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Migratory and Spawning Behavior of American Shad in the James River, Virginia

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MIGRATORY AND SPAWNING BEHAVIOR OF AMERICAN SHAD
IN THE JAMES RIVER, VIRGINIA

A Thesis

Presented to

The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of
Master of Science

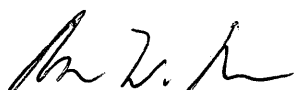
by

Aaron W. Aunins

2006

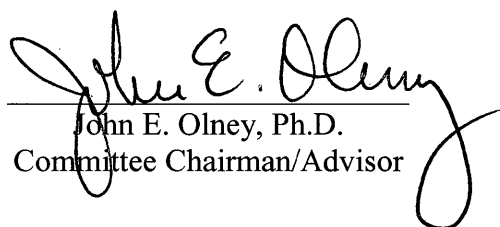
APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of
Master of Science



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PREFACE

The James River in Virginia historically supported productive and profitable fisheries for American shad (*Alosa sapidissima*) and other anadromous fishes but stocks have undergone severe declines due to overfishing and habitat degradation (Garman 1995; Freeman et al. 2003). The shad fisheries are currently under a harvest moratorium within the James River and other Chesapeake Bay tributaries (ASMFC 1999). A comprehensive restoration program began in Virginia in 1994 with the stocking of hatchery-reared larvae of Pamunkey River broodstock into the upper reaches of the James River above Boshers Dam (Olney et al. 2003). Fish passage has also been created at numerous locations within the fall line in Richmond and a fishway was opened at Boshers's Dam in 1999, restoring access to over 200 km of historical spawning habitat (Weaver et al. 2003). While the current restoration program has increased the numbers of shad returning to the James River and provided passage around obstructions, information on spawning behavior and habitats throughout the James River system are still largely unknown but needed for continued successful restoration efforts.

American shad have played an important cultural role in Virginia for centuries. In pre-colonial times, native populations undoubtedly exploited annual anadromous spawning runs and some tribal governments continue to harvest shad under colonial treaties that supercede the fishing ban (Olney et al. 2001). As early as 1607, American shad served as an important source of food for colonial settlers as evidenced by otoliths in archaeological excavations of pits and middens at Jamestown (Bowen and Andrews 2000). American shad and river herrings (*Alosa spp.*) also represent a valuable annual source of marine derived nutrients to riverine ecosystems (MacAvoy et al. 2001),

although the extent of this contribution by James River populations is not well known (Garman 1992).

Historical studies of James River shad have quantified commercial landings and fishing effort (Stevenson 1899) and used traditional tagging methods to estimate fishing mortality rate (Walburg and Sykes 1957) but there has been little attention to issues of biology and ecology. Modern fisheries management emphasizes the role of essential fish habitat (EFH), especially the protection of migration corridors, spawning sites and nursery grounds. Knowledge of these critical aspects of the biology of American shad on the James River is lacking. Acoustic and radio telemetry has recently been used to study the migratory movements (Bailey et al. 2004; Sprankle 2005; Olney et al. 2006) and spawning locations (Beasley and Hightower 2000; Hightower and Sparks 2003) of American shad in many Atlantic coastal rivers. The current study was designed to investigate the largely un-characterized spawning migration of American shad within the James River using acoustic telemetry and to enhance our understanding of reproduction in this depleted stock. Chapter 1 presents results of passive and active acoustic tracking used to assess movements during the upstream migration, subsequent residency period, and emigration. The study identified previously unobserved migration patterns and specific river reaches occupied during the residency period, and assessed the role of time of day and tidal stage on migratory movements. Spawning reaches of American shad within the James River are described in Chapter 2 using a combination of conventional ichthyoplankton techniques with active and passive acoustic tracking. These surveys represent the first investigation of the spawning grounds of American shad in the James River since hatchery restocking efforts began in 1994.

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CHAPTER 1

MIGRATORY BEHAVIOR OF
AMERICAN SHAD IN THE JAMES RIVER

Abstract

Acoustic telemetry was used to monitor the migratory behavior of American shad during the spawning run and subsequent residency within the James River, Virginia in spring 2005. Nine hydrophone monitoring stations extended 121 rkm upstream from the estuarine portion of the river at Hog Island (rkm 53) to just above Boshers' Dam Fishway (rkm 174) in non-tidal freshwater. Ninety-eight fish were tagged and released in the lower estuary. Fifty percent (n=49) of the tagged cohort was detected upstream of the lowermost hydrophone array. The remaining fish fell back and abandoned the migration. The tendency to continue with the upstream migration was not significantly related to age or spawning history ($p>0.05$). Similarly, there was no significant difference in the tendency to migrate upstream among individuals held in a holding pen for up to 4 hours ($p>0.05$). Three areas of residency were identified at Upper Brandon Plantation (rkm 94), Shirley Plantation (rkm 124) and Richmond Deepwater Terminal (rkm 148). Movements during the upstream migration were significantly related to flooding tides ($p<0.01$), and movements on the emigration were significantly related to ebbing tides ($p<0.01$). Thirty-nine fish resided on the mainstem of the river above Upper Brandon Plantation for an average of 28.8 days (SD = 8.2 days). Fish were detected at the mouths of two major tributaries (Appomattox and Chickahominy Rivers) but their presence in upstream reaches was not verified by active tracking. Ten fish either ceased transmitting detectable signals on the upstream migration or were not detected exiting the system at the lowermost monitoring station. Losses were attributed to natural or fishing mortality, or tag regurgitation. No tagged fish were detected above Boshers' Dam fishway.

Introduction

The American shad *Alosa sapidissima* is a migratory alosine clupeid, its native range extends along the east coast of the United States from the Saint Johns River, Florida to the Saint Lawrence River, Quebec (Leim 1924; Walburg and Nichols 1967). The species is anadromous, annually entering freshwater portions of coastal tributaries to spawn in spring following extensive coastal migrations. Populations spawning above 32° N show an increasing degree of iteroparity, whereas populations south of this latitude are entirely semelparous (Leggett and Carscadden 1978). The timing of entry of fish into tributaries during the spawning migration is largely influenced by water temperature, with peak catches associated with temperatures from 13-20 °C (Leggett and Whitney 1972).

Data from conventional mark-recapture studies have provided a description of the migratory route of American shad at sea and along the US Atlantic Coast (Talbot and Sykes 1958; Leggett 1973; Neves and Depres 1979). Dadswell et al. (1987) synthesized the results of years of tagging and trawl data from these and other studies into one generalized migratory pattern. In January and February, adult shad are distributed primarily in three offshore aggregations off of the coasts of Florida, the mid-Atlantic Bight, and Nova Scotia. Spawning begins in tributaries from Florida to South Carolina. In March and April movement is progressively northward, with spawning occurring in populations from North Carolina to the Bay of Fundy. In summer, shad occur in aggregations in the Bay of Fundy, the Saint Lawrence estuary, and in coastal waters of Newfoundland and Labrador. As fall approaches, shad begin to leave these areas and repeat the spawning migratory pathway (Dadswell et al. 1987). Site fidelity is reportedly

high (Melvin et al. 1986), with fish returning to their natal rivers and tributaries (Carscadden and Leggett 1975; Hendricks et al. 2002), although straying among rivers has been documented (Nichols 1960; Olney et al. 2006).

During the last century, stocks along the Atlantic coast have declined dramatically as a result of over-fishing, dam construction, and pollution (Freeman et al. 2003; Limburg et al. 2003). Historically, the Chesapeake Bay had one of the most productive shad fisheries. However, catch data show a steady decline in landings along the coast and in Virginia since the 1950's (Figure 1). Shad catches had declined from 11.2 million pounds in 1896 to 1.4 million pounds in 1960 (Walburg and Nichols 1967). A continued trend of declines in commercial landings within the James River and other Virginia tributaries throughout the 1980s and early 1990s prompted the imposition of a harvest ban for the Virginia portion of the Chesapeake Bay and its tributaries in 1994 (ASMFC 1999). Fishing effort then became more concentrated in coastal waters where ocean intercept fisheries harvested mixed stock assemblages of shad. Brown et al. (1999), analyzing mtDNA from American shad captured in coastal mixed stock fisheries off of Virginia and Maryland, determined that intercept fisheries significantly impacted stocks under restoration (James and Susquehanna Rivers) in some years, with the catch also containing individuals from northern, mid-Atlantic, and southern stocks. Due to concerns for impacts on already depressed populations, coastal ocean intercept fisheries were officially closed in December of 2004 as mandated by the Atlantic States Marine Fisheries Commission (ASMFC 1999).

Historically, American shad were abundant throughout the James River system, as evidenced by a productive fishery in the late 1800s. Stevenson (1899) provided a

detailed account of commercial activity of the United States American shad fishery in 1896 in an Atlantic coast survey extending from Florida to Maine. In the James River he reported catches of shad as far as 335 miles inland from the Chesapeake Bay, with total annual harvest in the main-stem James River estimated at ~325,000 fish. Catches within the Chickahominy and Appomattox Rivers, two main tributaries of the James, were also large (estimated at ~150,000 and ~12,000 fish, respectively). Stevenson described the Chickahominy River as “one of the finest shad streams of the United States for its size” (p. 185). Other significant Virginia fisheries were located in the York River (including its tributaries the Pamunkey and Mattaponi), and Rappahannock Rivers with annual harvests within these rivers of ~532,000 and ~351,000 fish respectively.

In 1994, Virginia initiated the construction of fish passage facilities as part of a restoration program to rebuild depleted stocks (Weaver et al. 2003). Inter-basin transfer of larvae from Pamunkey River broodstock into the James River has become an important component of the plan to rebuild the severely depleted James River stock (Olney et al. 2003), as well as creating access to previously inaccessible spawning habitat by building fishways such as the one at Boshers Dam, which restored access to 221.4 km of historical spawning habitat (Weaver et al. 2003). Other obstructions below Boshers Dam still exist, but have been breached to allow fish passage. The presence of American shad at the base of Boshers Dam has been confirmed by electro-fishing, and American shad have been observed using the fishway although passage efficiency is unknown (Weaver et al. 2003).

Monitoring to estimate the annual strength of the spawning run and the prevalence of hatchery fish has been conducted in the lower James River since 1998 (Olney et al.

2003). The results confirm the depleted status of the stock relative to historic catch rates, but indicate an overall increasing trend in catches since the inception of the monitoring program in 1998 until 2003, followed by a slight decrease in recent years (Olney and Delano 2006). Accompanying the initial increase in the catch index were increasing numbers of oxytetracycline (OTC) tagged hatchery shad in 1998-2003, indicating the hatchery program is working. The percentage of returning hatchery adults has declined during 2004-2005 from a peak in 2003 (Olney and Delano 2006). Electro-fishing and push-net monitoring by the Virginia Department of Game and Inland Fisheries (VDGIF) has detected few adult or juvenile American shad within the Appomattox and Chickahominy Rivers (Alan Weaver, VDGIF, personal communication).

In contrast to conventional mark-recapture techniques, telemetry methods provide information on fish behavior on finer spatial (m-km) and temporal scales (h-d). Some of the earliest research of American shad migratory behavior using acoustic telemetry was conducted by Leggett and his students in the 1970s (Leggett and Jones 1971; Dodson et al. 1972; Dodson and Leggett 1973). These studies provided estimates of swimming speeds, net avoidance behavior, influence of tidal phase on movements, and the usage of sight and smell to locate natal rivers in the northeast, especially the Connecticut River. In the 1980s, Barry and Kynard (1986) observed the behavior of tagged shad in the tailrace of a fishlift, and provided suggestions for improving fish passage at Holyoke Dam in the Connecticut River. More recent investigations have focused on describing in-river migratory movements, spawning habitat characteristics, and the effects of tagging and handling using both acoustic tags and radio tags in North Carolina rivers (Beasley

and Hightower 2000; Hightower and Sparks 2003), the Savannah River in Georgia (Bailey et al. 2004) and the York River, Virginia (Olney et al. 2006).

Migratory behavior of adult American shad in the James River has not been described but historic movements of native stocks are known to have been restricted by construction of dams in Richmond (Virginia) and on the Chickahominy River. Heavy industrial development (see Study Area description in Methods) has altered near-shore habitats and water quality, and may have influenced spawning site selection. It is likely that channel relocation and maintenance associated with commercial shipping have altered historic migratory pathways. Furthermore, stock composition of the migratory population has been significantly changed since the introduction of hatchery-raised fry from the Pamunkey River stock. As a result, the habits and habitats of native James River American shad may now be beyond our capacity to re-establish. Regardless, knowledge of the behavior of the current population can support informed management decisions regarding future protection of critical habitats and migratory pathways, location of present spawning grounds, efficacy of re-stocking efforts and fishways, advisability of time-of-year restrictions on channel maintenance, and future harvest regulations, especially designations of in-river sanctuaries associated with spawning grounds. To begin to address these important issues, we studied the movements of American shad throughout the James River system during the 2005 spawning run using acoustic telemetry (Figure 2). Our objectives were 1) to observe and characterize movement patterns throughout the James River system up to the fall line, including the use of tributaries that historically supported important fisheries; 2) to estimate residence time of spawners, identify river segments occupied during the residency period and document

emigration from the system; 3) to assess the extent of semelparity that exists within the James River population; and 4) to assess the influence of physical factors (temperature, time of day, tidal currents) on migratory movements.

Methods

Study area - The James River flows a distance of approximately 560 kilometers from its formation at the junction of the Cowpasture and Jackson Rivers in Botetourt County, VA to its mouth at Hampton Roads near the Port of Newport News, VA in Chesapeake Bay (Walburg and Sykes 1957). Tidal influence extends to the fall line in Richmond, VA at river kilometer (rkm) 158 just upstream of the 14th Street bridge (rkms are measured from the Hampton Roads Bridge Tunnel at the James River mouth upstream following the main shipping channel of the river excluding Jones Neck, Turkey Island, and Dutch Gap cutoffs). The fall line in Richmond is characterized by extensive rapids and riffle and pool habitat, with the river elevation dropping 30 m over 15 km (Garman and Nielsen 1992). The James River watershed drains 25% of the land area in Virginia (Vadas and Weigmann 1993) - an area of 27,018 sq km consisting of 19,119 sq km of forested land, and 4,605 sq km developed for agriculture (Chesapeake Bay Program 2004). The remaining 3,294 sq km are composed of open-water, wetlands, and developed areas (Chesapeake Bay Program 2004).

Development is most intense in reaches of the James River between Hopewell (rkm 120) to Richmond at the fall line (rkm 158). Various industrial facilities are located on both shorelines in this reach including a gravel pit and transfer station, cement plant, the Port of Richmond, wastewater treatment facilities, and a coal-fired power plant. This

region of the river is also characterized by heavy shipping traffic to the Port of Richmond and other industrial sites. To shorten the distance traveled by boat between Hopewell and Richmond, the natural path of the river has been altered by the construction of cutoffs at Turkey Island, Jones Neck, and Dutch Gap which were completed between 1933 and 1937 (Pleasants 1971). Above Richmond, Boshers Dam was constructed at rkm 172 in 1823 and denied access to all upstream American shad spawning habitats above the dam (Weaver et al. 2003). However with the opening of Boshers Dam Fishway in 1999, 221.4 km of historic main-stem spawning habitats became accessible for the first time since 1823 as far as the next migration barrier in Lynchburg, VA (Weaver et al. 2003).

Navigation through several reaches of the James River is maintained by channel dredging. Dredging frequency ranges from annually at the Richmond Deepwater Terminal turning basin (9 km downstream from the fall line), to every 20-25 years at City Point Shoal near the Appomattox and Hopewell (Keith Lockwood, United States Army Corps of Engineers (USACOE), personal communication). Recent studies using acoustic telemetry have investigated the influences of channel dredging on the upstream migratory behavior of American shad, although these results were inconclusive (Olney et al. 2005).

Capture Methods - American shad were captured with a haul seine operated by commercial fishers and a staked gill net used in an ongoing shad monitoring study (Olney et al. 2003). Gill net sets were 6-h in duration on 18 March 2005 and 15-h duration on 20 March 2005. Initial tagging efforts on 7 March through 20 March occurred in the lower James River near Ragged Island (Figure 3). However, few fish were captured at these sites. Operations were moved upstream on 21 March to Hog Island near the Surry

Nuclear Power Plant water discharge canal, approximately 37 km upstream of the Ragged Island haul location (Figure 4).

Fish captured in the gill net were gently removed from meshes and temporarily transferred to a holding pen before being placed into a ship-board tank with circulating seawater. Fish captured by haul seine were dip-netted directly from the holding pocket into the ship-board tank with the exception of 21 March, where fish were first transferred to a holding pen and then placed into the ship-board tank. Only healthy and vigorously swimming fish were selected from both gears. Prior to tagging, scales were removed from just below and posterior to the dorsal fin of all specimens for subsequent aging and determination of spawning history (Cating 1953). Acoustic tags were placed in the esophagus and gently pressed into the stomach using a slender wooden probe. In addition, a yellow conventional dart tag bearing the identity of the tagging program and indicating a monetary reward was inserted into the dorsal musculature just below the dorsal-fin base, although it is important to note that there is currently a ban on the harvest of American shad in the James River (ASMFC 1999). Tagging for each fish took place in two minutes or less. Fish were generally held in the tank prior to release to assess condition after tagging with the exception of the last tagging event on 21 March 2005, when fish were released immediately due to the large number in the holding pen ($n > 93$). Field notes describing the condition at release were recorded for each fish. Temperature, salinity, conductivity, dissolved oxygen, and pH was recorded at the release site with an YSI® water column profiler.

Passive Acoustic Monitoring Equipment - Passive acoustic equipment used in this study (Lotek Wireless, Inc., Toronto, Canada) included wireless hydrophones (WHS_1200) operating at frequencies of 149-151 MHz, receivers (SRX400) with W32CT firmware, and acoustic tags (CAFT11_2) with a battery life of approximately 100 days. Tags were 40 mm long, 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 emitted a code every five seconds unique to each individual tag, allowing up to 210 individuals to be detected and decoded on a single frequency.

Buoys and receivers were tested and installed on 4-8 February 2005 prior to the release of tagged fish. The period of deployment of hydrophones was 4 February through 27 May 2005 spanning 113 days. Hydrophones were attached to a braided metal cable and anchored in the desired position and depth within the river. The whole assembly was held upright in the water column by a buoy with the data transmitting antenna passing through the center.

Passive listening hydrophone arrays were deployed at 9 monitoring stations within the James River at variable distances apart (Figure 2). Based on channel morphology and width, the number of hydrophones at each station ranged from four hydrophones monitored by two receivers (at Kingsmill and Hog Island), two hydrophones and one receiver (at Upper Brandon Plantation and Sandy Point), or one hydrophone and one receiver (at the Richmond Deepwater Terminal, the entrance to the Chickahominy River, the entrance to the Appomattox River, Shirley Plantation, and the Virginia Power Boat Association). Range tests were conducted by tethering the battery portion of an acoustic tag to a string and placing it in the water at various locations

around the hydrophone by boat. All stations had an apparent minimum tag detection range of at least 500 meters upstream and downstream of the hydrophone. Signal detection in shallow water bordering the channel was weak or absent at some stations, but could be assumed negligible if shad migrate upstream following the river channel (as described by Leggett 1976; Katz 1986). We assumed that all fish had an equal chance of being detected and that all receivers (except those noted below) were equally efficient at decoding signals during the study.

Continuous records of acoustic tag detections were obtained using land-based receivers installed on private piers or constructed platforms. Receivers were maintained and data detection files were downloaded to a laptop computer from each receiver bi-weekly until 3 May 2005 when data were downloaded weekly. Debris from a storm event on 29 March caused the hydrophone at the Virginia Power Boat Association to be dislodged and transported 1 km downstream. This resulted in the loss of 17 days of data. Operation was restored on 14 April. Data sorting identified a number of short time periods when hydrophones at Hog Island, Upper Brandon Plantation, Sandy Point, and the Virginia Power Boat Association were not operating properly. With the exception of the hydrophone at the Virginia Power Boat Association, all sites with malfunctions were sites with two hydrophones. This usually resulted in a fish being detected only at one hydrophone.

Active tracking - On 20-21 April and 5 May 2005 active tracking was performed in the upper region of the study area using a Lotek LHP model operating in the 20-80 kHz detection range. Searches were conducted from Shirley Plantation to the fall line to

investigate movements of fish between hydrophone arrays, and to verify the presence of fish above Richmond Deepwater Terminal at the fall line. On 26 April, active tracking extended from Upper Brandon Plantation to Shirley Plantation. Listening with the directional hydrophone was accomplished every one to three kilometers. When a fish was detected, the time of detection, location (rkm), and tag identification number were recorded.

