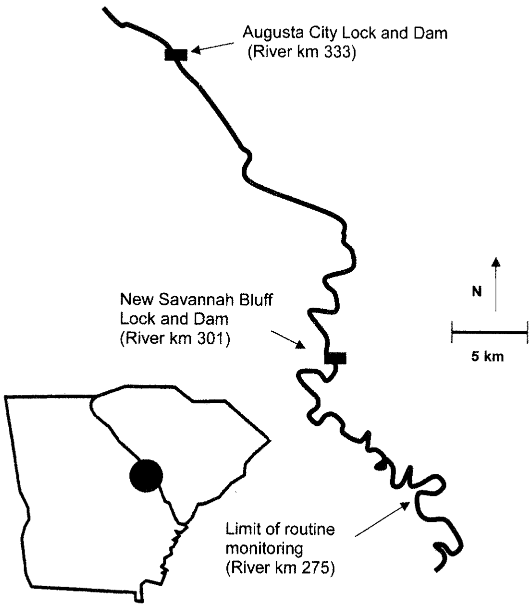

FIGURE 1.—Location of primary area of monitoring centered by the New Savannah Bluff Lock and Dam.

diel and seasonal behavior of migrating American shad when encountering the New Savannah BluffLock and Dam (NSBLD). Specifically, we investigated the proportion of the population that passed through the lock, retention time in the tailrace, and the diel and within-season movement patterns of American shad during their spring spawning run. In addition, we estimated the population size of American shad that reached NSBLD.

Study Area

The study area consisted of the Savannah River, South Carolina and Georgia, from the Augusta City Lock and Dam, located at river kilometer (RKM, measuring from the river's mouth) 333.5 to the influence of brackish water at about RKM 35, with emphasis on the river reach from RKM 275 to RKM 333.5 centered on NSBLD (Figure 1). NSBLD, located at RKM 301 just south of the city of Augusta, Georgia, is the most downstream obstruction to migration on the Savannah River. Completed in 1937 to enhance water control and navigation, the dam spans a 130-m section of the river. The low-head dam consists of five independent, 18-m-wide gates with a connected navigation lock on the Georgia abutment. The lock measures 17.1 m wide × 109 m long and has a lift capacity of 4.6 m.

The lock is operated in the spring of each year specifically to pass a variety of migrating fish, including striped bass *Morone saxatilis*, blueback herring *A. aestivalis*, and American shad. During this study, an average of five locking events for the purpose of fish passage were conducted each Monday from March through May between 0730 and 1600 hours. Each locking event consisted of the following sequence: (1) one lower door was fixed in the open position; (2) a fill valve was partially opened for at least 20 min to create a current in the lock thought to attract fish; (3) the lower door was closed; (4) the lock was filled; and finally (5) the upper doors were opened for at least 15 min. In order to operate the lock safely, a maximum head differential of 4 m was permitted. Consequently, on days prior to and during locking, discharge at NSBLD was increased to lower the water level above the dam and raise the water level in the tailrace.

Methods

Fifty-one fish in 2001 and 59 fish in 2002 were fitted with radio transmitters (Lotek Wireless, Newmarket, Ontario, Canada). To facilitate gastric implantation, transmitters were affixed to a flexible tube and inserted into the stomach though the mouth. The tube was then removed, leaving the antenna trailing from the mouth. Transmitters were coated in a water-soluble, nontoxic lubricant to reduce trauma during insertion. The sex of the fish was determined by applying gentle pressure to the abdomen to express eggs or milt. Transmitters were only inserted into robust, healthy fish. This process required less than 2 min per fish.

Three different radio transmitters were used in this study. In 2001, the transmitters were bottle shaped, measuring 9.2 mm in diameter and 20 mm in length and weighing 1.5 g in water, or measuring 10 mm in diameter and 32 mm in length, and weighing 2.1 g in water. The transmitters possessed a minimum battery life of 39 or 61 d, respectively. In 2002, the radio transmitters were cylindrical, measuring 11 mm in diameter and 36 mm in length, weighing 3.4 g in water, and possessing a minimum battery life of 110 d. All transmitters weighed less than 1% of the body weight of the smallest study fish.

