Transactions of the American Fisheries Society 135:889–896, 2006

DOI: 10.1577/T05-101.1

[Article]

Migratory Behavior of American Shad in the York River, Virginia, with Implications for Estimating In-River Exploitation from Tag Recovery Data

JOHN E. OLNEY,* ROBERT J. LATOUR, AND BRIAN E. WATKINS

Department of Fisheries Science, School of Marine Science, Virginia Institute of Marine Science, Gloucester Point, Virginia 23062, USA

DOUGLAS G. CLARKE

U.S. Army Corps of Engineers, Engineer Research and Development Center, 3909 Halls Ferry Road, Vicksburg, Mississippi 39180, USA

Abstract.—Tagging of American shad *Alosa sapidissima* may alter their migratory behavior, causing some tagged individuals to cease or delay the spawning run. In a tag recovery study designed to assess fishery impacts, this altered behavior would reduce the number of tagged fish available to the target fishery and would bias estimates of exploitation and fishing mortality rates. To investigate this possibility, we fitted 29 prespawning adults with acoustic tags and released the fish into the middle reaches of the York River, Virginia. Movements of individuals were remotely monitored at three hydrophone stations: (1) 7 river kilometers (rkm) downriver of the release site; (2) on the Mattaponi River, 48 rkm upriver of the release location; and (3) on the Pamunkey River, 56 rkm upriver of the release location. Almost half of the fish were apparently affected by capture, handling, and tagging, as they either abandoned their migration or delayed their upstream movements. The movements of some fish appeared to be unaffected by capture; these fish were not detected at the downriver station and were detected on the spawning grounds 2–5 d after release. Eighteen fish remained on the spawning grounds for 17–51 d (average = 34.4 d) and were last detected at the downriver location, presumably during their seaward migration. Of the 26 tagged fish that migrated to either tributary after release, 15 originally selected spawning grounds on the Mattaponi River and 11 selected the Pamunkey River. One fish occupied both tributaries for several weeks each, suggesting possible spawning at both locations. We conclude that tagging protocols designed to measure the impacts of fishing on American shad should include telemetry to assess altered migratory behavior.

The annual spawning run of American shad *Alosa sapidissima* in the York River, Virginia (Figure 1), consists of virgins (ages 3–7) and fish that have spawned in previous years (repeat spawners, ages 4–10) (Nichols and Massmann 1963; Maki et al. 2001; Olney et al. 2001). The run begins when maturing (prespawning) fish enter the mouth of the river in late January through late February and continues for approximately 4 months through mid-May (Olney et al. 2001) and, according to anecdotal accounts, perhaps as late as June. Postspawners (spent and partially spent individuals) exit the mouth of the river beginning in late March and continue to emigrate seaward through June (Olney and Hoenig 2001; Olney et al. 2001). American shad stocks in Virginia may be partially iteroparous (i.e., some proportion of the population dies after spawning; Garman 1992); however, there is no direct evidence of this phenomenon (e.g., spent carcasses on the shore) in the York River.

Once prespawning American shad have entered the lower Chesapeake Bay region (Figure 1), York River fish segregate from mixed-stock assemblages and migrate at least 130 river kilometers (rkm) up the estuary to freshwater spawning grounds (Bilkovic et al. 2002b). Adult American shad can swim at approximately 1–3 km/h (Dodson and Leggett 1973; Hightower and Sparks 2003). Thus, York River fish should appear on their spawning grounds about 2–5 d after entering the river. The spawning grounds are located in two tributaries, the Pamunkey and Mattaponi rivers, which converge at West Point, Virginia, to form the York River (Figure 1). The York River extends approximately 55 rkm from origin to mouth. American shad choose either tributary and spawn in upstream segments characterized by shallow depths, high dissolved oxygen, and relatively high currents (Bilkovic et al. 2002a). Fishes spawning in each tributary are believed to constitute separate substocks because there is no current evidence of mixing by spawners on either tributary.