Data Analysis - All detection data were imported into Microsoft Excel and into MATLAB using the SRX toolbox (Tom Grothues 2003, Rutgers University, personal communication) to identify periods of detection, and determine the validity of the codes.

The tendency of fish to migrate upstream or downstream in relation to holding time in the holding pen during tagging on 21 March was tested for significance with a 2x8 contingency table analysis using the chi-square statistic. The null hypothesis was that there was no difference in the tendency to migrate upstream or downstream versus the duration of holding time prior to release, i.e., fish released later were equally as likely to continue with the upstream migration. Similarly, the hour of release in relation to days until abandonment was tested for significance with a 4x4 contingency table analysis using the chi-square statistic among fish that did abandon the migration. The null hypothesis was that the hour of release had no significant effect on the number of days until abandonment. Days until abandonment were divided into the day of release, the day after release, 2-10 days after release, and greater than 10 days after release. Results from age and spawning history analysis of scales were used in two separate 2x2 contingency table analyses using the chi-square statistic with the applied Yates correction for

continuity (Zar 1999). The null hypotheses were that there was no difference in the tendency to migrate upstream between fish aged five and under and six and older, and between fish that were virgins or repeat spawners.

Movements upstream during the pre-spawning migration and movements downstream on the emigration were investigated with the Rayleigh test statistic following the analysis of Smith and Smith (1997) to determine if there was a significant relationship between migratory movements upstream or downstream with time of day, or tidal cycle. The null hypotheses were that movements upstream (or on the emigration) were random with respect to the time of day or tidal cycle. Time of day was expressed as a phase angle ranging from 0° at 12:00am, 180° at 12:00pm, and 360° at 12:00am (a full period of 24 hours). Tidal cycle was expressed as a phase angle ranging from 0° at high tide, 180° at low tide, and 360° at the next subsequent high tide. Tidal stage and duration was determined using the Tides and Currents version 2.0 program. Detections from all individuals over the entire study period were grouped for the analyses and analyzed by the software program Oriana version 2.02. Movements could only be inferred as upstream or downstream when a fish was detected at the next hydrophone array. Thus, the Rayleigh test was not applied to fish arriving at Richmond Deepwater Terminal, because they could not be detected upstream after passing the hydrophone there. However, movements downstream past Hog Island were interpreted as movements past the station, as it is reasonable to assume fish that had been tracked downriver on the emigration passed this site and exited the river.

River discharge data was obtained from the U.S Geological Survey (USGS) monitoring station on the James River near Richmond (USGS gauge 02037500,

provisional data, rkm 164). Mean daily discharge data for the study period in 2005 was displayed against the 25th and 75th percentiles of historic river flow, calculated as the mean of daily discharge values from 1934 until 2004. The study period was defined as the time between the release of the first acoustically tagged shad on 7 March until the last detection of an acoustically tagged shad on 19 May. River flow was considered normal if it fell between the 25th and 75th percentiles, above normal if it was above the 75th percentile and below normal if it was below the 25th percentile.

After all detection data were compiled for each fish, day after release (x-axis) was graphed against each hydrophone detection (y-axis) to generate a graphical depiction of the migratory pathway of each individual (Appendix 1). These movement plots were visually inspected for patterns and assigned to groups based on gross similarities such as residence in the same river reach, cessation of detection, etc. (see Results for final patterns and assignments). Although the primary objective of this analysis was to place fish into groups exhibiting similar gross movement patterns, fine-scale differences are still evident within and among different fish.

We used the following definitions in our analysis. Fallback behavior was defined as procession downstream after tagging, where the first detection of a tagged individual was downstream from the tagging site. Residence time on the spawning grounds in the James River was defined as the time between the first and last detection at Upper Brandon Plantation. This definition was based on the observation that fish committed to an apparent spawning residency period all resided above this location, with the exception of fish that may have spawned in the Chickahominy River. We estimated residence times only for those fish that were detected at Upper Brandon Plantation on the emigration,

presumably migrating seaward after the spawning run. Abandonment of the migration was defined as detection only at Hog Island, and/or absence of detection after tagging. Thus, fish that were released above Hog Island and were only detected there (or not detected at all) were assumed to have abandoned the migration. In addition, fish that were released below Hog Island and were not detected farther upstream were also assumed to have abandoned the migration. Transit times were defined as the time elapsed between the last detection at the lowermost hydrophone station (Hog Island/Kingsmill) and the first detection at the uppermost station reached. Similarly, exit transit times were defined as the time elapsed from the last detection at the uppermost hydrophone reached to the last detection at Hog Island. Transit times were only calculated for fish that exhibited residence times. Upriver minimum rates of travel in units of km/hr were calculated as the distance traveled between the lowermost monitoring stations at Hog Island to the uppermost station reached divided by the upriver transit time. Exit minimum rates of travel were calculated as the distance traveled between the uppermost station of last detection at the onset of the emigration and the last detection at Hog Island divided by exit transit time.

Results

Ninety eight American shad were tagged and released during seven sampling events (Table 1, Appendix 1). No fish were captured on three dates (14, 18, and 19 March 2005). Five fish were released during tagging events on 7-20 March 2005 downriver of the hydrophone array at Kingsmill/Hog Island (Table 1, Figure 3). Surface water temperatures on these days ranged from 6.2 (3/7/05) to 8.0 °C (3/18/05). One of

these five individuals (Fish 13) was never detected and is assumed to have abandoned the migration. The remaining four tagged fish were detected farther upstream, exhibiting minimum rates of travel of 4-7 days ($\bar{x} = 5.3$, $SD = 1.5$) to the first upstream hydrophone array at Hog Island. Of these four American shad, one abandoned the migration after reaching Hog Island (Fish 14), one ceased detection at Upper Brandon Plantation (Fish 3), and the remaining two proceeded upstream to later be detected at the Richmond Deepwater Terminal (RDT) (Fish 12, 15).

Hog Island Releases - On 21 March 2005, a haul seine was conducted just upriver of the Kingsmill/Hog Island hydrophone array in the thermal plume of the Surry Nuclear Power Plant (Table 1, Figure 4). The surface water temperature at the release site near the discharge was 14.7 °C while the ambient river temperature outside of the plume was 11.3 °C. Ninety-three American shad were tagged and released near the thermal discharge (Figure 4) over a period of four hours. Two fish (Fish 132, 114) were not detected again while the remaining 91 fish were all eventually detected at either the Kingsmill/Hog Island hydrophone array or at monitoring stations upstream. A chi-squared contingency table analysis showed no significant difference in the tendency of fish to proceed upstream or downstream versus the time released ($X^2 = 13.559$, $df = 7$, $p > 0.05$).

Of the 93 fish released, 86 (95%) exhibited fall back behavior (first detected at the Kingsmill/Hog Island transect). Twenty six of these 86 individuals (30%) fell back on the day of release, 52 (61%) fell back on the day after release, and 8 (9%) fell back within 2-8 days after release. Most of the fish that fell back ($n = 45$ or ~52%) did not resume the upstream migration and abandoned the migration. A chi-squared contingency table

analysis showed no significant relationship between the hour of release and the number of days to abandonment ($X^2 = 11.939$, $df = 9$, $p > 0.05$, i.e., fish tagged later were no more likely to abandon the migration on an earlier date than fish released at other times). One of the fish that abandoned the migration (Fish 92) was detected by collaborators monitoring releases of striped bass and summer flounder in Egg Harbor, New Jersey on 25 April 2005 (Tom Grothues, Rutgers University, personal communication). The fish was tagged on 21 March and was last detected at Hog Island on 3 April (~22 days travel to New Jersey). Five of the 93 fish released on 21 March did not fall back (Fish 35, 74, 82, 93, 130). The mean number of days until detection at Sandy Point for these individuals was 7.2 days (SD = 2.5).

River Discharge - Mean daily discharge remained above the 25th percentile during the entire study period, indicating no abnormally low flow conditions in spring 2005 (Figure 8). Mean daily discharge exceeded the 75th percentile on 19 of the 74 days (25.7%) of the study period, primarily during a large rain event on 29 March and 2 April causing high flows from 29 March to 9 April (Figure 8). These high flow conditions on 29 March displaced the hydrophone at the Virginia Power Boat Association downstream until it was recovered on 14 April.

Upstream Migratory Movements and Patterns - Half (49 of 98) of all tagged individuals proceeded upstream to the Chickahominy River or farther upriver past Sandy Point. Detection histories of these individuals were classified into 8 migratory patterns (Table 2, Appendix 2). Fish that were detected at the Chickahominy River station and

subsequently exited the system at Hog Island /Kingsmill were assigned as Pattern A (n=4). Three of these individuals (Fish 34, 195, 130) may have resided in the Chickahominy River for 20-29 days since they were not detected farther upstream. Two fish exhibited erratic upstream and downstream movements with no evidence of site-specific residence (Pattern B). Pattern C (n=2) included individuals that resided in the vicinity of Upper Brandon Plantation. Fish 120 was not detected upstream of Upper Brandon Plantation and resided there for approximately 16 days. Fish 131 migrated upstream briefly to Shirley Plantation at the end of a 31-day residence before exiting the river. Pattern D (n=5) represents individuals that resided for all or most of their time at Shirley Plantation. Pattern E (n=26) includes individuals that resided at or near RDT. The residency period at RDT ranged from 1-44 days ($\bar{x} = 16$, $SD = 11.6$). Pattern F (n=3 individuals) describes movements of fish that abruptly ceased detection on the upstream migration. No downstream movement was evident for any of these individuals before detection ceased. Fish 37 was detected by active tracking in the same location (ten kilometers below RDT) on 20 April, 26 April and 5 May. Its carcass or ejected tag may have settled there. Pattern G (n=3) was assigned to individuals that ceased detection during the residency period. Fish 32 appeared to move between Shirley Plantation and RDT before detection ceased. Fish 143 was detected 12 kilometers upstream of Upper Brandon Plantation on 21 April, 15 days after it was last detected at the Upper Brandon Plantation hydrophone array. Fish 145 resided for >20 days at RDT. Fish 145 was detected 1-2 km below the fall line by active tracking above RDT on 20 April and 5 May 2005 and was last detected at RDT on 11 May. Pattern H (n=4) describes fish that were

not detected during the emigration. All of these individuals reached Sandy Point on the emigration, but were not detected exiting the system at Hog Island.

Five fish were detected near the mouth of the Appomattox River but probably did not reside in the river. Four of these individuals (Fish 35, 43, 121, 193) were detected over 1 – 3 days, and one fish (Fish 101) was detected over ten consecutive days. This individual was detected while emigrating from the upper James River after residing for approximately 25 days farther upstream, suggesting that it did not enter the Appomattox River to spawn.

Active tracking was conducted on 20, 21, and 26 April and 5 May from just below Upper Brandon (rkm 96) to the fall zone at the 14th Street Bridge in Richmond (rkm 158). The upriver area extending from rkm 158 to Bosher's Dam is largely inaccessible by boat and was not searched. A total of 27 fish were detected by active tracking. Thirteen fish were located above RDT and below the Virginia Power Boat Association (Fish 12, 15, 39, 42, 45, 72, 82, 93, 101, 133, 145, 150, 156). One fish (male, Fish 150) was observed within the rocky fall zone at rkm 159 on 28 April by electro-fishing (Alan Weaver, VDGIF, personal communication). The fish was netted, examined, hand-held for photography, placed into an on-board tank with circulating river water, and then released with no apparent effects. On 6 May, it was detected proceeding back downstream past RDT, and exited the river past Hog Island on 16 May.

Usage of Bosher's Dam Fishway - No fish were detected at the Virginia Power Boat Association upstream of Bosher's Dam. A lapse in hydrophone coverage from 29 March to 14 April resulted in a gap of seventeen detection days. During this malfunction period,

23 fish were detected at RDT indicating that these individuals were potentially able to ascend the fishway and pass undetected while the hydrophone was inoperable. Eleven fish (Fish 15, 42, 44, 45, 72, 87, 122, 138, 157, 159, 183) reached RDT after the station was repaired. Six of these individuals (Fish 44, 72, 87, 138, 159, 183) were detected at RDT for a period of two-three days or less (Patterns B and E), and five fish were detected over more than three days (Pattern E). Thus, five fish were candidates to use the fishway while the gear was functioning but did not.

Movements in Relation to Time of Day and Tidal Cycle - Results of the Rayleigh test (Table 3) showed no significant relationship at any hydrophone station between migratory movements upstream or on the emigration in relation to time of day ($p > 0.05$). In contrast, a highly significant relationship between migratory movements and tidal cycle on the upstream migration was found at all stations ($p < 0.01$). The mean angle (μ) at all stations ranged from 245.54° - 304.18° indicating fish were actively moving upstream primarily on a flood tide. During the emigration, a highly significant relationship between downstream movements and tidal cycle was also found ($p < 0.01$) with the exception of the RDT and Sandy Point stations ($p > 0.05$). Mean angles (μ) ranged from 110.59° - 141.03° indicating fish generally moved downstream during an ebb tide.

Residence Time, Transit Time, and Minimum Rate of Travel - Residence times within the main stem of the James River averaged 28.8 d ($n= 39$ individuals, $SD = 8.2$ d, Appendix 3). Figure 6 depicts the mean residence time for individuals grouped by migratory

pattern. Upriver minimum rates of travel for these fish were highly variable and ranged from 0.08-0.90 km/hr (\bar{x} =0.35, SD=0.19, n=39, Appendix 3). Transit times on the upriver migration ranged from 3.4-37.6 days (\bar{x} =13.8, SD=7.6, n=39, Appendix 3). Figure 7 depicts the average upriver minimum rates of travel and transit times for individuals grouped by migratory pattern. Exit minimum rates of travel were faster and ranged from 0.28-3.17 km/hr (\bar{x} =1.71, SD=0.91, n=35, Appendix 3). Transit times during the emigration ranged from 0.79-14.0 days (\bar{x} =3.7, SD=3.4, n=35, Appendix 3). Figure 8 depicts the average exit minimum rates of travel and exit transit times in relation to migratory pattern.

Age and Spawning History - Age and spawning history of 91 tagged individuals is listed in Appendix 1. A chi-squared contingency table analysis to evaluate if the tendency to migrate upstream differed between individuals of ages five and under and six and older was not significant ($\chi^2 = 1.855$, df = 1, $p > 0.05$). Similarly, a chi-squared contingency table analysis of whether the tendency to migrate upstream differed between first time spawners or repeat spawners was not significant ($\chi^2 = 1.413$, df = 1, $p > 0.05$).

Discussion

The timing of the spawning run of American shad is largely influenced by water temperature (Leggett and Whitney 1972; Quinn and Adams 1996). Mature shad appear in the lower James River when surface temperatures reach 4 °C, and peak migrations occur between 8-14 °C (Olney et al. 2005). As a result of the unusually cold spring in 2005, river temperatures were low and our initial efforts to capture fish for tagging

yielded few fish. Large numbers of shad were not captured until sampling occurred in the warm-water plume of the Surry Nuclear Power Plant.

A large number (n= 86, 95%) of the tagged cohort released on 21 March exhibited fall-back behavior and many of these individuals (n=45) abandoned the migration. These behaviors have been described in almost all telemetry studies of the species, and are assumed to be induced primarily by capture and handling stress (Leggett 1976; Barry and Kynard 1986; Beasley and Hightower 2000; Hightower and Sparks 2003; Bailey et al. 2004; Olney et al. 2006). In the James River study, there was no statistically significant relationship between the time (days) to fallback and the hour of tagging on 21 March, suggesting confinement (up to 4 hrs) did not result in increased fall-back behavior. Similarly, statistical analysis of abandonment data showed that there was no significant relationship between holding time and the tendency to migrate upstream or abandon the migration. If holding time did influence migratory behavior negatively, fish released later after longer confinement would have been expected to be more likely to abandon the migration. Among the individuals that did abandon the migration, some did not do so for up to 19 days while remaining within the brackish waters of the warm-water plume of the power plant. It is not likely these fish were spawning since eggs and larvae are spawned in freshwater (Leim 1924; Massmann 1952; Bilkovic et al. 2002a; Bilkovic et al. 2002b). These fish were likely attracted to the warm waters of the plume because of the colder than average spring temperatures.

Some of the observed abandonment may be due to the presence of non-native fish in our sample. One fish that abandoned the migration after tagging on 21 March was detected on 24 April in Egg Harbor, New Jersey (Fish 92; Tom Grothues, Rutgers

University, personal communication). This behavior could represent an exploratory foray within the lower James River by a non-native individual. Walburg and Sykes (1957) reported that among 374 shad tagged near the James River mouth, 19 were re-captured in other Virginia tributaries, as well as within the Hudson and Connecticut Rivers. Olney et al. (2003) also reported strays at the river mouth based on river-specific OTC hatchery marks.

We found no significant relationship between age or spawning history and the tendency to continue with the upstream migration. Hightower and Sparks (2003) found that shad that migrated upstream after tagging were typically repeat spawners and ages 6-7, whereas American shad that did not resume the migration were first time spawners and ages 5-6. However, our results are similar to those of Olney et al. (2006) where abandonment was observed in either sex, in all classes, and in both virgin and repeat spawners.

River discharge was relatively normal in comparison to historic flow data. High flow conditions were not sufficient to overcome the upstream progress of migrating shad as individuals were detected reaching Richmond Deepwater Terminal during high flow periods. Similarly individuals downstream were detected moving to upstream hydrophones during high flow conditions. Katz (1986) documented acoustically tagged shad being flushed out of the Holyoke Pool in the Connecticut River during extremely high river flows of $2760 \text{ m}^3/\text{s}^{-1}$. Peak river flow in the current study was $1175 \text{ m}^3/\text{s}^{-1}$ which is less than half the value cited by Katz (1986) for pushing shad out of the system. Thus it is not likely that river flows impeded the upstream migration or prevented shad from migrating through the fall line region to the base of Boshers' Dam. Weaver et al.

(2003) found that increasing shad passage at Boshers' Dam was correlated with increasing daily mean discharge, with peak passage during three years of monitoring occurring at approximately $225 \text{ m}^3/\text{s}^{-1}$. River flow was above this value for over 70% of the current study period.

We found a significant relationship between upstream and downstream movements and tidal cycle along the migratory route. Upstream movements were strongly associated with flooding tides ($p < 0.01$); downstream movements were strongly associated with ebbing tides ($p < 0.01$). Our findings are not consistent with previous studies of American shad that characterized movements in relation to tides in the transition zone from saltwater to freshwater of the Connecticut River (Dodson et al. 1972; Dodson and Leggett 1973; Dodson and Leggett 1974). Dodson et al. (1972) described meandering behavior that they characterized as unrelated to tidal cycle within the estuarine portion of the river, with extensive meandering occurring near the salt wedge. Once shad entered freshwater and the upstream migration was initiated, there was no apparent relationship with tidal cycle, with migration continuous during periods of reverse and zero flow. In contrast, Dodson and Leggett (1973) found that shad homing to the Connecticut River from Long Island Sound tended to orient into the reversing tidal current, with greater swimming velocities during ebb tide conditions resulting in a net westerly displacement towards the mouth of the river. Leggett (1976) provided some active tracking data of shad within the freshwater portion of the Connecticut River. Leggett (1976) concluded that shad used a rheotaxic response to migrate upstream, with swim speeds consistently higher when shad were oriented upriver against the current. However, he also noted exceptions to this behavior where shad appeared able to orient

upriver during complete reversals of the rheotaxis cue. There appears to be no consensus on how shad utilize tides during the upstream migration. In our study, individual shad were often detected at a hydrophone station for one to several hours before initiating an upstream movement to the next hydrophone station upstream. This result suggests that shad were holding position within the river against an ebbing tide (otherwise they would be carried downstream past the hydrophone) until the tide switched and the shad migrated upstream with the flooding tide.

There was no relationship of detected movements with tidal cycle at the RDT and Sandy Point hydrophones. The RDT is within the primary residence area of most American shad in our study (n=31; Pattern E, G, and H) and within 9 km of the non-tidal fall line. Many fish moved upstream and downstream in this area without regard to tidal cycle, suggesting behavior on the spawning grounds may differ from movements on the upstream and downstream migrations. The Sandy Point hydrophones were within the upper limits of saltwater intrusion where meandering behavior might be expected. Dodson et al. (1972) reported meandering of tagged American shad at the saltwater-freshwater interface and suggested that this behavior was related to osmotic acclimation of fish prior to freshwater entry.