American shad were located with a portable radio receiver and a directional Yagi antenna. Positions were determined at least four times per week from the release date until the last week of May between NSBLD (RKM 301) downstream to at least RKM 275, and were recorded to the nearest 0.1 km. Fish that passed above NSBLD were located at least once per month up to the next barrier to migration at RKM 333.5. The passage efficiency of migrating American shad at NSBLD was based only on fish returning to the tailrace. A subsample of instrumented fish was located every 2 h from NSBLD to RKM 275 over continuous 48-h (2001) and 60-h (2002) periods beginning on May 7, 2001, and May 13, 2002. The hours between 0600 and 1800 hours were considered day, and those between 1800 and 0600 hours were considered night.

In addition to roving telemetry, fixed-station continuous monitoring of fish near the dam was conducted. In 2001, five antennas were mounted on the face of the dam and one was mounted on the wing wall of the upstream end of the navigation lock. In 2002, four antennas were mounted on the face of the dam, and three were mounted in the lock to monitor the entrance, middle, and exit. When an implanted fish was detected, a data logging receiver recorded the identification number, date, time, signal strength, and the receiving antenna number. In addition, average daily and hourly discharge and river stage information was obtained from the U.S. Geological Survey gauging station (02197000; provisional data) at NSBLD for 2001 and 2002.

Change in American shad location in relation to time after transmitter implantation and flow was analyzed by analysis of variance (ANOVA). Fisher's least-significant-difference test was used for comparison of least-squares means. Proportion data were analyzed using a chi-square test. Because multiple seasonal and hourly measurements were taken from individual American shad, a mixed model of repeated measures was used in seasonal and diel movement analysis. Year, sex, and flow were fixed effects, and fish was a random effect in the mixed model. American shad passage related to the number of times a fish returned to the area below the dam was analyzed by logistic regression. When assumptions of normality were not met, data were appropriately transformed. In all cases, transformations failed to change statistical outcomes and are therefore not presented.

We estimated the population size of adult American shad reaching NSBLD with the Peterson method for a randomly mixed population (Ricker 1975) using the equation

$$N = MC/R,$$

where N is the population size, M is the number of fish marked and released (adjusted for tag retention, differential migration, and survival), C is the number of fish in the recapture sample, and R is the number of fish recaptured (adjusted for reporting rate). We chose not to correct the equation using the Chapman modification, as the number marked and examined for marks was large. During the peak in American shad spawning migration in 2001 (between March 13 and April 9) and in 2002 (between March 11 and April 3), 739 and 812 adult migrating American shad, respectively, were marked (M) with either one or two internal anchor tags and released in the tailrace below NSBLD. All tagging was conducted between 0900 and 1500 hours. Fish were collected by boat electrofishing techniques. After capture, healthy fish were immediately tagged without anesthesia and released within 2 min of capture. Internal anchor tags imprinted with a unique identification number and a phone number to facilitate return were inserted just below the dorsal fin perpendicular to the pterygiophores.

A recreational fishery targeting American shad was used to collect fish for the recapture sample (R) during a 6-week period following marking. Recreational harvest (C) was estimated in 2001 and 2002 using standard creel survey techniques (Malvestuto 1983) in which over 23% and 38% of angling time, respectively, was sampled. Posters displayed at fishing access points instructed anglers to return tags to a local cooperating bait shop, or to call the phone number appearing on the tag and poster. The reward for a returned tag was an embroidered hat, coveted by the local anglers. In order to estimate reporting rate, tags were distributed to 25 anglers without added instructions as they exited the fishing area. We assumed anglers would treat these tags as they would tags recovered from captured fish. Twenty-two tags were returned, resulting in an estimated return rate of 88%. The number of recaptures was adjusted using this reporting rate.