Alosine fishes are regarded as very sensitive to capture and handling (Acolas et al. 2004). Thus, tagging may alter the migratory behavior of ripening fish, causing some tagged individuals to cease the

* Corresponding author: olney@vims.edu

Received April 11, 2005; accepted January 22, 2006
Published online June 26, 2006

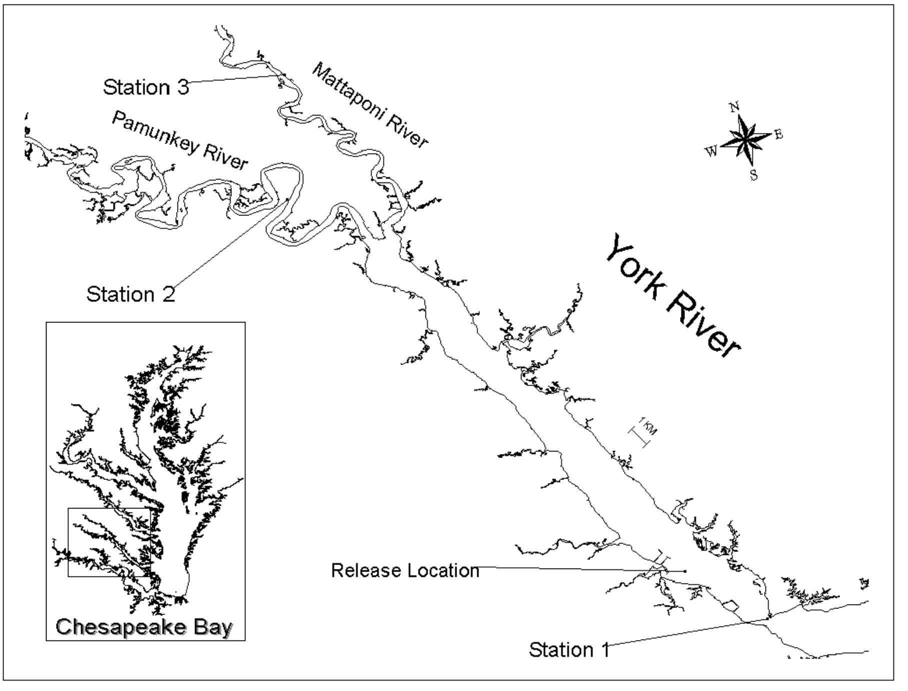

FIGURE 1.—Map of the York River system, Virginia, showing hydrophone locations downstream (station 1) and upstream (stations 2 and 3) of the release location of American shad tagged with acoustic transmitters during spring 2003.

spawning run and return to sea. This altered behavior would reduce the number of tagged fish available to the target fishery and would bias estimates of in-river exploitation rates. Evidence from previous tagging studies suggests that this bias exists. Nichols and Massmann (1963) tagged American shad at the York River mouth during the upriver migration in spring 1959. Of 842 tagged fish, 118 (14%) were recaptured shortly after release at locations other than the York River spawning grounds. Dodson et al. (1972), Barry and Kynard (1986), Moser and Ross (1993), Beasley and Hightower (2000), Acolas et al. (2004), and Bailey et al. (2004) observed fallback behavior (unexpected movement downstream toward marine waters just after tagging) in radio-tracked and acoustic-tracked allis shad *A. alosa* and American shad. In the Roanoke River, North Carolina, 12 of 17 American shad exhibited fallback behavior and 7 abandoned their upstream migration after radiotagging (Hightower and Sparks 2003). In ongoing conventional tagging studies on the Santee River, South Carolina, the percentage of returns within 30 d of release (i.e., "unexpected returns") from fisheries other than recreational anglers on or near the spawning grounds has been variable and sometimes has reached 50% (J. W. McCord, South Carolina Department of Natural Resources, unpublished data). In ongoing tagging studies on the Hudson River, New York, the percentage of unexpected ocean returns from fish tagged in the river varied from 0% to 67% during 1995–2001 (K. Hatalla, New York State Department of Environmental Conservation, personal communication).