There was no significant relationship between movements and time of day during the upstream migration or on the emigration. Dodson and Leggett (1973) found that countercurrent orientation was observed during daylight and darkness when shad were homing to Long Island Sound. While we did not observe countercurrent migration, our results are similar to those of Dodson and Leggett (1973) in that movements were related primarily to tidal cycle. Bailey et al. (2004) found that movements greater than 0.1 km/hr

were more frequent at night than during the day within the freshwater portion of the Savannah River, but noted that shad will seek lower velocity water at night than during the day (Theiss 1997, cited in Bailey et al. 2004). Barry and Kynard (1986) also noted tagged American shad moving out of the fast water of the Holyoke Dam tailrace at night and retreating to quieter water. Within the James River, passage of American shad through Boshers' Dam fishway was more frequent during the day than at night (Weaver et al. 2003).

Telemetry data suggest that the Chickahominy and Appomattox Rivers do not currently have large runs of American shad, a finding supported by independent electrofishing monitoring efforts (Alan Weaver, VDGIF, personal communication). Some individuals displayed a detection history that suggests possible residence within the Chickahominy River although their presence in upriver reaches was not confirmed by active tracking. In a pilot telemetry study in 2004, one American shad was detected within the upper reaches of the Chickahominy River by active tracking, where it eventually became stationary for a period of weeks and was assumed to have died or expelled its tag. In 2000, approximately one million hatchery-marked larvae were stocked into the Chickahominy (Tom Gunter, VDGIF, personal communication), and these releases may be the source of recent returns of mature fish. Historical data suggest shad runs within the Appomattox were small primarily due to pollution from the City of Petersburg (Stevenson 1896; Massmann 1952). Within the Chickahominy River, spawning runs were still large in the 1950's after the installation of Walker's Dam at Lanexa in 1943, suggesting most important spawning habitat is below the dam

(Massmann 1952). More investigation is needed to determine what factors are influencing the slow recovery of shad runs in these two tributaries.

Three fish exhibited rapid upstream and downstream movements before exiting the river after a period of residency. Olney et al. (2006) documented exploratory migrations into the adjacent Pamunkey River after a residence period within the Mattaponi River, although a rapid initial downstream movement was not reported. Other telemetry studies with extensive river coverage (Beasley and Hightower 2000; Hightower and Sparks 2002; Bailey et al. 2005) have not reported this behavior, although these were primarily semelparous populations. More investigation is needed to fully characterize post-spawning movements. Two individuals (Pattern B) moved upstream and downstream with no apparent site-specific residency. Altered migratory behavior induced by tagging may be a reason for these unusual movement patterns.

American shad use the fishway facility at Boshers' Dam and annual passage estimates have been increasing (Weaver et al. 2003). Detection of fish passage in our study was compromised due to a 17-d equipment failure of the hydrophone above Boshers' Dam. In our sample, only five individuals had sufficient opportunity (based on their late arrival at the RDT) to use the fishway while our hydrophone was operable. We expected 20-50% of our tagged cohort to migrate through the fishway based on recent hatchery prevalence data (Olney and Delano 2006) as only hatchery fish are stocked upstream of the dam. No fish were detected above the dam although there is a strong possibility some fish migrated through the fishway without detection. Passage efficiency has been investigated using telemetry within some other river systems. Barry and Kynard (1986) detected 50% of radio-tagged fish passing through the fish lifts at Holyoke Dam in

the Connecticut River and suggested many fish were repelled by turbulent water at the fish lift entrance. Sprankle (2005) documented low passage efficiency in the Merrimack River at the Boott Station fish lift, with 6% of radio-tagged fish successfully migrating upstream.

Residence times do not appear to vary appreciably with the distance migrated. Average residence times were similar among migratory patterns (B, C, D, E, H) ranging from 23.8 days to 31.5 days. The mean residence time of spawning American shad on the James River (28.8 d) is similar to an estimate of 32.4 days determined using acoustic telemetry in the York River system (Olney et al. 2006). Beasley and Hightower (2000) observed residency periods ranging from 13.8 – 69.7 days within the Neuse River. Average values of upstream transit times and minimum rates of travel were highly variable in the current study and no relationship among migratory patterns was evident due to the low sample sizes and high standard deviations among samples. Total average upstream transit times were 13.8 days (SD = 7.6) and upstream minimum rates of travel were 0.35 km/day (SD = 0.19). These values are similar to those values reported by Hightower and Sparks (2003) and Beasley and Hightower (2000) although we observed greater variability. In general, fish emigrating from points farther upstream took longer to emigrate than fish that resided downstream at Shirley Plantation or Upper Brandon. The average exit transit time of 3.7 days (SD = 3.4) and exit minimum rate of travel of 1.71 km/hr (SD = 0.91) were considerably faster than upstream estimates. Olney et al. (2006) reported similar patterns of exit behavior in the York River.

Results of this study identified three areas of residence within the main-stem James River at RDT, Shirley Plantation, and Upper Brandon Plantation. A majority of

the tagged cohort (n=31; Patterns E, G, and H) resided in the vicinity of RDT, extending to the fall line (9 km upstream). Thirteen of these fish (including one detected by VDGIF) were identified above RDT up to the fall line by active tracking. Five fish resided in the vicinity of Shirley Plantation but below RDT (Pattern D), a region which extends approximately 24 km (excluding cutoffs). None of these individuals were detected at RDT, but two were detected three kilometers below the RDT hydrophone by active tracking on separate dates. Three cutoffs exist within this reach, and one individual (Fish 122) was detected at the mouth of Dutch Gap Cutoff. However, the three cutoffs were not actively searched and some individuals may have migrated into these areas. Only two individuals (Pattern C) resided in the vicinity of Upper Brandon Plantation. Several small tributaries empty into this river reach including Ward's Creek, Herring Creek, Queens Creek, and Powell's Creek. In March 2006, Fish 38 (Pattern D) from the 2005 study was captured within Wards Creek, a small tributary of the James approximately 3 km upstream of Upper Brandon Plantation, suggesting some of these tributaries may support runs of shad, although the extent of these runs is unknown.

No habitat suitability indices have been developed for anadromous species in the James River system. Optimal ranges of habitat variables have been assumed to be similar between different river systems for American shad eggs and larvae (Bilkovic et al. 2002a). Within the Mattaponi and Pamunkey rivers, American shad eggs were collected primarily in reaches with 60% or greater forested shoreline but no eggs were collected in river reaches with high erosion (35-45%). Similarly, reaches with greater than 40% agricultural land use showed declines in egg abundance (Bilkovic et al. 2002a). All three of the areas of residence in this study, while they may contain extensive urbanization and

industrialization, appear to contain some suitable reaches as identified by shoreline and land use characteristics identified by Bilkovic et al. (2002a).

Our identification of residence areas at RDT, Upper Brandon, and Shirley are not consistent with earlier assessments. The construction of Boshers Dam in 1823 (Weaver et al. 2003) extirpated the upstream shad runs. Massmann (1952) suggested that important spawning areas of American shad did not extend into areas of the river above Hopewell. The extension of runs into areas above Hopewell evidenced by current telemetry data may be a result of hatchery introductions. More investigation is needed to determine if these residence areas are now composed of wild and hatchery fish, a pattern that could result in introgression of the two stocks. Recent studies using micro-satellite markers (Brown et al. 2000) appear promising in their ability to distinguish native James River fish and hatchery fish of Pamunkey River origin and may allow identification of disjunct residence areas or different migratory behavior patterns among hatchery and wild shad.

Ten fish (~20% of 49 upstream migrants) migrated upstream but did not exit the system. Their disappearance is attributed to natural or fishing mortality, regurgitation of the tag or a combination of these factors. These individuals were last detected while moving up-river (Pattern F, n= 3), during their residency period (Pattern G, n= 3) or while emigrating (Pattern H, n= 4). We observed these individuals at multiple stations during the study. Repeat spawning in the James River stock is frequently observed (Olney and Delano 2006) and most of our sample survived the spawning migration to exit the river. American shad in the James River reach a maximum age of 11 years (Olney and Delano 2006) and their scales often bear erosion marks indicative of previous spawns

(using the methods of Cating 1953). The degree of semelparity is not known, and carcasses of spent fish have not been observed in the James River (Garman 1992). Semelparity has been observed in the Delaware River (Chittenden 1975) and may be a characteristic of some mid-Atlantic stocks that undergo extensive migrations. An active catch and release recreational fishery exists in the James River. If the fish that disappeared in our sample were landed, they were not reported. There have been no studies of hooking mortality of James River shad. Commercial fisheries exist in the James River for striped bass (staked gill net, pound net, haul seine), catfish (pound net, trot-line, pots) and river herring (dip nets). American shad are a known bycatch of these fisheries, but no tagged individuals were reported. Studies that have documented death after tagging (Bailey et al. 2004) have noted that it usually occurred quickly (within hours of tagging). Regurgitation has been noted previously in telemetry studies (Bailey et al. 2004; Acolas 2004). Acolas et al. (2004) reported that acoustically tagged large female allis shad (*Alosa alosa*) may be more likely to regurgitate tags than smaller male shad. In our sample, 8 of the ten lost fish were female and 2 were male.

American shad stocks in the James River have not recovered from years of overfishing and habitat loss. Additional information is needed to address the efficiency of Boshers' Dam fishway, usage of upstream habitats above the fall line, and utilization of cutoffs during the upstream migration. A detailed account of adult spawning locations, preferences, and larval and juvenile rearing habitat may aid in understanding the factors that are influencing the slow recovery.

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Table 1. Summary of sampling dates, locations, commercial gear used to capture and tag American shad (*Alosa sapidissima*), number released, and surface water temperature within the James River, Virginia, spring 2005.

Date	Location	Gear	Species	# Released	Surface water Temp. °C at collection site
3/7/05	Near James River Bridge (above bridge)	Haul seine	<i>A. sapidissima</i>	1	6.2
3/7/05	Near James River Bridge (below bridge)	Haul seine	<i>No shad captured</i>	0	6.2
3/14/05	Near James River Bridge	Haul seine	<i>No shad captured</i>	0	6.6
3/18/05	Near James River Bridge	Gill-net	<i>No shad captured</i>	0	8.0
3/19/05	Near James River Bridge	Haul seine	<i>No shad captured</i>	0	6.7
3/20/05	Near James River Bridge	Gill-net	<i>A. sapidissima</i>	4	7.5
3/21/05	Hog Island	Haul seine	<i>A. sapidissima</i>	93	14.7
TOTAL:				98	Range 6.2 - 14.7

Table 2: Migratory patterns of the 49 acoustically tagged American shad (*Alosa sapidissima*) that proceeded upstream and were detected at the Sandy Point or Chickahominy hydrophones.

Migratory Pattern	Fish/Tag number
A: Only detected at the Chickahominy River	34,62,130,195
B: Rapid upstream and downstream movements with no evidence of site specific residence	72,87
C: Resided primarily at Upper Brandon Plantation	120,131
D: Resided Primarily at Shirley Plantation	38,53,121,193,204
E: Resided primarily at Richmond Deepwater Terminal	15, 25,33,36,39,42,43,44,45,46,47,74,82,93,101,111,116,122,133,138,150,152,156,159 157,183
F: Abruptly ceased detection on the upstream migration	3,37,110
G: Ceased detection after a residency period of 5-35 days at the last station reached	32,143,145
H: Ceased detection on the emigration	12,20,35,170

Table 3: Summary of upstream and downstream movements of American shad (*Alosa sapidissima*) in relation to time of day and tidal cycle. The length of the mean vector is denoted as r (a value of zero indicates a random distribution, 1 indicates all values converging on one value), μ is the mean angle, p is the probability, and n is the number of movements.

TIME OF DAY:

<u>Upstream</u>	<u>HI</u>	<u>SP</u>	<u>UB</u>	<u>SHI</u>	<u>---</u>
r	0.138	0.043	0.167	0.219	
μ	4:36 AM	12:25 PM	8:52 AM	9:31 AM	
p	0.291	0.871	0.234	0.122	
n	65	74	52	44	
<u>Downstream</u>	<u>HI</u>	<u>SP</u>	<u>UB</u>	<u>SHI</u>	<u>RDT</u>
r	0.175	0.044	0.043	0.214	0.267
μ	3:55 AM	12:38 PM	11:54 AM	9:15 AM	6:42AM
p	0.061	0.933	0.074	0.185	0.102
n	91	36	40	37	32

TIDAL CYCLE:

<u>Upstream</u>	<u>HI</u>	<u>SP</u>	<u>UB</u>	<u>SHI</u>	<u>---</u>
r	0.397	0.504	0.517	0.379	
μ	283.57°	304.18°	299.57°	245.54°	
p	<0.001	<0.001	<0.001	0.002	
n	65	74	52	44	
<u>Downstream</u>	<u>HI</u>	<u>SP</u>	<u>UB</u>	<u>SHI</u>	<u>RDT</u>
r	0.476	0.265	0.449	0.388	0.069
μ	141.03°	164.51°	122.68°	110.59°	77.73°
p	<0.001	0.079	<0.001	0.003	0.862
n	91	36	40	37	32

Figure 1: Atlantic Coast and Virginia American shad (*Alosa sapidissima*) landings from 1950 until the 1994 Virginia moratorium.

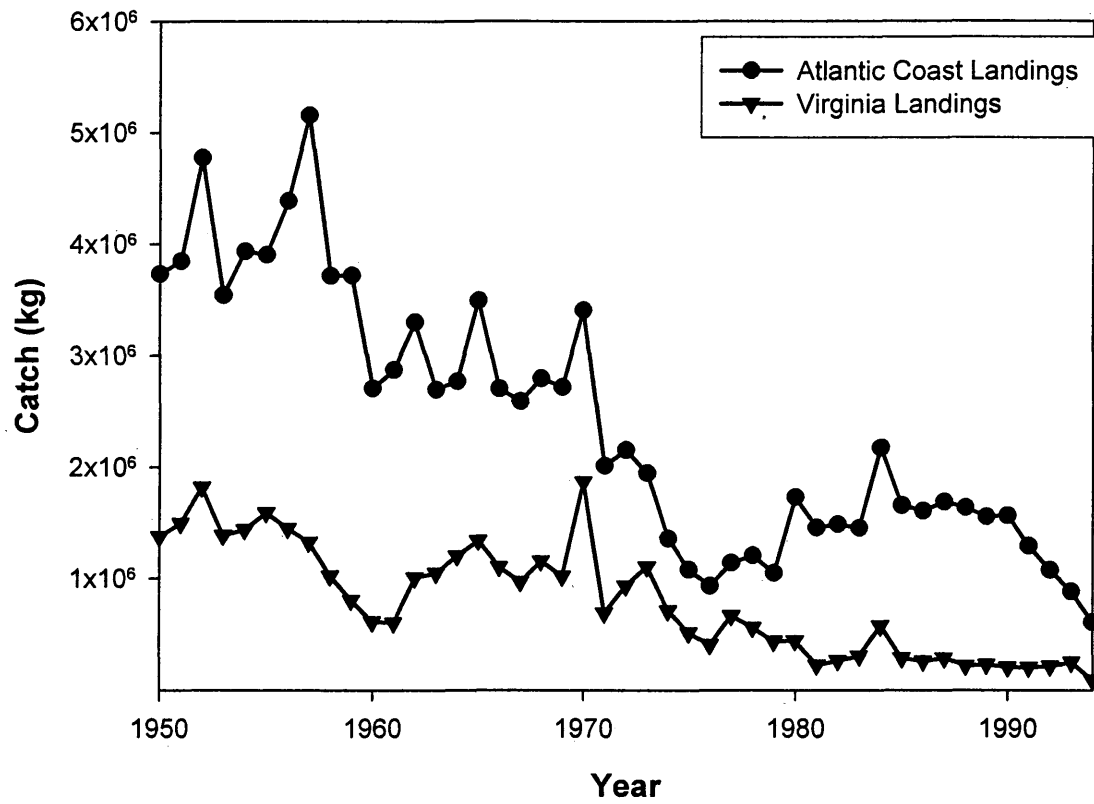


Figure 2: Map of the James River indicating locations of passive hydrophone monitoring stations and distances between hydrophone arrays.

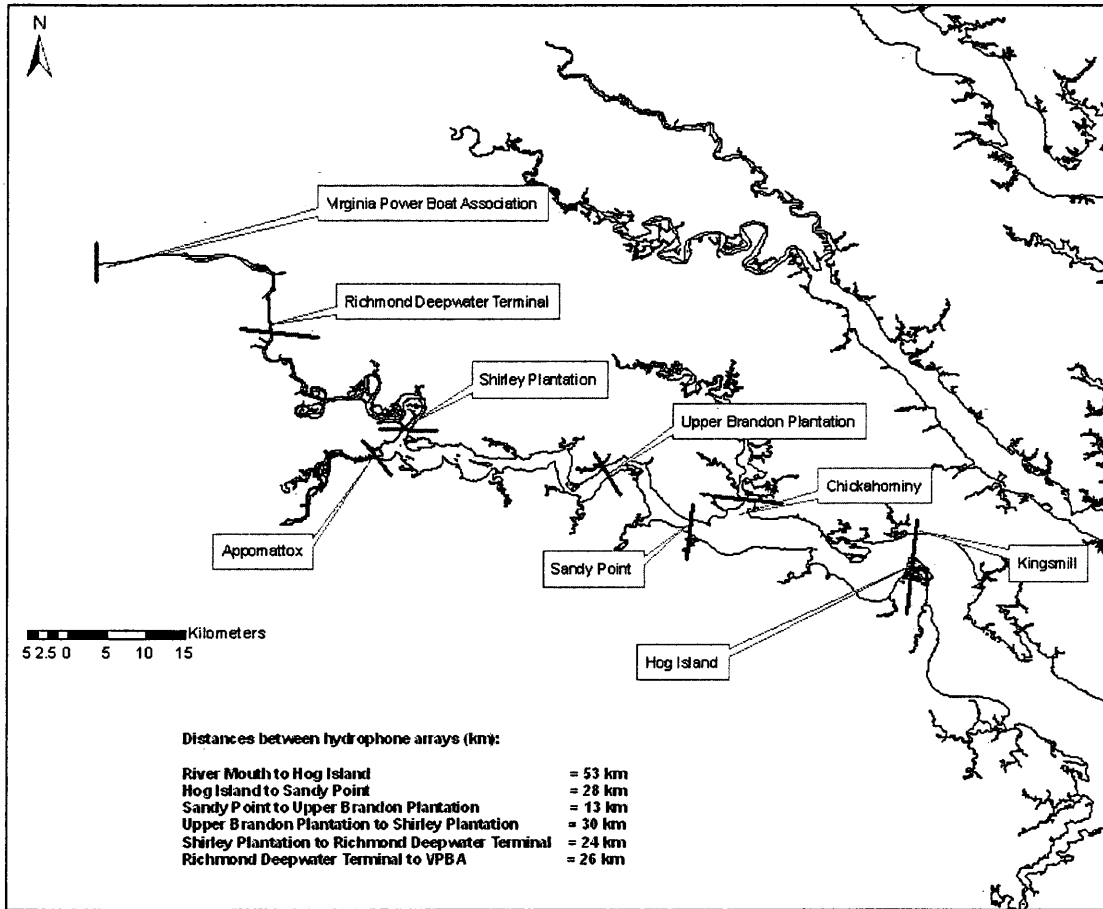


Figure 3: Capture, tagging, and release locations of American shad (*Alosa sapidissima*) near Ragged Island in the Lower James River.