The number of marked fish was adjusted for tag retention, differential migration, and mortality. Tag retention was based on returns of double-tagged fish (n = 16), and was estimated at 94%. Differential migration and mortality was estimated from the proportion of fish implanted with radio transmitters that died or migrated downstream and did not return to the dam, and was estimated to be 26% in 2001 and 47% in 2002, resulting in 74% and 53% retention of tagged fish to the study area, respectively.

The combination of these adjustments for tag reporting, tag retention, and emigration resulted in

TABLE 1.—Study year, number of American shad implanted with radio transmitters (N), number that expelled transmitters at point of tagging (Failure), number that died as a result of tagging or handling stress (Mortality), number that did not make a downstream movement after radio implantation (Remained), number that returned to the tailrace after making initial downstream movement, and number that did not return to the tailrace during the remainder of the season at the New Savannah Bluff Lock and Dam, Savannah River. Different letters indicate significant differences between years.

					Moved downstream	
Year	N	Failure	Mortality	Remained	Returned	Did not return
2001	51	3	7	1	29 z	10
2002	59	2	8	1	11 y	37

TABLE 2.—Distance and rate of downstream movements associated with handling by tagging date in 2001 and 2002 of American shad implanted with radio transmitters at the New Savannah Bluff Lock and Dam, Savannah River. Similar letters indicate no significant differences within year and column. Ranges are given in parentheses.

Release date	N	Distance (km)	Rate (km/d)
		2001	
Mar 22	14	19.3 (5.0–30) z	4.0 (0.4–7.5) z
Mar 27	6	26.0 (6.1–30) z	6.8 (1.5–15.0) y
Apr 19	19	7.4 (1.2–24.9) y	1.8 (0.3–5.0) x
		2002	
Mar 18	10	24 (7.4–30) z	5 (1.6–7.5) z
Apr 1	18	21.7 (2.1–30) z	5.5 (0.5–10.0) z
Apr 15	20	19.0 (4.3–30) z	4.3 (0.8–10.0) z

bias adjustment coefficients of 61% in 2001 and 44% in 2002. As the numbers of fish examined for tags was small with respect to population size, confidence intervals (95%) were estimated according to Ricker (1975) for large samples, based on a Poisson distribution of recaptures.

Results

In 2001, three study fish rejected the implanted radio transmitters immediately after tagging, and seven died within 5 d of implantation as a result of handling or tagging (Table 1). The remaining 40 fish were located an average of 20.2 (range = 5–51) times. One fish remained near the point of release, while 39 moved downstream from 1.3 km to greater than 30 km within 5 d of transmitter implantation. Although 29 fish returned to the tailrace during the study period, 10 did not. One fish continued moving downstream and moved below the area of daily tracking after 5 d. In 2002, two study fish rejected the implanted radio transmitters immediately after tagging, and eight died within 5 d of implantation as a result of handling or tagging. The remaining 49 fish were located an average of 16.8 (range = 4–60) times. One fish remained near the point of release, while 48 moved downstream from 2.1 km to greater than 30 km within 7 d of transmitter implantation. Although 11 fish returned to the tailrace during the study period, 37 did not. Sixteen of those continued moving downstream and moved below the area of daily tracking within 12 d. An angler in the tailrace captured one fish that returned 31 d after release.

In 2001, fish moved downstream an average of from 7.4 to 26.0 km, depending on the implantation date (Table 2). Fish tagged earlier in the season moved downstream a greater distance and at a greater rate than fish tagged late in the season (Table 2). In 2002, fish implanted on different dates moved an average of 19.0 to 24.0 km downstream; however, we were unable to detect an effect of release date on distance or rate of downstream movement. We were unable to detect an effect of sex on the proportion of fish that made an initial downstream movement or that later returned to the dam in either year. More fish moved upstream to the area of the dam after transmitter implantation in 2001 than in 2002.