We examined movements of prespawning American shad that were tagged with acoustic transmitters and subsequently detected via passive hydrophone arrays placed above and below the release point in the York River, Virginia. To investigate the phenomenon of altered behavior induced by capture and tagging, we estimated the proportion of fish that did not subsequently complete their spawning migration on the York River. In addition, we sought to describe migratory pathways and behavior of York River fish, especially the choice of spawning tributary, residence duration on the spawning grounds, and the possibility that individual fish might utilize more than one spawning tributary during the season.

Methods

American shad were captured in the spring of 2003 in a research pound net located in the middle reaches of the York River (Figure 1). The net was fished on slack current before flood tide. After the net was pursed, fish were dipnetted and placed into a floating live car. Healthy and vigorous fish were measured, tagged, and held in a circular shipboard tank with circulating seawater for up to 30 min before release. Scales were removed from each specimen before tagging for subsequent aging and determination of spawning history (Cating 1953). Acoustic tags were inserted through the esophagus into the upper alimentary canal via a slender wooden probe. Tagged fish were released on six dates in March. Our previous studies have shown that American shad captured at this time are all ripening fish (Olney et al. 2001). Gender was estimated in the field. Prespawning females are usually longer, deeper bodied, and heavier than males and have fuller abdomens.

Acoustic equipment used in this study (Lotek Wireless, Inc., Toronto, Canada) included wireless hydrophones (WHS_1200) that operated at frequencies of 149–151 MHz, receivers (SRX_400) with W32CT firmware, and acoustic tags (CAFT11_2) that had a battery life of approximately 100 d. Tags were 40 mm long and 11 mm in diameter and weighed 8 g in air and 4.3 g in water. Tags transmitted at a frequency of 76.8 kHz and relayed a code unique to each individual tag. The code was transmitted at 5–6-s intervals by each tag. Each hydrophone was attached to an independent buoy with a data-transmitting antenna. Continuous records of acoustic tag detections were obtained via land-based receivers and antennas installed on private piers or specially constructed platforms. Hydrophones and receivers were installed and tested just before release of tagged fish and were deployed for 100 d (3 March–10 June 2003). Receivers were maintained and data were downloaded twice weekly.

Hydrophones were positioned at three stations in the York River upstream and downstream of the fish release point (Figure 1). An array of four hydrophones was deployed across the York River at Gloucester Point just upstream of the Coleman Bridge, or 7.4 rkm downstream of the release site (station 1; Figure 1). At this point, the York River is approximately 1 km wide and has an average depth of 20 m. Two receivers were positioned on each side of the river at station 1. Two hydrophones were also deployed upstream: one (station 2) in the Pamunkey River, 48.1 rkm upstream of the release site, and one (station 3) in the Mattaponi River, 55.6 rkm upstream. At stations 2 and 3, the rivers are approximately 0.5 km wide and have an average depth of 10 m. The distance from the release site to the confluence of the tributaries at West Point was 33.3 km.

The collected data were imported into a spreadsheet, and individual tag codes were checked for authenticity. Data sorting identified a limited number of periods when station 2 was not receiving properly. Malfunctions were temporary (never lasting more than several hours) and only lowered receiver effectiveness without terminating reception. These events could have resulted in failure to record weak tag signals at that location. Regardless, we assumed that all fish had an equal chance of being detected and that all receivers were equally efficient at decoding signals during the study.

We used the following definitions in our analysis. Fish that exhibited fallback behavior were first detected at the downriver hydrophone array after release. Transit time was the number of days from release to the first detection upstream. Residence time was the number of days between the first and last detections at the upriver monitoring site. We estimated residence times only for fish that were last detected at station 1; these fish were presumably migrating seaward after the spawning run. Exit time was the number of days between the last detection upstream and the last detection downstream.