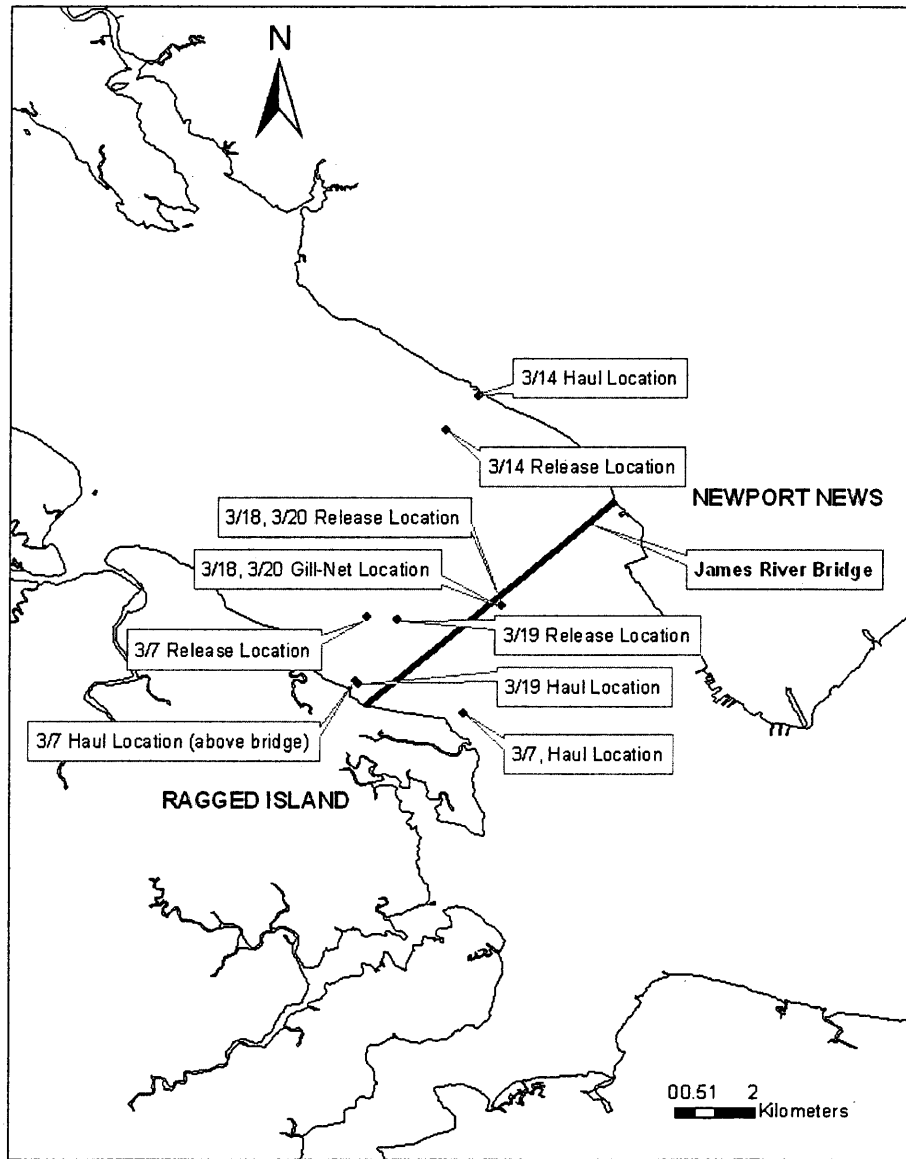


Figure 4: Capture and release locations of American shad (*Alosa sapidissima*) near Hog Island on 21 March 2005.

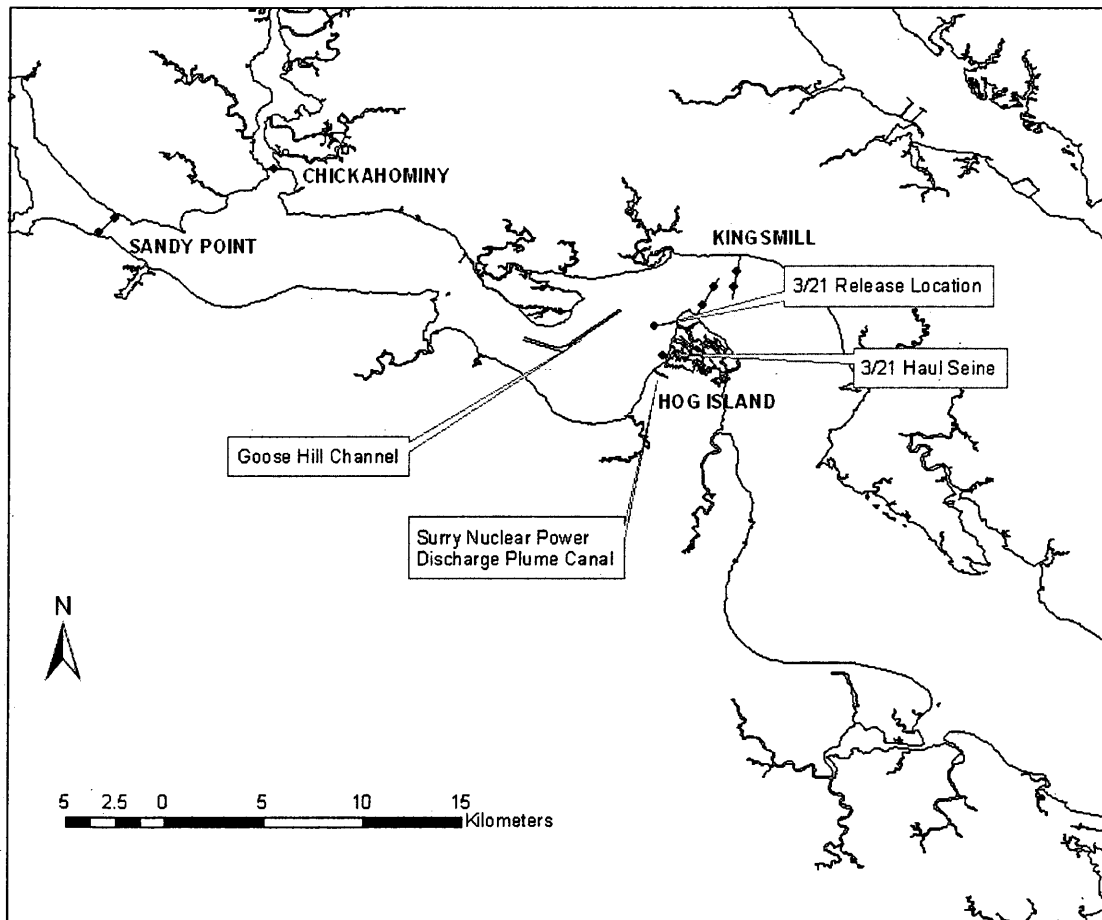


Figure 5. River discharge (m^3/s^{-1}) in 2005 as measured from the United States Geological Survey gauge in the James River near Richmond (Station 02037500). The 25th and 75th percentiles of historic discharge are measured from data collected at the same station from the period 1934-2004.

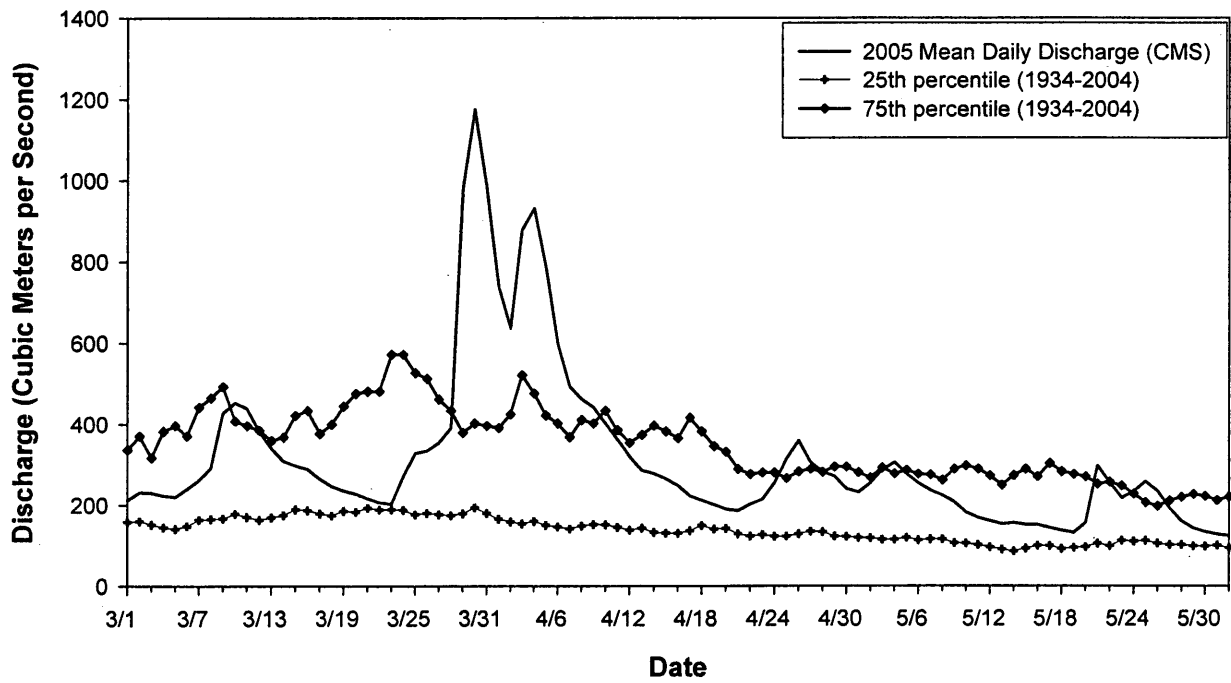


Figure 6. Mean residence time among individual American shad (*Alosa sapidissima*) assigned to different migratory patterns

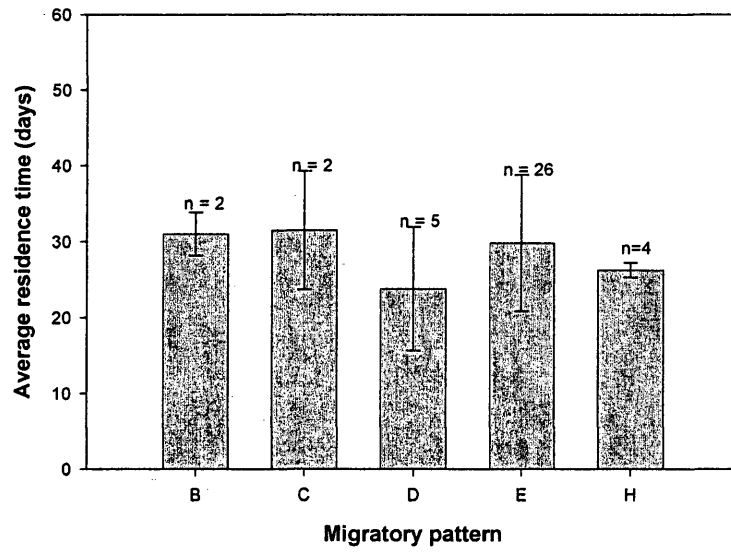
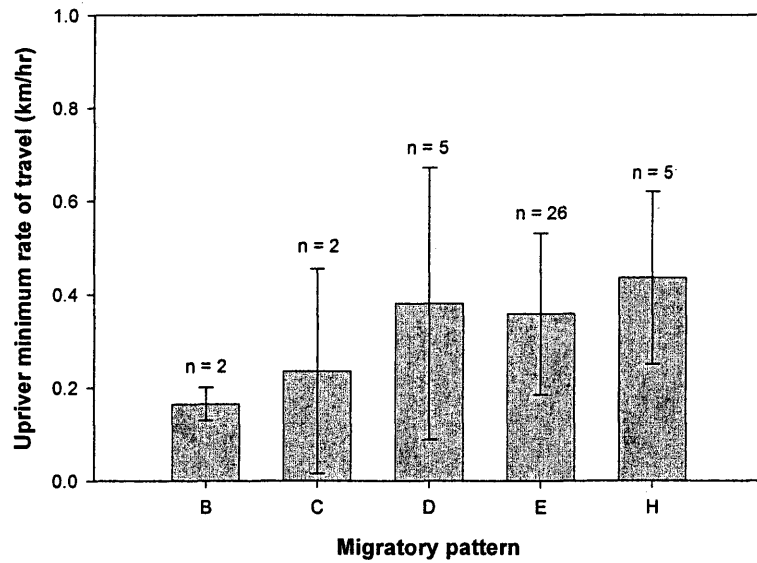


Figure 7. Mean upriver minimum rates of travel (a) and transit times (b) among individual American shad (*Alosa sapidissima*) assigned to different migratory patterns

a)



b)

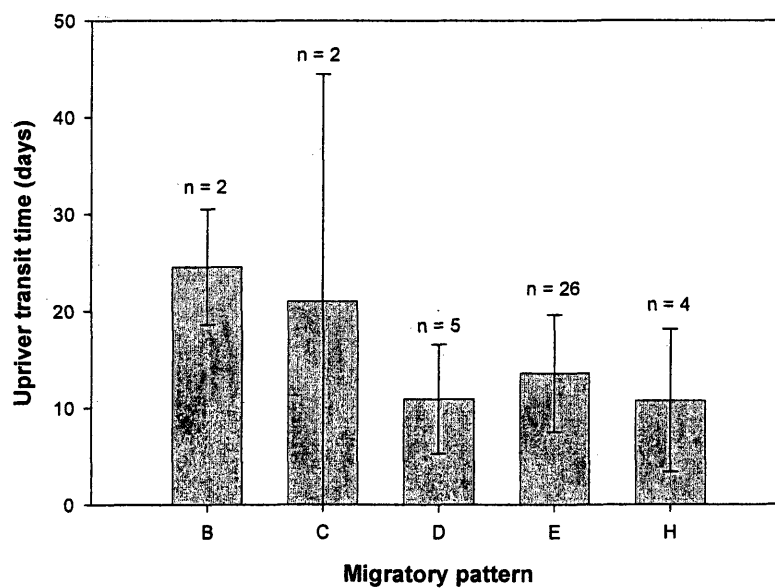
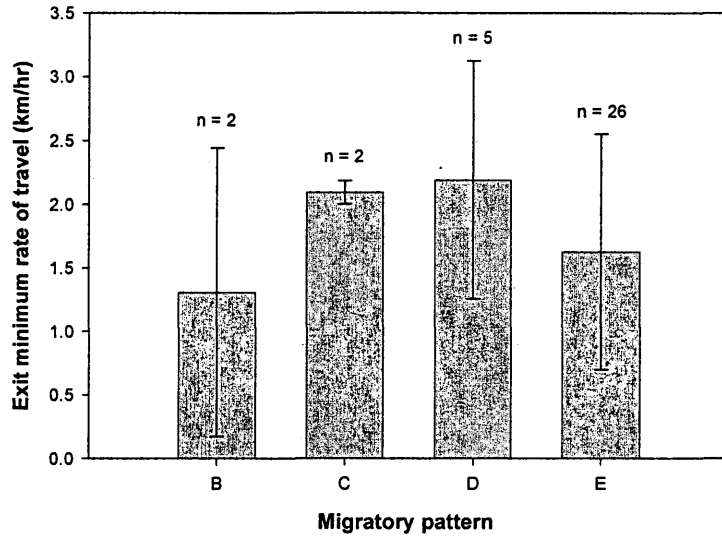
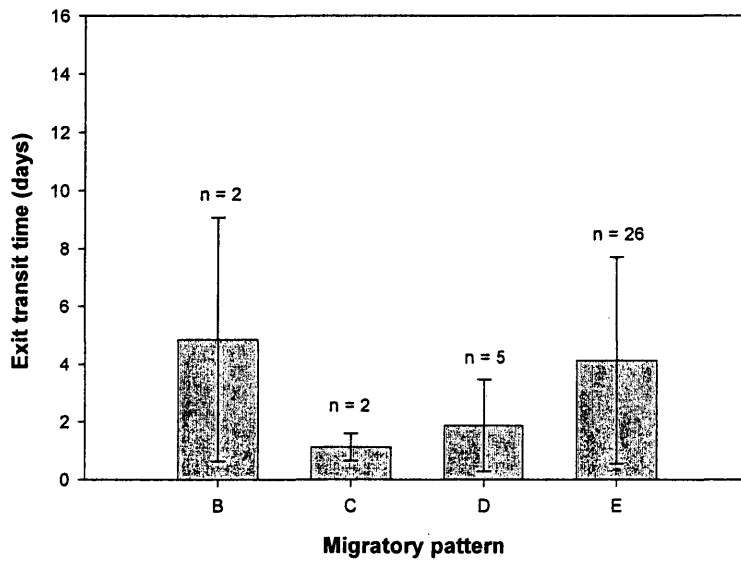


Figure 8. Mean exit minimum rates of travel (a) and transit times (b) among individual American shad (*Alosa sapidissima*) assigned to different migratory patterns

a)



b)



CHAPTER 2

SPAWNING OF AMERICAN SHAD IN THE JAMES RIVER

Abstract

Ichthyoplankton surveys were used to identify spawning areas of American shad within rkms 90 -158 at the fall line in Richmond, Virginia. Fish eggs and larvae were collected in anchored and towed nets during six cruises in April and May 2005. Active tracking searches were performed concurrently with ichthyoplankton sampling on four of the cruises, and passive telemetry data were collected from three receivers within the study area to identify tagged fish in areas where eggs and larvae were sampled. Eggs were collected from rkms 124.5 – 154.5, and yolk-sac larvae were collected from rkms 124.5 – 158 by both gears. Anchored nets collected more eggs ($n=76$) than bongo nets ($n=26$) and towed nets captured more yolk-sac larvae ($n=770$) than anchored nets ($n=3$). Peak densities (number/100m³) of eggs occurred at rkms 137.5 and 143.5. Peak densities of yolk-sac larvae were collected at rkms 135.5 and 149.5. The principle spawning grounds were located in a 33.50-km reach from rkm 124.5 – 158 at the fall line, a finding consistent with active tracking relocations and patterns of residency determined by passive acoustic monitoring of individuals within this reach. Densities of larvae were often high and extremely variable within the principle spawning grounds ($\bar{x}=32.7/100\text{m}^3$, $SD = 37.7/100\text{m}^3$). Measures of juvenile abundance in the lower James River by an independent seine survey targeting various finfish species have been zero in most years, suggesting larval and/or juvenile survival may be low.

Introduction

Every spring, American shad (*Alosa sapidissima*) ascend embayments, rivers and tributaries to spawn in tidal and non-tidal freshwater reaches (Leim 1924). At the southern end of the range in Florida, spawning runs begin in January and at the northern end of the range in Quebec, spawning runs begin in June and July (Limburg et al. 2003). A latitudinal gradient of iteroparity exists along the coast with populations on the southern end of the range being entirely semelparous, whereas populations northward of 32° N show an increasing degree of iteroparity (Leggett and Carscadden 1978). The duration of most spawning runs is approximately two to three months, but varies subject to weather conditions (Limburg et al. 2003). Within the James River, Virginia, the spawning run takes place from approximately mid-March until late May (Olney and Delano 2006).

American shad are broadcast spawners and spawning activity is believed to peak during the afternoon and nighttime (Massmann 1952; Marcy 1972; Chittenden 1976). Chittenden (1976) described American shad spawning behavior observed by lantern light within the Delaware River. One large shad (presumably female) in shallow water was joined by a small fish (presumably male). This was followed by a brief splash and rattling sound at the surface with the fish then swimming away. These noises could be heard throughout the river and occurred in water as shallow as 15 cm (Chittenden 1976). Similar behavior has been observed among other alosine fishes. In the Garrone River (France), an annual abundance index of allis shad (*Alosa alosa*) spawners is determined by recording and enumerating these splashes termed 'bull splashes' (Baglinière et al. 2003).

During spawning, semi-demersal eggs are deposited freely within the water column where they are dispersed by currents and eventually sink and become lodged in the substrate or gently roll along the bottom (Massmann 1952; Mansueti and Hardy 1967). Marcy (1972) determined that in the Connecticut River fertilized shad eggs can travel from one to four miles away from the spawning location based on water velocity and developmental stages of sampled eggs. Shad appear to actively select reaches of the river that may retain eggs in favorable habitats. In the Mattaponi and Pamunkey Rivers, Bilkovic et al. (2002a) found that spawning generally occurred in upriver and mid-river areas with high width:depth ratios. It was hypothesized that these river reaches may represent optimal spawning habitat because of high DO and currents that may inhibit siltation of eggs, but promote transport of larvae to productive feeding environments (Bilkovic et al. 2002a).

Water temperature influences time to hatch for eggs and growth rates of larvae, proceeding faster at higher temperatures, and slower at cooler temperatures. At temperatures of 12 °C hatching can take up to 17 days, whereas at 27° C hatching occurs within approximately 2 days (Jones et al. 1978). Once hatching occurs, larval survival is highest at water temperatures ranging from 15.5-26.1 °C and pH>7 (Klauda et al 1991). The stage duration of yolk-sac larvae is 4-7 days, and post-yolk-sac larvae have a stage duration of 21-28 days again dependent on water temperature (Jones et al. 1978). Metamorphosis and the onset of salinity tolerance occur at approximately 45 days post-hatch (Zydlewski and McCormick 1997).

Adult American shad within various river systems exhibit differences in spawning habitat preference. Beasley and Hightower (2000) reported American shad spawning at

depths from 0.30–1.83m and currents of 0.06-1.28m/s over a gravel or bedrock substrate in the Neuse River, North Carolina. Hightower and Sparks (2003) found American shad in the Roanoke River, North Carolina, selected spawning grounds with a mean depth of 2.5m and a mean current velocity of 0.63 m/s over substrates composed primarily of gravel, cobble, bedrock, and sand. In the Mattaponi and Pamunkey Rivers, Bilkovic et al. (2002a) found that shad spawning occurred primarily in areas characterized by shallow depths (<5m), and current velocities of 0.3-1.0 m/s. Chittenden (1976) reported that in the Delaware River, spawning occurred preferentially in shallow riffle habitats instead of pools. In the James River however, little information is available to characterize or locate the spawning habitat.