We were unable to detect a between-year difference in the distance moved on a daily basis

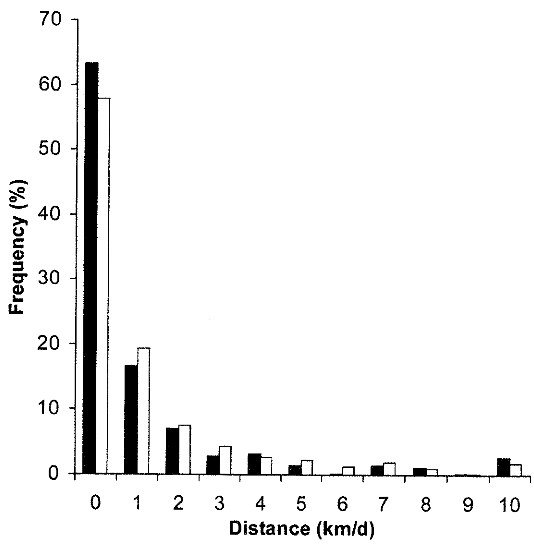

FIGURE 2.—Frequency distribution of distance moved (interval midpoint) in 2001 (solid bars) and 2002 (open bars) of American shad implanted with radio transmitters near the New Savannah Bluff Lock and Dam, Savannah River.

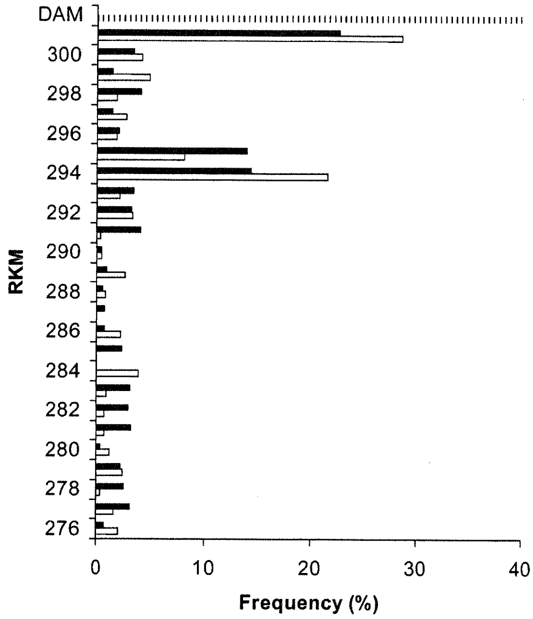

FIGURE 3.—Frequency distribution of relocations over the interval from river kilometer (RKM) 275 to RKM 301 in 2001 (solid bars) and 2002 (open bars) by individual American shad implanted with radio transmitters near the New Savannah Bluff Lock and Dam (hatched bar), Savannah River.

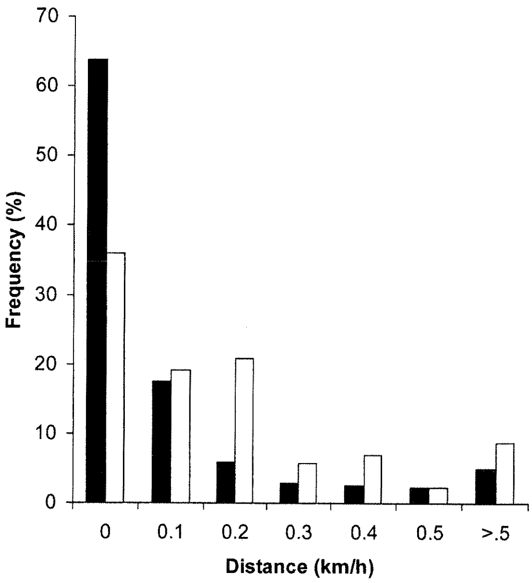

FIGURE 4.—Frequency of hourly movement (interval midpoint) in 2001 (solid bars) and 2002 (open bars) during a 48–60-h period of intense study of American shad implanted with radio transmitters near the New Savannah Bluff Lock and Dam, Savannah River.

when the effect of individual variation was controlled. The distribution of daily movement was highly skewed (Figure 2). In both years, the modal daily movement distance was less than 1 km. Movements greater than 5 km/d were generally associated with fish rapidly returning upstream after their initial downstream movement. In 2001, the proportion of fish moving over 0.2 km/d increased with flow. In 2002, we were unable to detect an effect of flow on the proportion of fish that moved over 0.2 km/d. Males and females did not move different distances on a daily basis in either year when the effect of individual variation was controlled.