Results

Twenty-nine American shad, including 3 males (391–438 mm fork length) and 26 females (404–529 mm), were tagged and released. Surface water temperatures at the release site during the 6 d of tagging were 6.1°C on 7 March, 6.7°C on 11 March, 7.9°C on 18 March, 9.1°C on 22 March, 11.6°C on 25 March, and 12.1°C on 25 March. We tagged 7 virgins and 22 repeat spawners ranging from age 5 to 9; most were members of the 1998 ($N = 13$ fish), 1997 (7 fish), and 1996 (7 fish) year-classes.

The movements of 13 American shad (44.8% of tagged fish) were apparently affected by capture, handling, and tagging, because these fish were detected first at the downriver hydrophone array (station 1) after release, exhibited extended transit times of 6–36 d (average = 11.4 d), or both. Two of these fish were detected only at station 1 after release and did not resume their upstream movements. Another of these affected fish was detected upstream (station 2) 36 d after release but probably did not spawn because it left the spawning tributary within 1 d and exited the York River thereafter. One individual did not exhibit fallback behavior but was included in this group because it was first detected upstream 14 d after release. Thus, 3 American shad (10.3% of the sample) abandoned the spawning migration and did not spawn in the York River system, and 10 American shad (34.5% of the sample) were delayed in their movements upstream.

We judged the migrations of 16 American shad (55.2% of the sample) to be largely unaffected by capture, handling, and tagging. These fish did not exhibit fallback behavior and had shorter transit times (1–5 d; average = 3.1 d) than those of affected fish. Two individuals reached station 2 on the Pamunkey River within 1–2 d of release; this distance would require average swimming speeds of 1.0–2.0 km/h. Of the five unaffected fish that required 5 d to reach the upriver hydrophone, all were first detected at station 3, approximately 8 rkm farther upstream than station 2. For these individuals, the required average swimming speeds were lower (0.46 km/h) but were still within the range of swimming speeds reported for migrating American shad (Dodson and Leggett 1973).

In all, 26 fish migrated to either tributary after release; 15 of these fish (57.7%) originally selected the Mattaponi River, and 11 (42.3%) originally selected the Pamunkey River. Although patterns of tributary selection were not consistent throughout the period of release, 8 of 12 American shad chose the Pamunkey River before 22 March, and 11 of 14 chose the Mattaponi River after that date.

Eighteen fish remained upstream of station 2 or 3 for more than 14 d and were last detected at station 1, presumably during their seaward migration. Most fish emigrated from the York River (i.e., they were last detected at station 1) in early to mid-May (14 of 18 fish). Exit time for these fish averaged 4.6 d (SE = 0.77) and ranged from 1 to 10 d. Estimates of residence ranged from 17 to 51 d (mean = 32.4 d, SE = 2.3). The average Mattaponi River residence time of 29.9 d (SE = 2.3, $N = 11$ fish) did not differ significantly (t-test, $P > 0.05$) from the average Pamunkey River residence time of 36.4 d (SE = 4.5, $N = 7$ fish). We were unable to account for eight fish (four individuals on each tributary) that migrated to the spawning grounds but were not detected as leaving the rivers. All of these fish were at large for more than 80 d before termination of the experiment. We did not conduct mobile or manual searches to locate these individuals.

Five fish were detected as occupying both tributaries (Figure 2). Two individuals (fishes 116 and 100) initially resided on the Mattaponi River (about 30 d each) and then entered the Pamunkey River for a short period (>3 d) before exiting the York River system. The movements of a third fish (fish 138) mirrored this pattern, but the fish was never detected again after entering the Pamunkey River. Another individual (fish 133) entered the Pamunkey River briefly (>2 d) but eventually selected the Mattaponi River and was never detected again. Interestingly, one fish (fish 157) displayed extended residence on both tributaries (Pamunkey River, 15 d; Mattaponi River, 23 d) before exiting the system. Judging from these residence times, this female had the opportunity to spawn on both tributaries.