Spawning takes place in tidal fresh water and in some cases extended hundreds of kilometers inland in systems such as the James River before dams blocked access to upstream spawning habitat (Stevenson 1899). Limburg and Ross (1995) investigated growth and mortality rates of larval American shad at different salinities, and concluded that estuarine salinities neither depress nor elevate growth rates or mortality of larval American shad when compared with freshwater habitat. They hypothesized that spawning within the Hudson River occurs in freshwater to give larvae access to greater food resources and avoidance of estuarine predators (Limburg and Ross 1995). However, Zydlewski and McCormick (1997) found that American shad do not develop salinity tolerance until the onset of metamorphosis, suggesting a physiological necessity for spawning within freshwater.

The selection of optimal rearing habitat is an important factor influencing larval growth, survival, and consequently recruitment (Werner 2002). Crecco et al. (1983)

determined that mortality of larval American shad within the Connecticut River is higher than juvenile mortality suggesting year class strength is established in the larval stage, highlighting the importance of quality rearing habitat to larval growth and survival. Ross et al. (1997) investigated habitat use and feeding ecology of riverine Juvenile American shad in the upper Delaware River. Juvenile shad were found distributed within SAV beds, riffle, riffle pools, eddies, and channels. However no significant relationship was found between habitat type and juvenile abundance, suggesting juveniles can utilize a variety of riverine habitat types (Ross et al. 1997). Bilkovic et al. (2002a) described retention of larvae in mid-river segments of the Pamunkey and Mattaponi Rivers where tidal excursion is lowest. Spawners also appeared to select river reaches with extensive deadfall from shoreline vegetation where many food items of larval and juvenile shad originate (Bilkovic et al. 2002a).

Unfortunately, little work has been done to characterize current habitat conditions in the tidal freshwater portion of the James River. Analyzing historic aerial photographs of the James River, Moore (2000) determined that submerged aquatic vegetation (SAV) has been largely absent in the tidal freshwater portion of the James River since the 1940's. Such areas may have been historically important rearing habitat for larval and juvenile fishes (Werner 2002). In contrast, other Virginia tributaries that serve as important spawning and nursery habitat for anadromous fishes (the Pamunkey, Mattaponi, and Rappahannock Rivers) are relatively unaltered (Bilkovic 2002a; Boger 2002).

Ichthyoplankton surveys have been used to document spawning activity, characterize spawning habitat, and locate spawning reaches of American shad

(Massmann 1952; Marcy 1972; Gadomski and Barfoot 1998; Bilkovic et al. 2002a; Bilkovic et al. 2002b). Sampling methods have included passive filtering anchored nets (Massmann 1952; Marcy 1972, Gadomski and Barfoot 1998), and towed plankton nets (Gadomski and Barfoot 1998; Bilkovic et al. 2002a; Bilkovic et al. 2002b). A bow mounted push net developed by Kriete and Loesch (1980) was used by Bilkovic et al. (2002a) and Bilkovic et al. (2002b) to collect American shad ichthyoplankton on the Mattaponi and Pamunkey Rivers. Telemetry methods have also recently been used to help identify and characterize spawning areas (Beasley and Hightower 2000; Hightower and Sparks 2003). Beasley and Hightower (2000) monitored the movements of striped bass and American shad throughout the Neuse River North Carolina and recorded habitat characteristics in regions where shad spawning was observed. Hightower and Sparks (2003) performed plankton tows in areas of the river where tagged adults had been detected, and was able to confirm spawning activity by the presence of eggs and larvae.

While considerable information exists describing the historical range and distribution of fishing effort for American shad within the James River system (Stevenson 1899; Walburg and Sykes 1957; Walburg and Nichols 1967; Weaver et al. 2003; Olney et al. 2003), little is known about the location of important spawning reaches. Massmann (1952) conducted an ichthyoplankton survey using anchored nets within the James River mainstem up to Turkey Island Cutoff near Shirley Plantation, and within the Appomattox and Chickahominy Rivers. In the main-stem James River, he collected three shad eggs in the Turkey Island and Hopewell areas. In the Chickahominy River, two eggs were collected. Massmann (1952) noted that Walker's Dam in the Chickahominy had been constructed in 1943, but catches within the river remained high

since then suggesting areas below the dam are the primary spawning areas. Two eggs were collected within the Appomattox River, but Massmann (1952) hypothesized that domestic and industrial pollution diminished the importance of the Appomattox as productive spawning habitat. In a later study describing the James River, Walburg and Sykes (1957) cited Massmann's work and described shad as spawning within the mainstem James River below Hopewell. Historically, shad ascended to the junction of the Cowpasture and Jackson Rivers in Botetourt County over 560 km inland, suggesting spawning took place in these reaches as well. A popular catch and release fishery for hickory (*Alosa mediocris*) and American shad has developed at the fall line in Richmond, suggesting some spawning may be occurring there. American shad have been observed using the fishway at Boshers' Dam above the fall line, but no eggs or larvae have been collected upstream to identify areas of spawning (Weaver et al. 2003).

In this study, we used ichthyoplankton surveys to identify spawning reaches of American shad in the upper James River, extending from just below Upper Brandon Plantation to the fall line in Richmond (Figure 1). Our objective was to identify river reaches within this area where spawning of American shad occurs. In addition we compared data on the presence or absence of eggs or larvae to telemetry results to confirm spawning activity in areas where acoustically tagged fish were found to reside.

Methods

Ichthyoplankton Collections- Ichthyoplankton samples were collected with bongo nets and passive filtering anchored nets. The bongo frame was fitted with two conical 335 μ m mesh plankton nets (60 cm mouth diameter, 5:1 tail to mouth ratio). A flow-meter was

mounted within the mouth of one of the nets to estimate the volume of water filtered. All tows were stepped oblique with the exception of tows at rkm 158 below the fall line where depths of 5-6 ft only permitted shallow subsurface tows. For stepped oblique tows, tow times were 3-6 min at sampling depths ranging from 15-55 ft (\bar{x} =29, SD=7.8). Surface tows were 3-5 min in duration.

We modified Massmann's (1952) original anchored net design by placing the net approximately 1 m off of the bottom as opposed to directly on the bottom. Anchored nets consisted of a 50-cm diameter net ring outfitted with conical 1 mm mesh nets with a tail to mouth ratio of 5:1. The nets were held upright in a fishing position by a buoy at the surface, as well as a buoy attached at the upper portion of the net. Sampling depth was adjusted by adding or removing detachable sections of rope above the net though the length of rope from the bottom of the net to the anchor remained constant for all samples. All anchored net samples were collected along the edge of the river channel to avoid shipping traffic at depths ranging from 10-30 ft (\bar{x} =20, SD=7.2). Flowmeters were not used with the anchored nets. Anchored net sets ranged in duration from 1 hour to 6 hours and 22 minutes on 12, 20, and 21 April (\bar{x} =3:23, SD=1:41). On 26 April, anchored net sets were considerably shortened and lasted from 14 to 40 minutes (\bar{x} =29 min, SD=13 min). All net samples were fixed in the field in a 10% formaldehyde solution. For all bongo net tows, the contents from both nets were combined into one sample.

The study area was divided into thirteen 5-km strata beginning at rkm 90 and samples were collected within each stratum from rkm 90 to rkm 158 at the fall line (Figure 1). Bongo stations were randomly selected within each stratum on 12 and 28 April. Anchored nets were set at fixed stations (rkms 135.5, 140.5, 145.5, 150.5, and 155.5) on 12, 20, and 26 April. Two additional stations were sampled on 12 April at

rkms 124.5 and 129.5. Anchored nets were only deployed in the lower part of the study area on 21 April at rkms 90.5, 95.5, 100.5, 105.5, 110.5, and 115.5. Bongo net tows were conducted where fish were detected on 20, 21, 26 April and 5 May based on the presence of acoustically tagged fish detected by active tracking. If fish were not detected within a stratum, tow location was selected randomly.

Water column profiles were taken at selected sample sites at the surface, mid-water, and maximum depth with an YSI[®] water column profiler measuring salinity, conductivity, DO, pH, temperature, and depth on each cruise.

Sample Sorting and Identification - Whole samples were sorted for alosine eggs and larvae using a stereomicroscope. Larvae were placed into labeled vials and preserved in 70% alcohol. Eggs were preserved in 10% formalin.

Yolk-sac larvae of American shad and hickory shad were separated from larval herrings (*Alosa* spp.) based on size at hatching following Jones et al. (1978). Herring larvae hatch at approximately 2.5-5.0 mm notochord length (NL) while yolk-sac larvae of American shad (5.7-10.0 mm NL) and hickory shad (5.2-6.5 mm NL) are larger. Larvae of American shad and hickory shad were distinguished using total myomere counts (55-57 for American shad, 44-52 for hickory shad, see Jones et al. 1978). Myomere counts of some specimens fell between this reported range. In this case, larvae with total myomere counts ≥ 53 were assigned as American shad. American shad eggs were separated based on the characteristics described by Lippson and Moran (1972), Jones et al. (1978), and Wang and Kernehan (1979). Eggs of both striped bass (*Morone saxatilis*) and American shad were identified in James River samples. Both species have large (>2.5 mm

diameter) eggs with large perivitelline spaces. Eggs of American shad lack the characteristic oil globule of striped bass eggs and are easily identified (see above references). The primary spawning areas of these species are disjunct in Virginia rivers; striped bass spawn in areas downstream of American shad (Grant and Olney 1991; Bilkovic et al. 2002b). In some samples taken above the striped bass spawning areas, we found damaged (often split chorions) eggs that lacked intact embryos or yolk. These were enumerated as eggs of American shad since they were not likely to be eggs of striped bass at these locations. Eggs and larvae are reported as numbers/hr in anchored net sets; eggs and larvae are reported as numbers/100m³ in bongo net collections.

Results

Samples were collected over six cruises in April and early May (Table 1, Appendix 4). A total of 65 samples was collected, 23 with anchored nets and 42 with bongo nets over a 68-km portion of the James River. The average surface water temperature was 16.8 °C (range 14.9-19.6 °C, SD= 1.2 °C), values within the reported range for American shad spawning.

American shad eggs (n=102) were collected from rkm 124.5–154.5 in the area extending from Shirley Plantation to 4 rkm below the fall line in Richmond with both anchored nets and bongo nets. The total number of eggs/hr or densities of the total number of eggs collected in bongo nets are depicted in Tables 2-3 and Figures 2-3. In anchored nets, peak numbers occurred at rkm 145.5 (n= 71, 10.5/hr); in bongo nets, peak density occurred at rkm 137.5 (n = 5, 6.13/100m³).

American shad yolk-sac larvae ($n = 773$, 5.1 – 6.8 mm NL) were collected from rkm 124.5 to 158 at the fall line, a portion of the river encompassed by egg distribution. Anchored nets collected 3 yolk-sac larvae (Table 2, Figure 2) from rkm 135.5–155.5 with the highest number/hr at rkm 155.5 ($n = 1$, larvae/hr = 0.40). Most yolk-sac larvae were collected by bongo net ($n = 770$) in reaches extending from rkm 124.5 – 158 (Table 3; Figure 3). The highest densities of yolk-sac larvae were collected at rkm 135.5 ($n = 122$, larvae/100m³ = 139.59). Post-yolk sac larvae ($n = 30$, 6.7-12.7 mm NL) were found sporadically in collections downstream to rkm 95.

Eight bongo tows were collected at locations within rkms 135.5-158 where tagged fish were detected by active tracking (Table 4). All of these samples contained either eggs, yolk-sac larvae, or a combination indicating spawning activity at locations where tagged fish were present. Data from passive acoustic hydrophones indicated that 34 of 39 acoustically tagged individuals (87%) were detected during the residency period at Shirley Plantation (rkm 124) and RDT (rkm 148). Thus, spawning activity occurred where a majority of acoustically tagged fish resided during the spawning migration.

Discussion

The principal spawning grounds of American shad on the James River are located in a 33.5-km reach extending from Shirley Plantation (rkm 124.5) to the fall line (rkm 158) at Richmond, Virginia. The highest densities of eggs and larvae were collected in this region, the same river reach where most acoustically tagged individuals resided following the spawning migration (Patterns D, E, G, H, Chapter 1). The habitat in the area up to the fall line is primarily a narrow deep channel bordered by steep banks. The substrate is primarily silt, mud and organic matter (personal observation). While this river

reach is heavily industrialized, there is a relatively consistent buffer of trees and deadfall along the shore in some areas, although the extent of these characteristics was not rigorously quantified. Treed buffers and deadfall are habitat characteristics associated with high egg and larval densities in the Mattaponi and Pamunkey Rivers (Bilkovic et al. 2002a). In other systems, spawning activity of American shad has been reported in river channels with sand or gravel substrates at depths between 0.91 and 12.19 meters (Walburg and Nichols 1967). The fall line habitat 9 rkm upstream of RDT contains numerous islands, creeks, rocks, and shallow habitats where eggs or larvae spawned by American shad upstream may have been retained, and numerous American shad yolk-sac larvae were collected just below the white water at the fall line. These reaches are largely inaccessible to plankton sampling or active tracking but contain areas that are described as suitable spawning habitat in other river systems (Chittenden 1976; Beasley and Hightower 2000; Hightower and Sparks 2003). At least one of our tagged fish was captured by electrofishing within the fall line region.

Some acoustically tagged American shad resided between Upper Brandon (rkm 94) and Shirley Plantation (rkm 124.5, Pattern C, Chapter 1) but eggs were not collected in this area. American shad larvae ($n=9$) collected in this reach were post-yolk-sac stage and probably originated from points upstream. Our plankton collections in this region were dominated by eggs and larvae of striped bass. Grant and Olney (1991) found the peak of striped bass spawning activity was generally located in reaches between Upper Brandon and Shirley Plantation. Bilkovic et al. (2002b) found that peak striped bass spawning activity took place below areas of peak American shad spawning with little spatial overlap on the York River system. The reach extending from Upper Brandon to

Shirley Plantation is approximately 30 km and the habitat is composed primarily of a continuous deep channel, bordered by extensive flats. The substrate is primarily sand, mud, and silt (personal observation). The shoreline is mostly wooded up to Hopewell (approximately 25 km upstream of Upper Brandon) although there are numerous cleared areas. If American shad were spawning in the area around Upper Brandon, then eggs were not accounted for in our samples.

The spawning grounds of American shad in the James River may have shifted upriver since the 1950s due to a significant change in stock composition. This conclusion is based on comparisons of our data with the historic account of spawning by Massmann (1952). In his study, shad spawning did not extend upriver beyond Turkey Island cutoff near Shirley Plantation. Massmann (1952) concentrated his sampling efforts to the region of the river below this area and did not sample upstream. His choice of sampling areas was based on the spatial extent of commercial fishing activity in the river. At the time, most ripe shad were captured in drift nets at or below Hopewell, Virginia (rkms 120-124). Landings of American shad in the 1950s were substantial, exceeding 1×10^6 lbs in some years (Walburg and Sykes 1957). It is not likely that spawning habitats have expanded considerably since the 1950s given that current abundance of James River shad is believed to be low compared to historic levels (Olney and Delano 2006). Our detection of principal spawning areas upriver of the City of Hopewell may be a result of recent relocation of spawning habitat by hatchery-produced adults and their progeny. The hatchery components of the current population in the James River presumably migrate to their natal habitats above Boshers' Dam, although the efficiency of the passageway is unknown.

The location of hypothesized spawning reaches may have been biased if eggs or larvae had drifted from the original spawning location. The influence of physical factors such as depth, current, substrate composition, and sinuosity likely affect egg and larval distribution. Bilkovic et al. (2002a) documented tidal excursions of 3.2 rkms in the Mattaponi and Pamunkey Rivers, leading to the assumption that egg and larval dispersal could be extrapolated between stations 3.2 rkms apart. We made the assumption that the collection of larvae was indicative of spawning within the sampled 5 km stratum although tidal excursion was not quantified.

Anchored nets captured more eggs than bongo nets. American shad eggs are semi-demersal and may have been more susceptible to capture closer to the bottom. The filtering efficiency of anchored nets probably decreases with the sampling duration from fouling by organic debris, and bottom current speeds are also likely less than surface current speeds. Numbers of yolk-sac larvae captured by anchored nets ($n = 3$) were considerably smaller than the numbers captured by bongo net ($n=770$). This is likely due to the large mesh size of 1 mm, where the thin yolk-sac larvae may have been extruded through the meshes, or a function of the spatial distribution of yolk sac larvae within the water column.

The average size of American shad yolk-sac larvae in our samples was 5.8 mm NL (SD = 0.41, range 5.1-6.8 mm NL). This average size is at the lower end of the range of 5.7 - 10 mm NL hatching size reported by Jones et al. (1978), and may be due in part to shrinkage of larvae in preservative. There are no studies of the effects of preservatives, on the shrinkage of American shad larvae. Bilkovic et al. (2002b) reported minimum American shad yolk-sac larval lengths of 6.1 and 6.6 mm TL in the Mattaponi and

Pamunkey rivers respectively. Estimates of shrinkage of Atlantic herring larvae (*Clupea harengus*, 9-19 mm live length) due to preservative and capture effects were 10 % (Fox 1996). Compensating for shrinkage of 10% among American shad larvae collected in the current study would still yield a small average size but within the published size limit reported by Jones et al. (1978). Chambers and Leggett (1996) concluded that size variation of larvae in marine populations is largely due to maternal origin and environmental conditions experienced by the female. However, the size and physical condition of spawning adult female American shad in the current study was not assessed and the maternal contribution to egg and larval size of American shad is not known. Intact American shad eggs (n=3) ranged from 2.9 – 3.4 mm in diameter, which is above the minimum size reported by Jones et al. (1978) of 2.5-3.8 mm diameter. More investigation is needed to evaluate the role of shrinkage of American shad larvae in preservative and the potential for maternal effects on size at hatching.

Juvenile American shad are rarely collected in extensive monthly seine surveys in the James River targeting striped bass and the index of juvenile abundance (JAI) of American shad has been zero in most years. The seine survey has been shown to correlate well with a push-net survey on the adjacent Mattaponi and Pamunkey Rivers (Wilhite et al. 2003). The average larval density in the current study of 32.7/100m³ is similar to the value reported in the Mattaponi River of 32.8/100m³ (Bilkovic et al. 2002b). Higher yolk-sac larval densities and low numbers of juveniles suggest larval and or juvenile survival may be low below Boshers' Dam. Above the dam, survival of hatchery-released larvae is higher since hatchery-marked juveniles are routinely collected there (Alan Weaver, VDGIF, personal communication) and mature hatchery-released

cohorts are returning in large numbers (Olney et al. 2003). Crecco et al. (1983) determined age-specific growth and survival rates for larval and juvenile American shad within the Connecticut River. Survivorship curves indicated that 70-85% of losses occur among larvae ages 4-9 days, suggesting American shad recruitment in the Connecticut River is largely determined in the larval stage, as juvenile survivorship was positively correlated with adult recruitment (Crecco et al. 1983). Houde (1997) determined the physiological mortality rate M/G (mortality/growth) for American shad in the Connecticut River based on data from Crecco et al. (1983). The age at transition where $M/G = 1$ was reached at a size of about 12mm shortly after first feeding and before metamorphosis (Houde 1997).

The possible causes of high larval or juvenile mortality in the James River are unknown. Physical parameters recorded at sampling locations were consistently above the threshold value of 5.0 mg/L for dissolved oxygen and $pH > 6.7$ (Klauda et al. 1991; Appendix 4), which have been identified as thresholds for the survival of American shad eggs and larvae. Anthropogenic challenges, especially poor water quality associated with industrialization in the spawning reaches, could be impacting growth and mortality. Natural factors important to the recruitment process such as predation, habitat, food availability, and river flow require more investigation. If larval survival is low below Boshers' Dam, then the potential for full recovery of the James River stock could be compromised. In the absence of successful reproduction in the river below Boshers' Dam, the current population may be dependent on hatchery replenishment.

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Table 1: Spatial and temporal coverage of American shad (*Alosa sapidissima*)

ichthyoplankton samples collected in the James River, 2005. Abbreviations are: A, anchored net; B, bongo net.