In 2001 and 2002, American shad were not uniformly distributed over the study area but were predominantly grouped in two areas (Figure 3). Approximately 25% of the locations were above RKM 300 and within 1.5 km of the dam. An additional 30% of the locations were between RKM 294 and RKM 295. This stretch consists of a series of tight bends with low-grade sand banks protected by two current-deflecting wing dikes. The section also contained two intermittent streams that were dry during most of the study period.

In 2001, 17 American shad were located an average of 20.5 (range = 5–25) times during 25 consecutive 2-h tracking periods. One fish was passed upstream by the navigation lock during this 2-d intensive study period. In 2002, seven American shad were located an average of 27.1 (range = 25–30) times during 30 consecutive 2-h tracking periods. Mean movement during the study period was greater in 2002 (0.19 ± 0.018 km/h [mean ± SE]) than in 2001 (0.10 ± 0.013 km/h; Figure 4). In both years the proportion of fish that moved more than 0.2 km per 2-h interval was greater at night (mean = 45%) than during the day (mean = 23%). We were unable to detect an effect of flow on diel movement in either year when the effect of individual variation was controlled.

In 2001, flow fell within the lower 5th percentile of the 96-year historical daily flow level during 45% of the study period, and was less than the 96-year mean daily flow level during 98% of the study period (Figure 5). In 2002, flow fell within the lower 5th percentile of the 96-year historical daily flow level during 64% of the study period and was less than the 96-year mean daily flow level during 100% of the study period. Flow was greater in 2001 than in 2002, but most of the variation between years was due to an early season rain event in 2001. No substantial rain events were recorded during the 2002 study period.

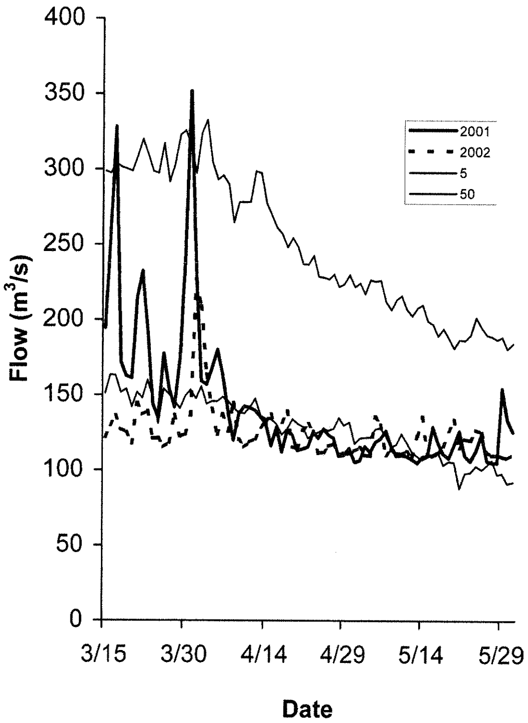

FIGURE 5.—Flow from a U.S. Geological Survey gauge at the New Savannah Bluff Lock and Dam, Savannah River. Light lines represent the 5th and 50th percentiles of historic flow,the heavy solid line represents flow in 2001, and the heavy broken line represents flow in 2002.