Discussion

Prespawning American shad do not feed during their migration up the York River (Walter and Olney 2003), and there is no evidence that individuals naturally delay their directed movements to the York River spawning grounds. Although mixed stocks may occur at the mouths of rivers and in large embayments along the U.S. East Coast, straying of individuals into middle and upper portions of nonnatal rivers and spawning areas is rare, based on multiple years of recapture of hatchery fish bearing river-specific marks (Hendricks 1995; McBride et al. 2005). Adverse weather conditions (especially sharp declines in temperature or late-spring warming) might delay or alter migrations of American shad, but these conditions were not present during our study.

Thus, we conclude that increases in transit times of affected fish in our study were not due to feeding forays before spawning and that the unexpected abandonment of spawning migrations by some fish was not due to natural causes or straying by nonnative individuals.

The high proportion of American shad affected by capture, handling, and tagging in our trials and in those of other investigators (Hightower and Sparks 2003) suggests that tagging protocols designed to estimate impacts of fishing should include concurrent monitoring to assess altered migratory behavior. Remote sensing techniques are ideal for this purpose. Altered migratory behaviors include abandonment of upstream movement, fallback downstream of the release location, and delay in upstream movements after tagging. Analytical methods used to derive exploitation rate estimates from tag recovery data for American shad require modifications to accommodate for altered migratory behavior because of the assumption that the tagged population is representative of the target population (Brownie et al. 1985).

The Atlantic States Marine Fisheries Commission requires assessment of fishing mortality for stocks under exploitation (ASMFC 1999). Thus, in-river tag recovery studies are currently used to estimate harvest rates by recreational and commercial fisheries for American shad in several states (e.g., New York, South Carolina, and Georgia). In these studies, fish are captured, tagged, and released below the fishing grounds but well within the natal river of each stock. Investigators assume that the tagged population is destined to proceed upriver to spawn and is not of mixed-stock origin. The tag recovery rate for prespawning fish in year i ($f_{p,i}$) can be modeled as (Hoenig et al. 1998)

$$f_{p,i} = \phi \lambda u_{p,i}, \qquad (1)$$

where ϕ is the probability that a fish will survive the tagging process with the tag intact in the short term, λ is the tag reporting rate, and $u_{p,i}$ is the exploitation rate in year i. Both ϕ and λ are assumed to be constant over time and must be estimated independently; this is