Strata	12 April		20 April		21 April		26 April		28 April		5 May	
158 (fall line)			B				B		B		B	
155	A		A				A					
150	A	B	A	B			A	B		B		B
145	A	B	A	B			A	B		B		B
140	A	B	A	B			A	B		B		B
135	A	B	A	B			A	B		B		B
130		B						B		B		B
125	A									B		
120	A									B		
115					A	B				B		
110					A	B				B		
105					A	B				B		
100					A	B				B		
95					A	B				B		
90					A	B				B		
	A:7	B:5	A:5	B:5	A:6	B:6	A:5	B:6	A:0	B:14	A:0	B:6

Table 2: Total number of American shad (*Alosa sapidissima*) eggs and larvae collected by anchored nets within the James River, 2005

rkm	Number of samples	Sampling Duration	Eggs	Yolk-sac larvae	Post yolk-sac larvae	Eggs/hr	Yolk-sac larvae/hr	Post yolk-sac larvae/hr
155.5	3	2:29	0	1	0	0	0.40	0.00
150.5	3	4:24	3	0	0	0.68	0.00	0.00
145.5	3	6:47	71	1	0	10.47	0.15	0.00
140.5	3	8:28	1	0	0	0.12	0.00	0.00
135.5	3	10:07	1	1	1	0.10	0.10	0.10
129.5	1	5:30	0	0	0	0	0.00	0.00
124.5	1	6:22	0	0	0	0	0.00	0.00
115.5	1	1:00	0	0	2	0	0.00	2.00
110.5	1	1:41	0	0	0	0	0.00	0.00
105.5	1	2:41	0	0	0	0	0.00	0.00
100.5	1	3:30	0	0	1	0	0.00	0.29
95.5	1	4:34	0	0	2	0	0.00	0.44
90.5	1	5:51	0	0	0	0	0.00	0.00
TOTAL	23	63 hrs 24 min	76	3	6	11.37	0.65	2.82

Table 3. Total density of American shad (*Alosa sapidissima*) eggs and larvae captured by bongo net within the James River, 2005

rkm	Number of samples	Total volume filtered	Eggs	Yolk-sac larvae	Post yolk-sac larvae	Eggs/100m ³	Yolk-sac larvae/100m ³	Post yolk-sac larvae/100m ³
158	4	227.4	0	161	0	0	70.80	0
154.5	4	387.3	1	58	0	0.26	14.98	0
152.5	1	55.7	1	1	0	1.80	1.80	0
149.5	2	121.6	0	104	1	0	85.53	0.82
147.5	1	82.8	0	6	0	0	7.25	0
146.5	2	249.7	0	7	0	0	2.80	0
143.5	2	161.9	6	110	0	3.71	67.94	0
142.5	2	147.3	2	65	1	1.36	44.13	0.68
141.5	1	71.5	0	3	0	0	4.20	0
139.5	2	181.8	6	13	0	3.30	7.15	0.00
138.5	1	62.3	0	35	2	0	56.18	3.21
137.5	1	81.6	5	17	1	6.13	20.83	1.23
135.5	1	87.4	0	122	1	0	139.59	1.14
134.5	1	102.4	0	8	0	0	7.81	0
133.5	2	174.5	1	28	3	0.57	16.05	1.72
132.5	1	92.2	3	21	5	3.25	22.78	5.42
127.5	1	60.3	0	7	5	0	11.61	8.29
124.5	1	55.5	1	4	1	1.80	7.21	1.80
119.5	1	65.5	0	0	0	0	0	0
118.5	1	102.3	0	0	0	0	0	0
111.5	1	72.5	0	0	0	0	0	0
110.5	1	108.4	0	0	0	0	0	0
109.5	1	56.2	0	0	1	0	0	1.78
105.5	1	88.7	0	0	0	0	0	0
102.5	1	93	0	0	1	0	0	1.08
100.5	1	92.3	0	0	1	0	0	1.08
99.5	1	121.8	0	0	0	0	0	0
96.5	1	61.8	0	0	1	0	0	1.62
93.5	1	72.3	0	0	0	0	0	0
91.5	1	71.4	0	0	0	0	0	0
TOTAL	42	3409.4	26	770	24	22	588.62	30

Table 4: Locations of bongo net tows where American shad (*Alosa sapidissima*) eggs or yolk-sac larvae were collected concurrent with active tracking.

Row	Date	Gear	rkm	Eggs	Yolk-sac larvae	Post-yolk-sac larvae	Detected fish
1	4/20/2005	Bongo	135.5	0	122	1	116, 25
2	4/26/2005	Bongo	138.5	0	35	2	37
3	5/5/2005	Bongo	139.5	1	11	0	37
4	4/26/2005	Bongo	142.5	2	56	1	121
5	4/20/2005	Bongo	149.5	0	93	0	15
6	4/20/2005	Bongo	154.5	1	53	0	12, 82, 42, 145, 39
7	5/5/2005	Bongo	154.5	0	5	0	156
8	4/20/2005	Bongo	158	0	141	0	45, 133
	TOTAL	8 tows		4	516	4	14

Figure 1. Study area within the James River indicating locations of passive hydrophone stations, and 5 km strata.

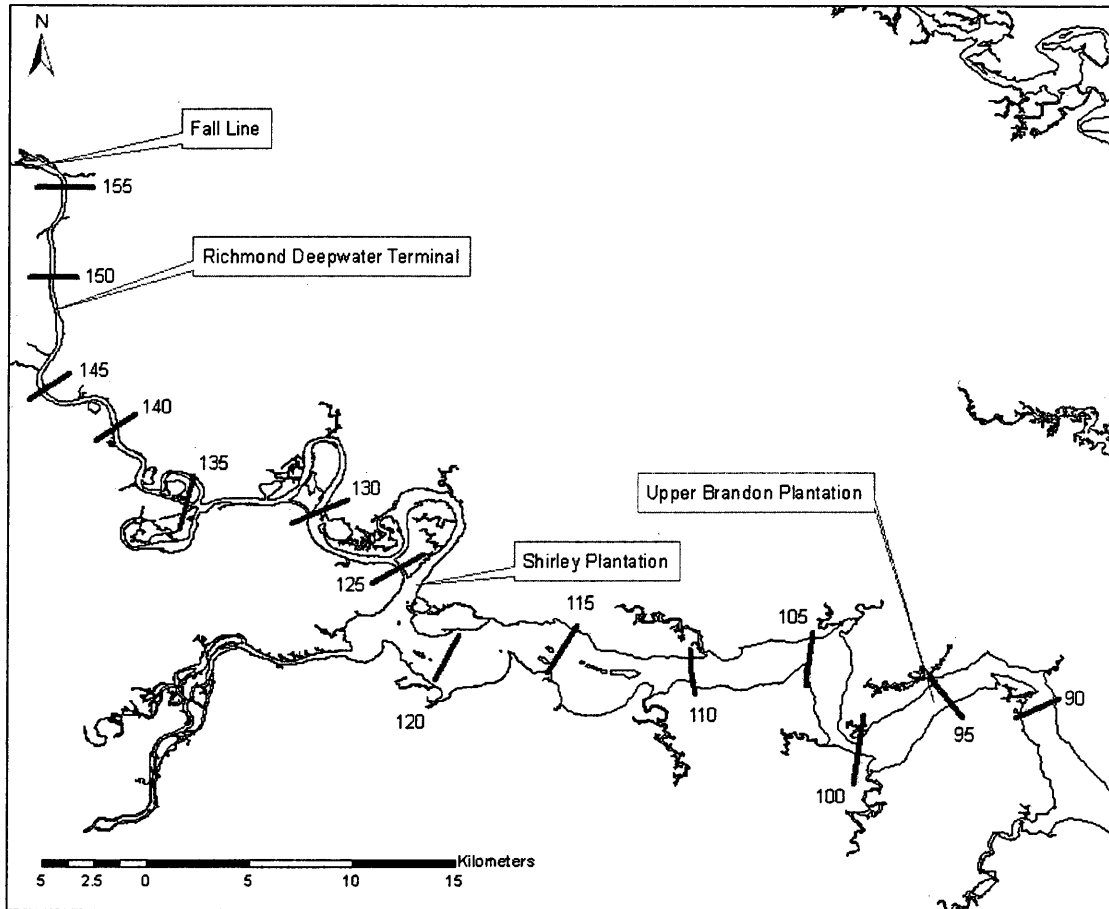


Figure 2: Spatial distribution of American shad (*Alosa sapidissima*) eggs, yolk-sac larvae, and post yolk-sac larvae captured by anchored nets

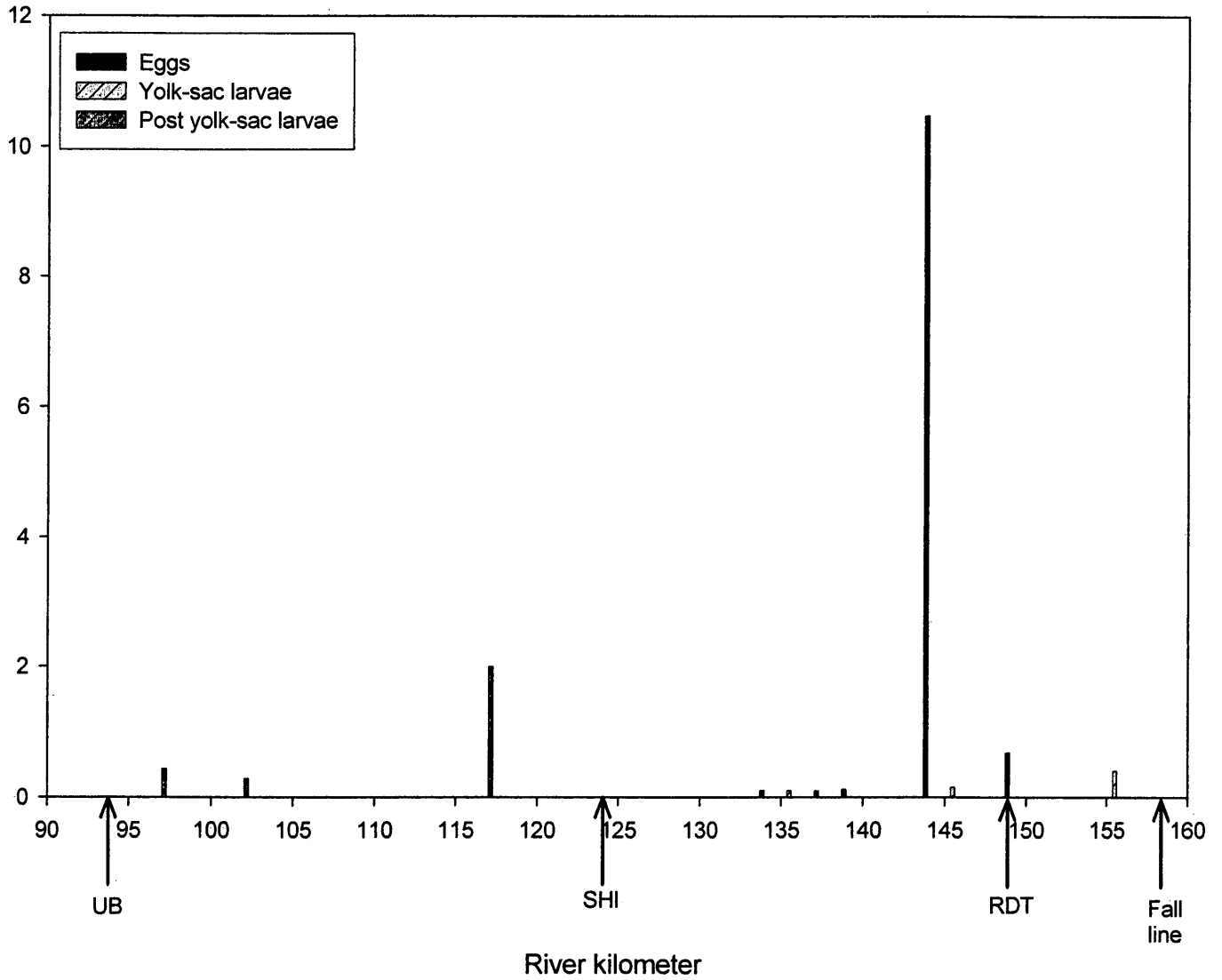
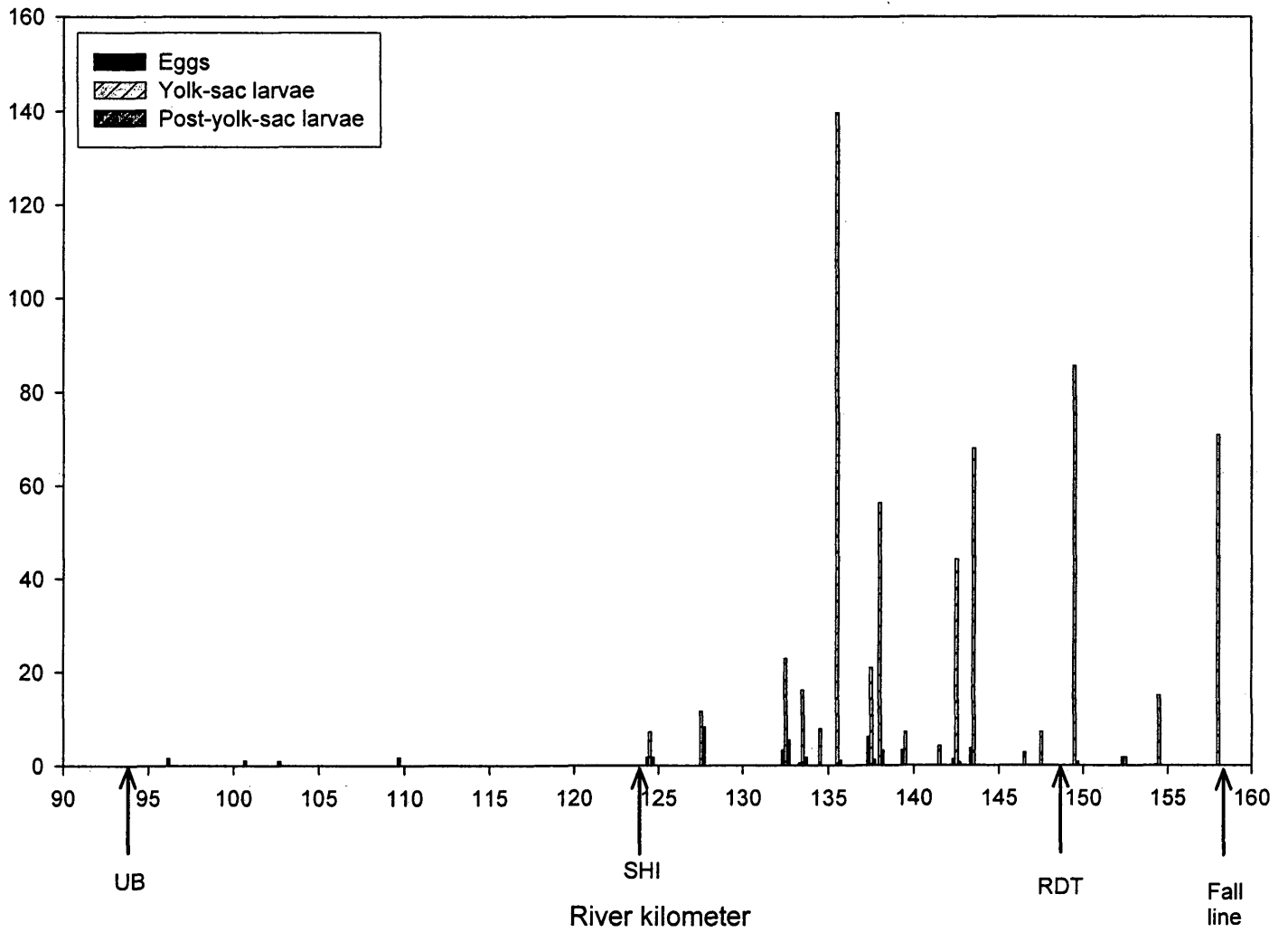


Figure 3: Spatial distribution of the total densities of American shad (*Alosa sapidissima*) eggs, yolk-sac larvae, and post yolk-sac larvae capture by bongo nets



APPENDIX 1

Table 2: Summary of mark-recapture data for American shad (*Alosa sapidissima*) released with acoustic tags in the James River, Virginia in spring 2005. Residence time is defined as the time between the first and last detection at Upper Brandon Plantation. Individuals with estimates of residence time were last detected at the Upper Brandon site, presumably migrating seaward. Individuals without estimates of residence time were not detected exiting the spawning tributary. For age, regenerated scales are denoted as Regen. and insufficient quantities as Insuff.

Fish	Water Temp °C	Release Date	Gear	Date of last detection	FL	Sex	Age	Spawning Marks	Residence Time
3	6.2	3/7/2005	HS	3/16/2005	465	F	7	3	
12	7.5	3/20/2005	SGN	4/25/2005	440	F	4	0	27
13	7.5	3/20/2005	SGN		465	F	6	1	
14	7.5	3/20/2005	SGN	4/2/2005	440	F	7	3	
15	7.5	3/20/2005	SGN	4/23/2005	500	F	6	1	23
16	14.7	3/21/2005	HS	3/30/2005	600	F	Regen.		
18	14.7	3/21/2005	HS	3/21/2005	470	F	Regen.		
19	14.7	3/21/2005	HS	3/21/2005	400	M	3	0	
20	14.7	3/21/2005	HS	4/24/2005	458	F	Regen.		25
21	14.7	3/21/2005	HS	3/21/2005	490	F	6	2	
22	14.7	3/21/2005	HS	3/22/2005	543	F	11	5	
23	14.7	3/21/2005	HS	3/21/2005	445	F	5	0	
24	14.7	3/21/2005	HS	4/7/2005	460	F	6	2	
25	14.7	3/21/2005	HS	4/22/2005	488	F	6	1	22
26	14.7	3/21/2005	HS	3/22/2005	412	M	4	0	
27	14.7	3/21/2005	HS	3/21/2005	430	M	5	2	
28	14.7	3/21/2005	HS	3/22/2005	442	F	5	1	
29	14.7	3/21/2005	HS	4/1/2005	448	F	5	0	
30	14.7	3/21/2005	HS	3/31/2005	480	F	6	0	
31	14.7	3/21/2005	HS	3/30/2005	478	F	6	0	
32	14.7	3/21/2005	HS	4/19/2005	475	F	6	0	
33	14.7	3/21/2005	HS	4/30/2005	460	F	6	0	25
34	14.7	3/21/2005	HS	4/19/2005	462	F	7	2	
35	14.7	3/21/2005	HS	4/24/2005	375	M	3	0	27
36	14.7	3/21/2005	HS	4/25/2005	477	F	6	2	24
37	14.7	3/21/2005	HS	4/7/2005	425	F	6	1	
38	14.7	3/21/2005	HS	4/22/2005	460	F	Insuff.		15
39	14.7	3/21/2005	HS	4/26/2005	438	F	7	4	26
40	14.7	3/21/2005	HS	3/23/2005	458	F	5	1	
41	14.7	3/21/2005	HS	3/23/2005	530	F	8	2	
42	14.7	3/21/2005	HS	5/14/2005	525	F	9	3	44
43	14.7	3/21/2005	HS	4/23/2005	442	F	5	1	22
44	14.7	3/21/2005	HS	4/21/2005	485	F	7	2	24
45	14.7	3/21/2005	HS	5/16/2005	400	UNKN.	4	1	34
46	14.7	3/21/2005	HS	4/25/2005	385	M	4	0	25
47	14.7	3/21/2005	HS	5/17/2005	440	F	7	3	48
52	14.7	3/21/2005	HS	3/28/2005	465	F	6	1	
53	14.7	3/21/2005	HS	5/1/2005	438	F	8	4	26