In 2001, 43 locking events for fish passage were completed between April 2 and May 21, while in 2002, 47 locking events for fish passage were completed between March 18 and May 29. Based on fish that remained in the tailrace or returned to the dam after transmitter implantation, a total of 30 (2001) and 12 (2002) study fish could potentially pass through NSBLD. Of those, a higher percentage of fish were passed in 2001 than in 2002 (Table 3). Fish that did not pass upstream made several return trips to the area below the dam. However, we were unable to detect a relationship between the number of times fish returned to the area below the dam and passage. In 2001, fish were passed during all times of lock operation. In 2002, the one fish passed moved through the lock at 1300 hours.

Although we tagged and examined a relatively large number of fish each year, relatively few fish were recaptured (Table 4). After adjusting for tag loss, mortality, differential migration, and reporting rate, the population size of American shad near NSBLD was estimated at 157,685 (95% confidence interval [CI] = 82,654–259,365) in 2001 and as 217,077 (95% CI = 107,776–393,335) in 2002.

Discussion

All but two fish moved downstream after transmitter implantation. This stress response to handling and transmitter implantation is referred to as fallback (Moser and Ross 1993). Past studies with American shad have attributed fallback to low water temperature (Moser and Ross 1993), poor condition of fish (Sparks and Hightower 1998), or a flight response due to handling (Barry and Kynard 1986). We observed a slightly higher frequency of mortality and transmitter rejection than has been observed in other telemetry studies of American shad using similar methods (Moser and Ross 1993; Beasley and Hightower 2000). High mortality in late-stage migrating American shad implanted with transmitters may be attributed to reduced energy stores following migration (Glebe and Leggett 1981; Leonard and McCormick 1999). In 2001, American shad implanted with radio transmitters and released earlier in the season exhibited a stronger fallback response and moved downstream faster and further than fish released later. These results are similar to those observed by Moser and Ross (1993) and are likely because of lower water temperature. However, this trend was

TABLE 3.—Percentage (by year) of fish passed or not passed (95% confidence interval [CI]) upstream through the navigation lock, mean number (range) of times fish returned to the area below the New Savannah Bluff Lock and Dam, mean number (range) of days fish spent in the area below the New Savannah Bluff Lock and Dam, and mean number (range) or days after implantation that fish passed successfully at the New Savannah Bluff Lock and Dam. Similar letters indicate no significant differences within columns.

Year	Passage	*N*	Passage (%)	Times returned (d)	Residence time (d)	Time since implantation (d)
2001	Passed	16 z	53 (35–71)	1.3 (1–3) z	9.5 (1–28) z	17.9 (4–48)
	Not passed	14	47 (29–65)	1.9 (1–9) z	9.6 (1–63) z	
2002	Passed	1 y	9 (0–25)	1 (1)	9 (9)	18 (36)
	Not passed	11	91 (75–100)	2.1 (1–8)	14.7 (2–36)	

TABLE 4.—Study year, marking period, recapture period, unadjusted number of fish marked (M), number of fish marked adjusted for mortality fallback and tag loss (M_a), number of fish examined for marks (C), unadjusted number of fish recaptured (R), number of fish recaptured adjusted for return rate (R_a), population estimate, and 95% confidence intervals (CIs) of population estimation for American shad at the New Savannah Bluff Lock and Dam.

Year	Marking period (d)	Recapture period (d)	M	M_a	C	R	R_a	Estimated N	95% CI of N
2001	27	42	739	451	3,337	9	9.54	157,685	82,654–259,365
2002	23	42	812	357	5,152	8	8.48	217,077	107,776–393,335

not consistent between years. In 2002, fish moved downstream faster and further than in 2001, often moving beyond the routinely tracked area. Fish were also less likely to return to the dam in 2002. While transmitter size was increased in 2002, it is unlikely this caused a major effect on differential migration. Transmitters represented less than 2% of the body weight of the fish and are similar to transmitters used in other American shad telemetry studies (Sparks and Hightower 1998; Beasley and Hightower 2000). It is more likely that drought conditions resulted in flows that were insufficient to attract or retain fish at the dam.