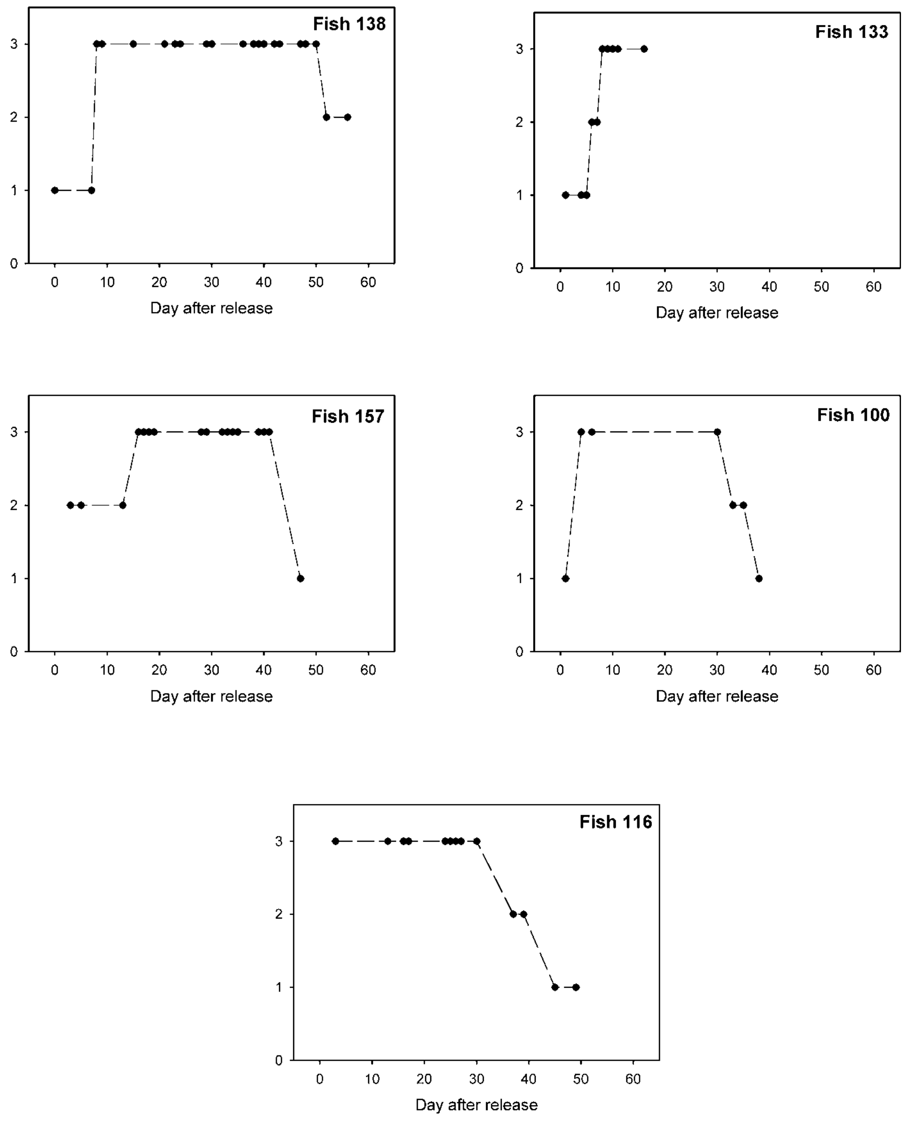

FIGURE 2.—Individual locations and detection times (days after release) for five acoustic-tagged American shad that occupied both the Pamunkey and Mattaponi rivers, Virginia, during their spawning migration in spring 2003. Hydrophone receivers were located downstream (station 1: lower York River, Virginia) and upstream (station 2: lower Pamunkey River; station 3: lower Mattaponi River) of the York River release location (see Figure 1).

generally done by conducting holding trials (Latour et al. 2001) and a high-reward tagging experiment (Pollock et al. 2001). Equation (1) leads to the following exploitation rate estimator:

$$\hat{u}_{p,i} = \frac{r_i/N_i}{\hat{\phi}\hat{\lambda}}, \tag{2}$$

where N_i is the number of tagged fish in year i and r_i is the tabulated number of tag recoveries in year i from fish tagged in that year. Given that tagged American shad exhibit altered behavior that can lead to emigration from the study area, a modified tag recovery rate model is needed, namely,

$$f_{p,i} = (\phi\lambda u_{p,i})\delta_i, \tag{3}$$

where δ_i is the probability that a fish captured, tagged, and released in year i will continue the spawning migration. A modified exploitation estimator is easily obtained from equation (3), that is,

$$\hat{u}_{p,i} = \frac{r_i/N_i}{\hat{\phi}\hat{\lambda}\hat{\delta}_i}. \tag{4}$$

Although equation (4) adjusts for the bias imposed by emigration of tagged individuals from the study area, use of that model is limiting because its application represents independent annual tag recovery studies. An improved approach would be to collect tag recovery data in a multiyear context. This type of study design has the potential to (1) improve the precision of exploitation rate estimates and (2) allow derivation of estimates of other important population parameters (e.g., natural mortality rate).

Recently, Pollock et al. (2004) developed a multiyear model structure to estimate mortality rates (both fishing and natural) and tag reporting rates by combining telemetry and tag recovery data. In many respects, we view the Pollock et al. (2004) approach as an ideal study design for assessing American shad populations, provided that modifications can be imposed to allow for abandonment or delay in upstream migration. In their general formulation, Pollock et al. (2004) assumed that there is no emigration of tagged individuals out of the study area. However, the authors noted that the telemetry approach could be used to detect emigration, which is coincident with our recommendations. The incorporation of altered migration (abandonment or delay) would require changing the model structure of the multiyear tag recovery component of the combined approach and can be accomplished without great difficulty.