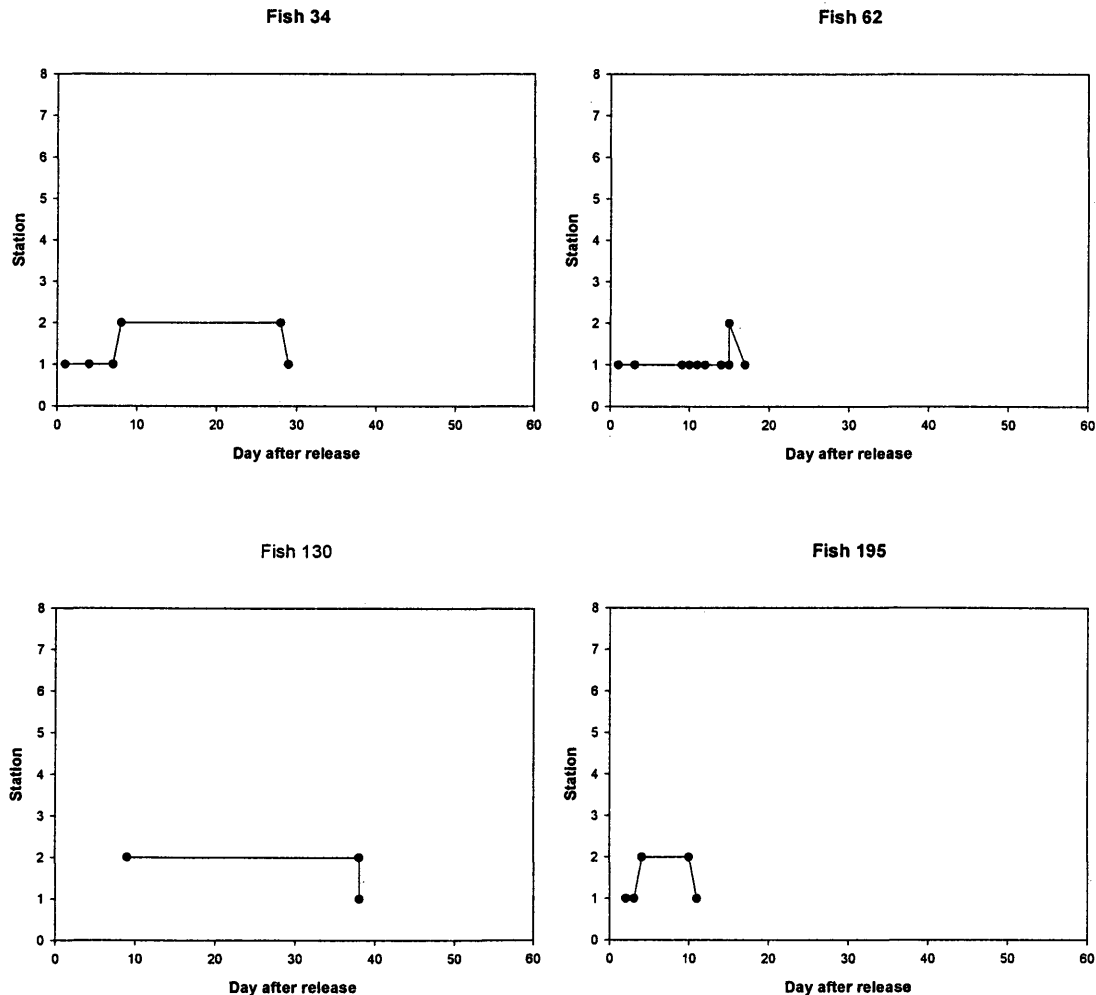
Fish	Water Temp °C	Release Date	Gear	Date of last detection	FL	Sex	Age	Spawning Marks	Residence Time
58	14.7	3/21/2005	HS	4/9/2005	482	F	5	1	
59	14.7	3/21/2005	HS	4/2/2005	472	F	Insuff.		
60	14.7	3/21/2005	HS	3/22/2005	455	F	5	1	
61	14.7	3/21/2005	HS	3/21/2005	540	F	9	3	
62	14.7	3/21/2005	HS	4/7/2005	422	F	5	1	
63	14.7	3/21/2005	HS	4/6/2005	475	F	6	0	
64	14.7	3/21/2005	HS	3/26/2005	418	M	4	0	
72	14.7	3/21/2005	HS	5/5/2005	480	F	6	1	33
73	14.7	3/21/2005	HS	3/22/2005	345	M	3	0	
74	14.7	3/21/2005	HS	4/23/2005	500	F	7	1	23
75	14.7	3/21/2005	HS	3/31/2005	410	UNKN.	5	2	
80	14.7	3/21/2005	HS	3/31/2005	460	F	5	0	
82	14.7	3/21/2005	HS	5/8/2005	505	F	9	4	43
83	14.7	3/21/2005	HS	3/22/2005	535	F	10	5	
86	14.7	3/21/2005	HS	3/22/2005	375	M	5	2	
87	14.7	3/21/2005	HS	4/27/2005	468	F	6	2	29
88	14.7	3/21/2005	HS	3/26/2005	500	F	7	1	
90	14.7	3/21/2005	HS	3/30/2005	505	F	7	3	
92	14.7	3/21/2005	HS	4/3/2005	435	UNKN.	7	3	
93	14.7	3/21/2005	HS	5/2/2005	441	F	5	1	33
94	14.7	3/21/2005	HS	3/22/2005	428	F	5	1	
100	14.7	3/21/2005	HS	3/21/2005	375	M	Regen.		
101	14.7	3/21/2005	HS	5/11/2005	450	F	6	1	35
102	14.7	3/21/2005	HS	3/31/2005	418	F	6	2	
103	14.7	3/21/2005	HS	3/25/2005	450	F	6	1	
109	14.7	3/21/2005	HS	3/22/2005	415	F	6	1	
110	14.7	3/21/2005	HS	4/7/2005	478	F	6	1	
111	14.7	3/21/2005	HS	5/4/2005	515	F	9	4	31
114	14.7	3/21/2005	HS		390	M	5	1	
115	14.7	3/21/2005	HS	3/22/2005	470	F	6	0	
116	14.7	3/21/2005	HS	5/1/2005	476	F	7	2	31
117	14.7	3/21/2005	HS	3/29/2005	490	F	7	1	
120	14.7	3/21/2005	HS	4/24/2005	476	F	7	2	26
121	14.7	3/21/2005	HS	5/7/2005	500	F	8	2	36
122	14.7	3/21/2005	HS	5/9/2005	418	M	5	0	29
129	14.7	3/21/2005	HS	3/22/2005	385	M	5	1	
130	14.7	3/21/2005	HS	4/28/2005	418	UNKN.	5	2	
131	14.7	3/21/2005	HS	5/8/2005	395	M	Regen.		37
132	14.7	3/21/2005	HS		360	M	3	0	
133	14.7	3/21/2005	HS	5/19/2005	455	UNKN.	6	3	52
138	14.7	3/21/2005	HS	4/24/2005	460	F	7	1	18
143	14.7	3/21/2005	HS	4/7/2005	360	M	4	0	
144	14.7	3/21/2005	HS	3/22/2005	500	F	6	2	
145	14.7	3/21/2005	HS	5/11/2005	444	F	6	3	
150	14.7	3/21/2005	HS	5/16/2005	375	M	4	0	36
152	14.7	3/21/2005	HS	4/27/2005	452	F	6	0	24
154	14.7	3/21/2005	HS	3/22/2005	457	F	5	0	
156	14.7	3/21/2005	HS	5/10/2005	450	F	5	0	32

Fish	Water Temp °C	Release Date	Gear	Date of last detection	FL	Sex	Age	Spawning Marks	Residence Time
157	14.7	3/21/2005	HS	5/1/2005	467	F	6	1	25
159	14.7	3/21/2005	HS	4/29/2005	465	F	7	3	30
169	14.7	3/21/2005	HS	3/27/2005	399	UNKN.	4	0	
170	14.7	3/21/2005	HS	4/29/2005	454	F	5	1	26
178	14.7	3/21/2005	HS	3/31/2005	382	M	3	0	
183	14.7	3/21/2005	HS	4/25/2005	396	UNKN.	4	0	17
193	14.7	3/21/2005	HS	4/30/2005	475	F	6	3	24
195	14.7	3/21/2005	HS	4/1/2005	460	F	6	2	
203	14.7	3/21/2005	HS	3/22/2005	417	F	5	0	
204	14.7	3/21/2005	HS	4/22/2005	399	UNKN.	5	0	18
205	14.7	3/21/2005	HS	3/22/2005	445	F	4	0	
210	14.7	3/21/2005	HS	4/3/2005	440	F	4	0	

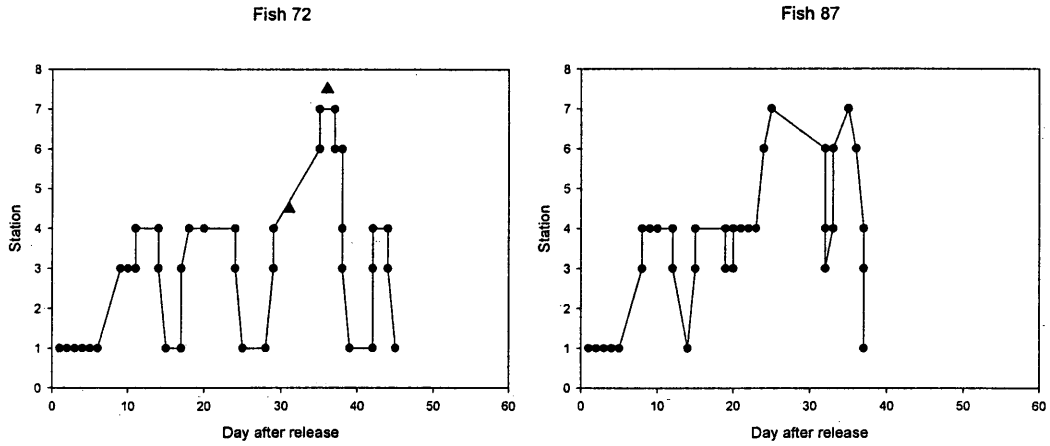
APPENDIX 2

Detection histories for all American shad (*Alosa sapidissima*) (n=49) that proceeded upstream past Hog Island. Fish are grouped into migratory patterns (A-H) as described in the results section of Chapter 1. Active tracking relocations are indicated with red triangle symbols where applicable. Day after release (x-axis) is the number of days between the release date and detection at each hydrophone. Stations (y-axis) are numbered consecutively upstream as 1) Hog Island/Kingsmill; 2) Chickahominy; 3) Sandy Point; 4) Upper Brandon Plantation; 5) Appomattox; 6) Shirley Plantation; 7) Richmond Deepwater Terminal; and 8) Virginia Power Boat Association

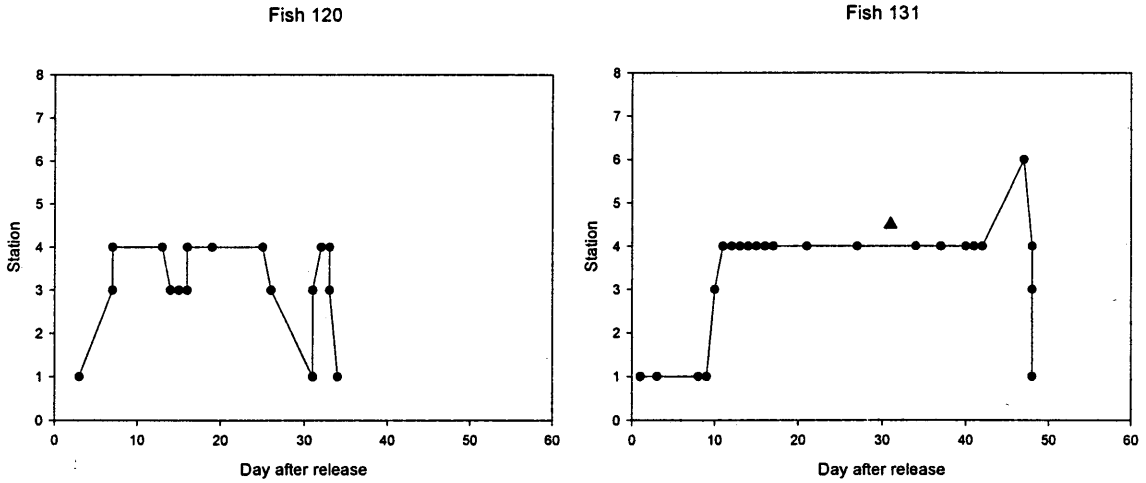
A: Only detected at the Chickahominy River



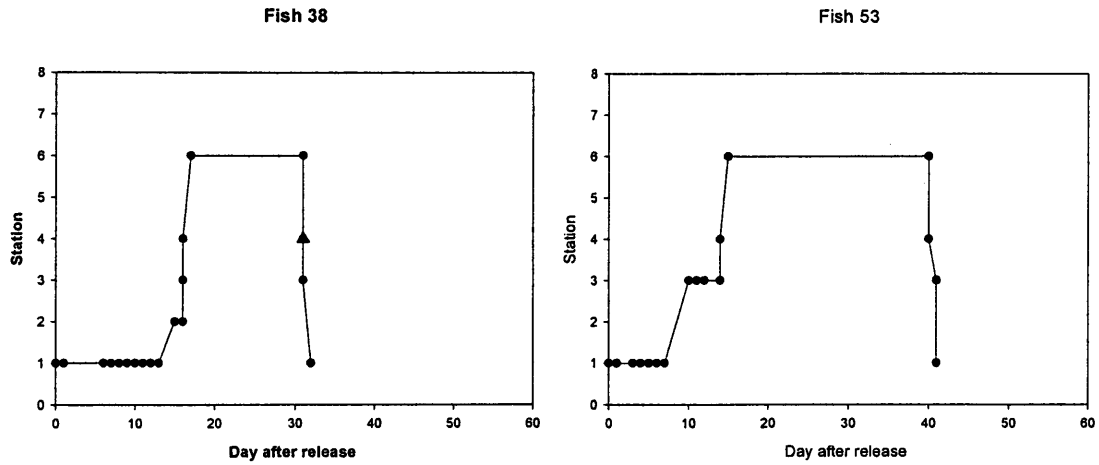
B: Rapid upstream and downstream movements with no evidence of site specific residence



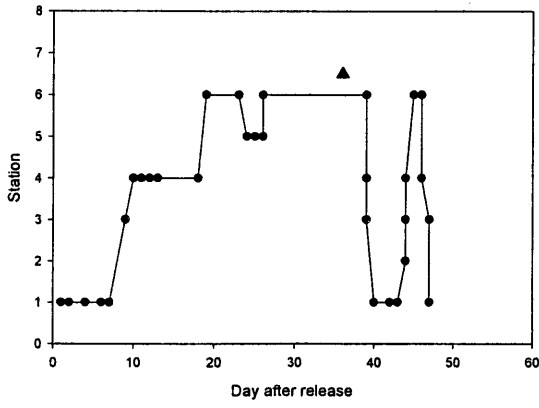
C: Resided primarily at Upper Brandon Plantation



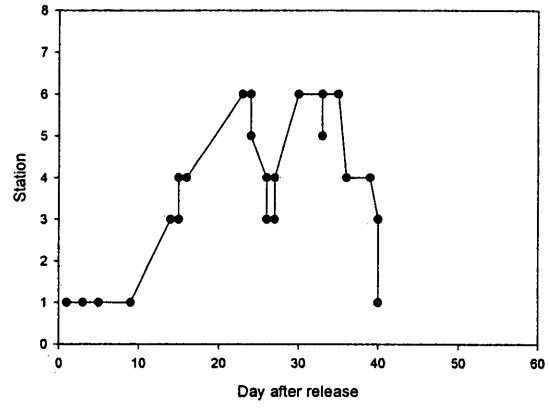
D: Resided Primarily at Shirley Plantation 15, 44, 138, 159, 183.