Fish in this study were impeded from moving upstream to more suitable spawning habitat; therefore, the limited movement observed was not unexpected. The observed movement was similar to the movement of American shad that have already reached their spawning grounds (Sparks and Hightower 1998; Beasley and Hightower 2000; Moser et al. 2000). In 2001, the proportion of fish moving greater than 0.1 km/h was related to flow, but no effect was found in 2002. In 2002, flow never approached the long-term mean seasonal flow, and thus could not be effectively evaluated. Movements over 5 km were often associated with relocation to a higher-use area or a return upstream after fallback. No late-season out-migration was observed, except when associated with fallback. American shad in the Savannah River are assumed to be completely semelparous (Leggett and Carscadden 1978); therefore, out-migration was not expected.

We observed American shad concentration in two areas. The first area was located just below the dam. American shad have been reported to use sand and gravel areas below an obstruction for spawning (Walburg and Nichols 1967; Beasley and Hightower 2000). As the area below the dam appeared to have suitable spawning substrate, fish were likely using this area for spawning as well as for staging prior to upstream migration attempts. The habitat in the area of the second concentration of fish appears to be similar to that used by spawning shad in other rivers (Liem 1924; Walburg and Nichols 1967). The area had a slightly deeper main channel, and more expansive, shallow flats than did the adjacent reaches of the Savannah River. Fish were primarily located along current breaks in this stretch. American shad are known to prefer areas of reduced or nonturbulent flow for resting (Barry and Kynard 1986).

Continuous diel monitoring indicated that movements greater than 0.1 km/h were more frequent at night than during the day. The movements during the diel tracking periods were likely related to spawning and moving to areas of more suitable water velocity. American shad will use higher water velocity during the day than at night (Theiss 1997), but spawning is thought to occur mainly after sunset or on overcast afternoons (Liem 1924; Walburg and Nichols 1967). Some fish made repeated long distance (>1 km/h) movements that did not seem to be related to time of day. These fish may have been meandering in an attempt to find passage upstream.

Passage efficiency and numbers of implanted American shad returning to NSBLD was highest in the first year of study. Over 50% of the fish that returned to the dam were passed even though the lower gates were open for less than 15 h. This percentage represents remarkable passage efficiency when related to another lock structure that had lower gates open for well over 1,000 h (Moser et al. 2000). Although the locking season was expanded in 2002, low returns to the dam made passage difficult to assess. Even the low percentage of fish that passed in 2002 (9%) represents a very high passage rate, as lower gates were open for less than 20 h. Passage and percentage of fish returning to the dam in either year compare favorably with the general range of passage in a similar study conducted on a low-elevation lock and dam system on the Cape Fear River, North Carolina (Moser et al. 2000).

The efficient passage at NSBLD may be due to the bottom topography of the area directly below the dam. A midchannel gravel bar splits the main channel into two smaller channels. The larger, deeper channel leads directly to the lock entrance. American shad follow the main river channel during migration, often using the lower one-third of the water column (Witherell and Kynard 1990). Barry and Kynard (1986) found that turbulent flows could confuse and deter fish from an area. The turbulent flow within 30 m of the dam may have caused fish to repeatedly move downstream and upstream, increasing the time spent in the main channel. This orientation could lead to a higher probability of encountering the lock entrance and passing upstream.

In both years, the population size of American shad reaching NSBLD was similar. The population estimates for either year are similar to the Altamaha River system (D. Harrison, Georgia Department of Natural Resources, personal communication). Numbers of American shad reaching NSBLD were similar to the observed numbers at a fish lift in South Carolina (Cooke and Leach 2002); however, those values are highly variable and were assessed by numbers of fish that successfully pass through the lock. Mark–recapture studies on migrating fish are inherently difficult because of high interannual variation, difficulties in capture, and potential biases. Most mark–recapture studies are conducted in cooperation with commercial gill-net fisheries, and often assess all fish that enter rivers, not only those that reach spawning grounds. Mark–recapture studies, in conjunction with telemetry, are valuable to the assessment of differential movement and may provide more realistic estimates of populations.

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