Clupeid fishes are highly adapted for sound detection, and some are considered to be hearing specialists (Helfman et al. 1997; Popper 2003). Alosine clupeids can detect ultrasonic sounds to over 200 kHz, and American shad may have the widest hearing range of any fish (Popper 2003). Thus, sounds produced by acoustic tags are probably detected by tagged American shad and may alter their behavior. Studies that compare migratory behavior in American shad that are monitored with sound-producing and nonsound-producing telemetry could be useful for evaluating this possibility, but none have been conducted to date. It is important to note that fallback behavior in tagging studies of this species has been observed in studies that use acoustic, radio, and conventional external tags, suggesting that sound is not the principal cause of this phenomenon.

Spawning history, age, date of release, and water temperature at release did not appear to be factors influencing whether fish were affected by tagging. Hightower and Sparks (2003) found that radio-tracked American shad exhibiting fallback behavior were virgins of age 5–6. In our trials, delayed or abandoned spawning migrations were observed in both sexes, in all ages, and in both virgins and repeat spawners. Field notes by tagging personnel indicated that all fish released in our trials were healthy, and most were in vigorous swimming condition when released. Thus, it may not be possible to predict which tagged fish will be affected by field protocols.

Alternating spawning between rivers by individual American shad within a spawning season has not been reported previously. In our trials, 5 of 18 American shad that migrated to the spawning grounds and then exited the York River system had entered both the Mattaponi and Pamunkey rivers. One of these individuals exhibited behavior that suggested spawning activity in both tributaries, but this possibility requires further study. In the other four cases, fish entered the secondary tributary for a short period, either before or after spawning.

Some postspawning fish exited the spawning grounds quickly, making the downstream migration in 1–2 d at swimming speeds equivalent to the upstream migration rate of 1–2 km/h. Others lingered in the middle–lower estuary for 3–10 d. Mean exit time was greater than mean transit time for unaffected fish, and out-migrants were often detected on successive days or over a 2–5-d period at the downstream station. Walter and Olney (2003) reported that American shad resumed feeding soon after spawning in the York River system and that opossum shrimp *Neomysis americana* accounted for almost all stomach contents. They further observed that variability in stomach fullness was high, indicating that not all fish actively fed. Dadswell et al. (1987) observed that ripening fish migrated at faster rates than did postspawning fish, an observation attributed to feeding by postspawners to optimize growth. Our data on out-migration timing and duration are consistent with these observations. Temporary residence and feeding in the middle to lower estuary are important refractory processes for postspawning American shad in the York River that facilitate partial reclamation of lost energy reserves and promote iteroparity (Walter and Olney 2003).

Acknowledgments

We thank commercial fishers R. Kellum, T. Kellum, S. Kellum, and W. Lett for their assistance in capturing American shad. M. Sisak (Lotek Wireless, Inc., Toronto, Canada) provided invaluable technical assistance and advice. We acknowledge the contributions of K. Reine and C. Dickerson (Engineer Research and Development Center, Vicksburg, Mississippi), who set up and deployed the buoyed hydrophones and assisted in equipment maintenance. Thanks to T. Barbose, S. Olsson, and the Waterman's Museum of Yorktown, Virginia, for permission to deploy data-receiving equipment on private property. We thank P. Crewe, A. Hyle, and J. Goins for help in the field. This research was supported in part by a cooperative research award from the U.S. Fish and Wildlife

Service's Wallop–Breaux Program through the Marine Recreational Fishing Advisory Board of the Virginia Marine Resources Commission (grant F-116-R-5). This is contribution number 2748 of the Virginia Institute of Marine Science.

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