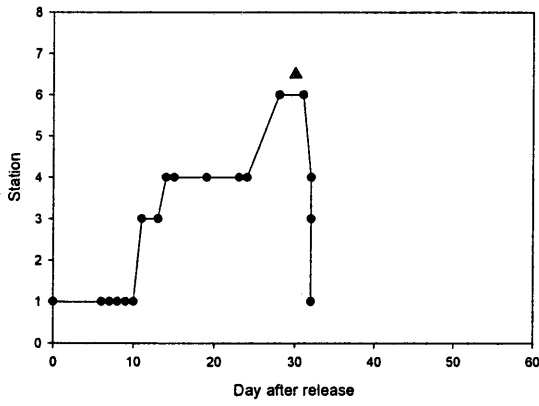
Fish 121



Fish 193

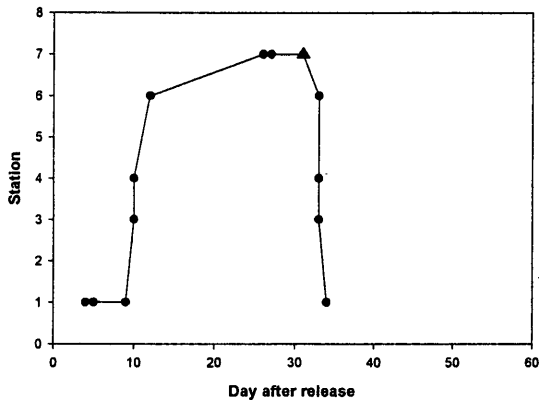


Fish 204

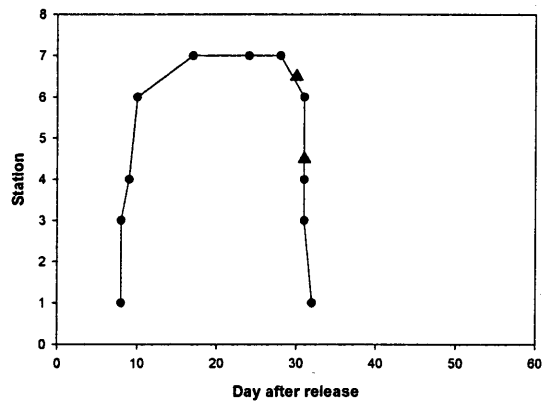


E: Resided primarily at Richmond Deepwater Terminal

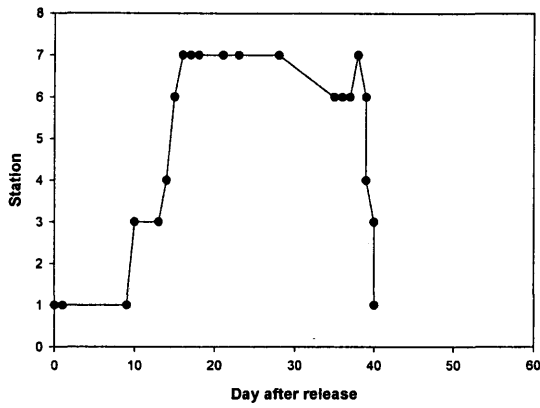
Fish 15



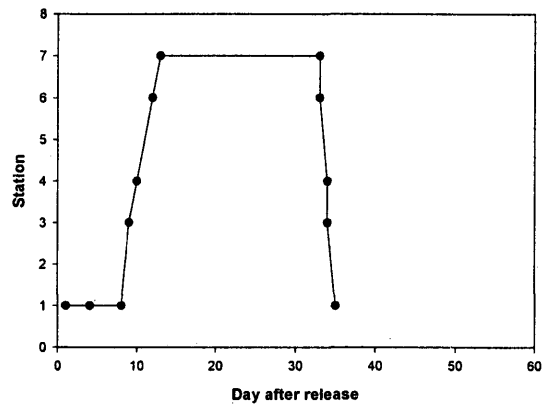
Fish 25



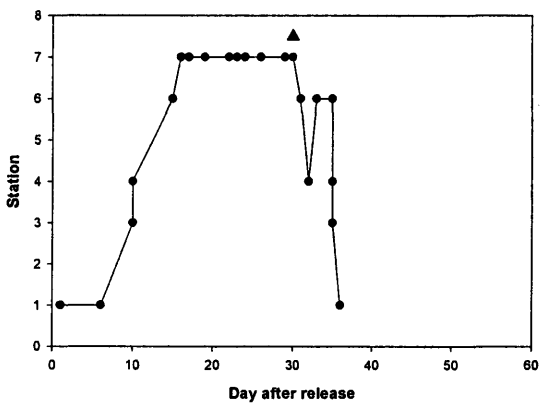
Fish 33



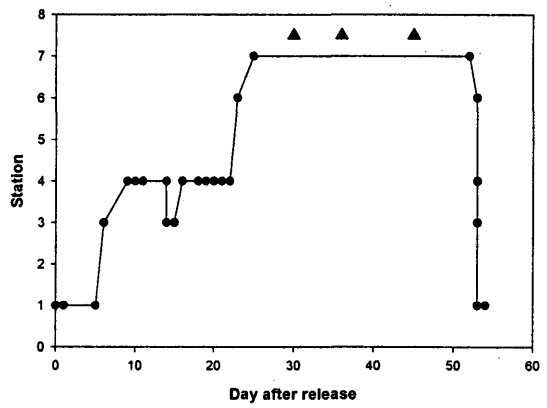
Fish 36



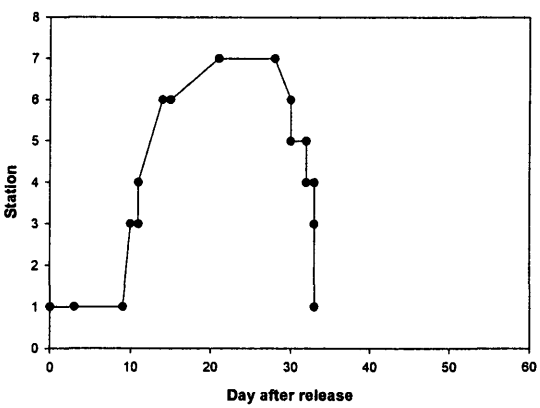
Fish 39



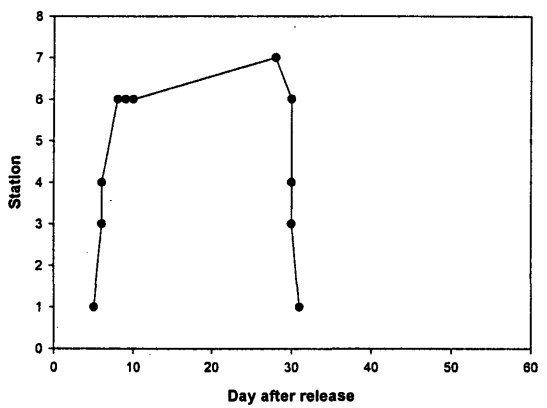
Fish 42



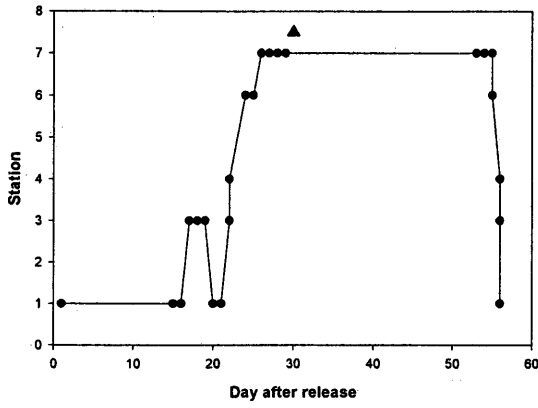
Fish 43



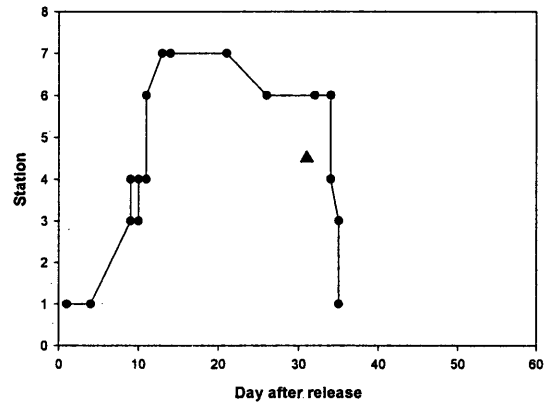
Fish 44



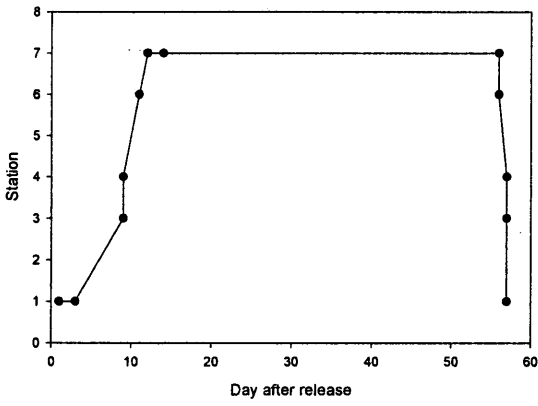
Fish 45



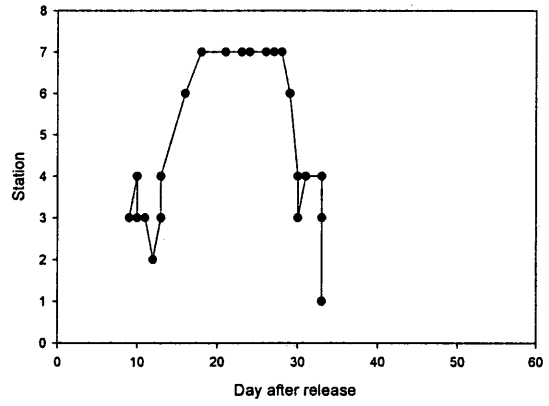
Fish 46



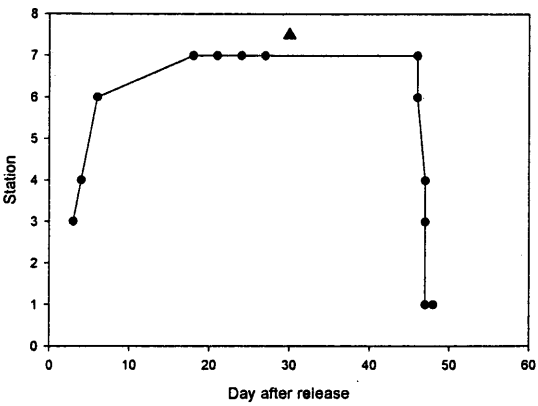
Fish 47



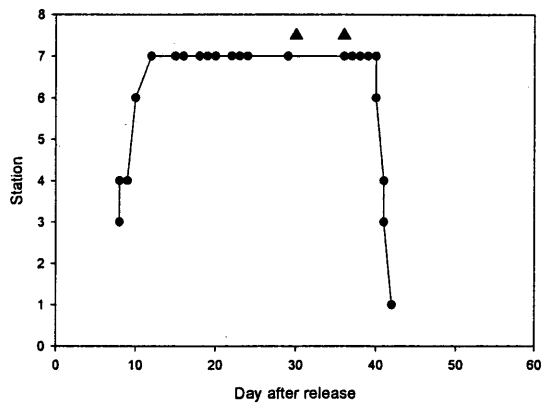
Fish 74



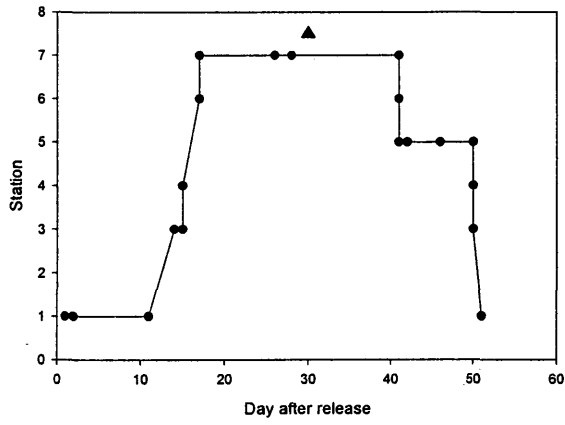
Fish 82



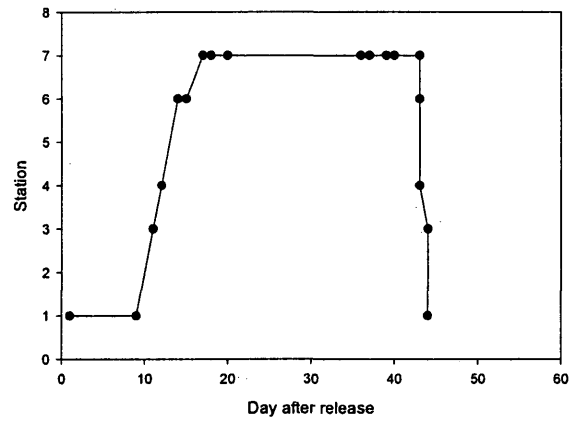
Fish 93



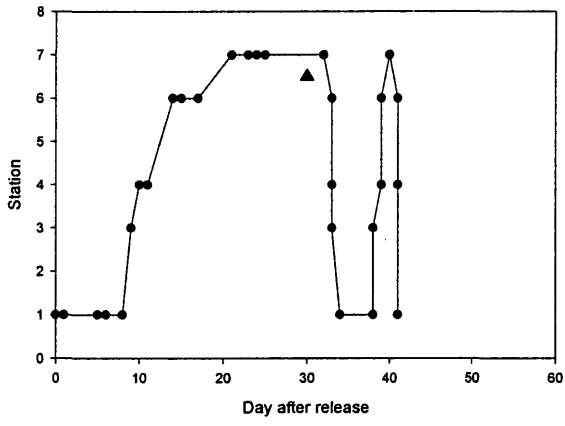
Fish 101



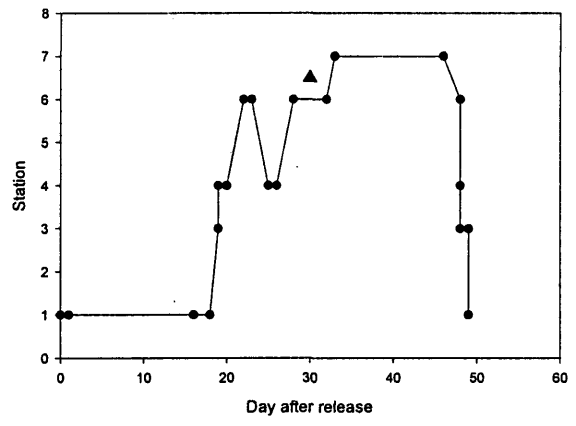
Fish 111



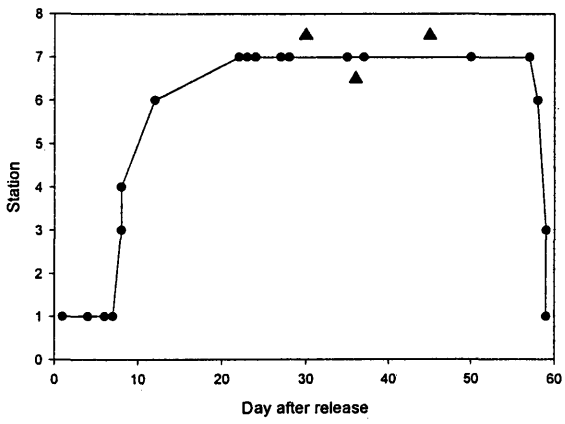
Fish 116



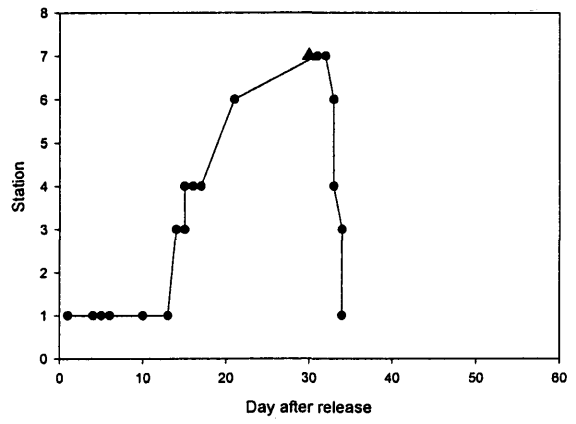
Fish 122



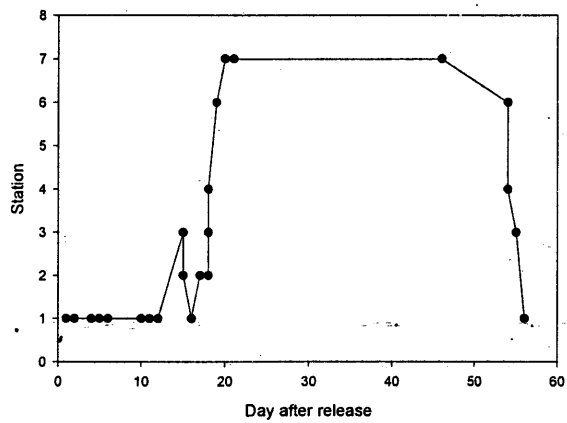
Fish 133



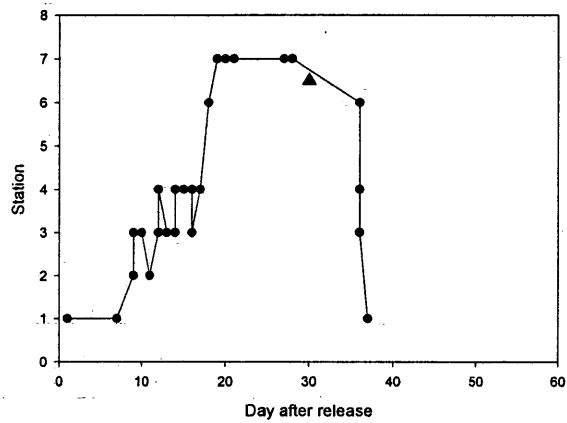
Fish 138



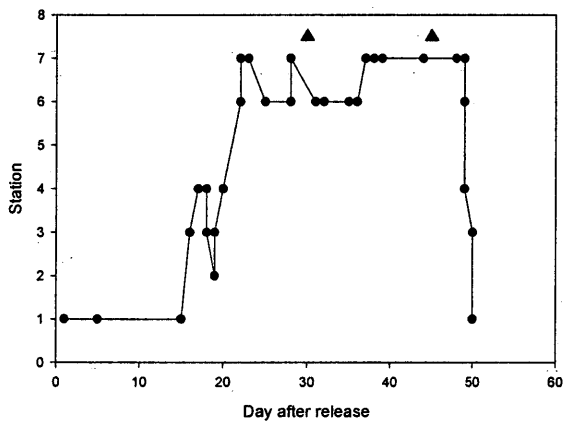
Fish 150



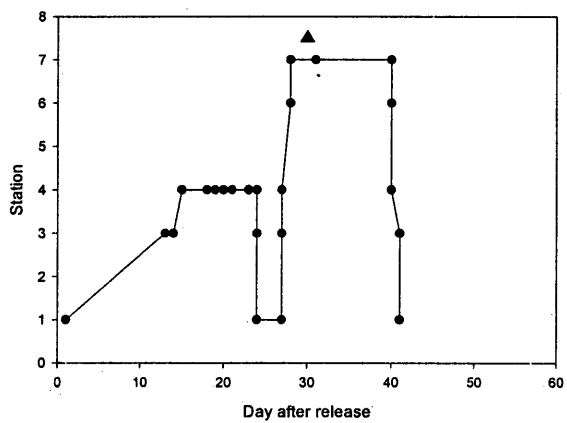
Fish 152



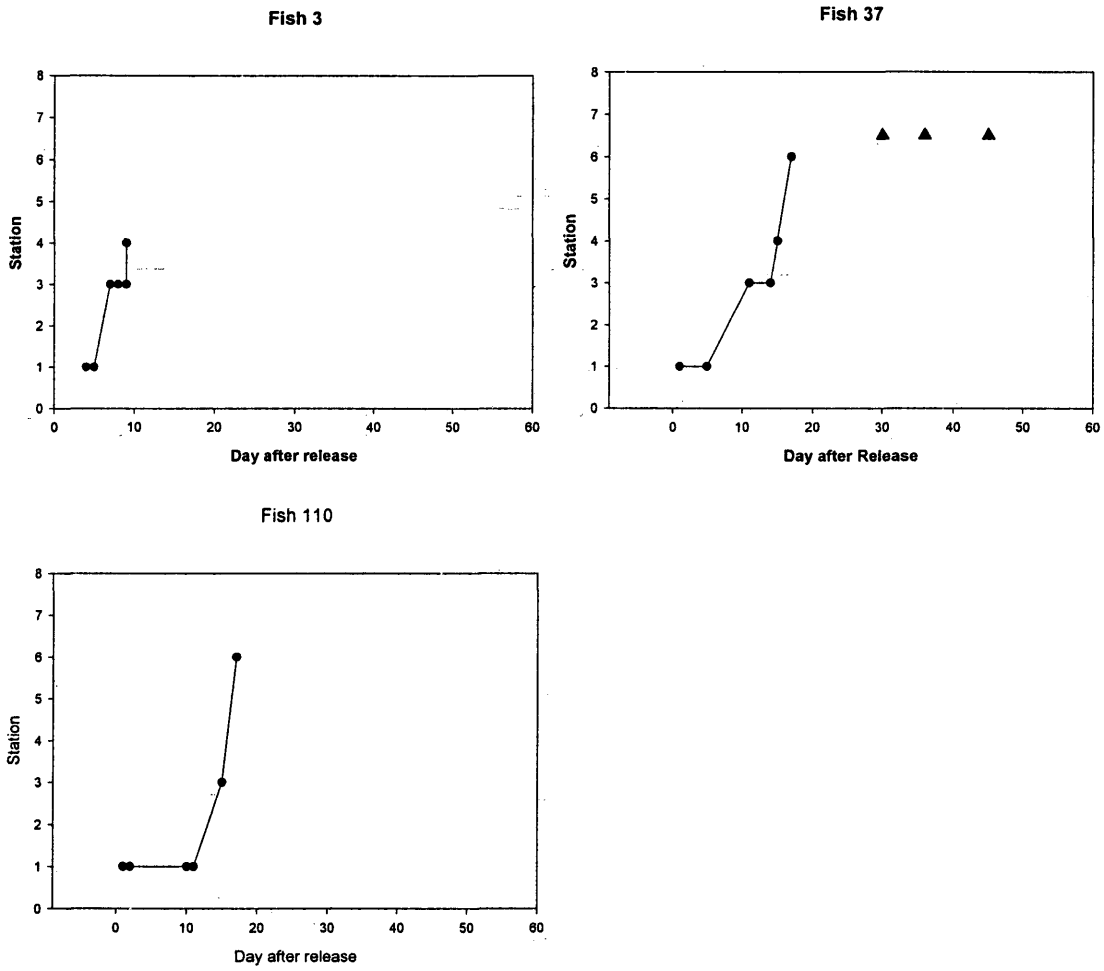
Fish 156



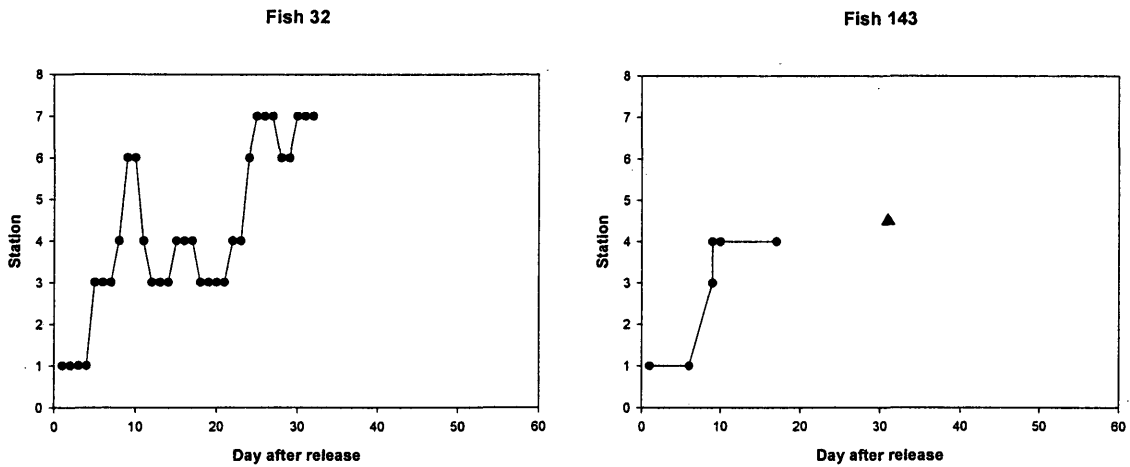
Fish 157



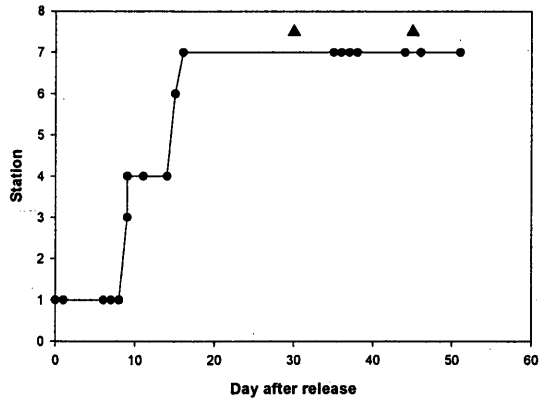
F: Abruptly ceased detection on the upstream migration:



G. Ceased detection during the residency period:

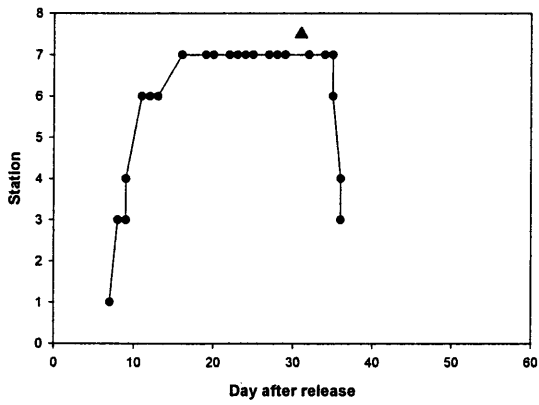


Fish 145

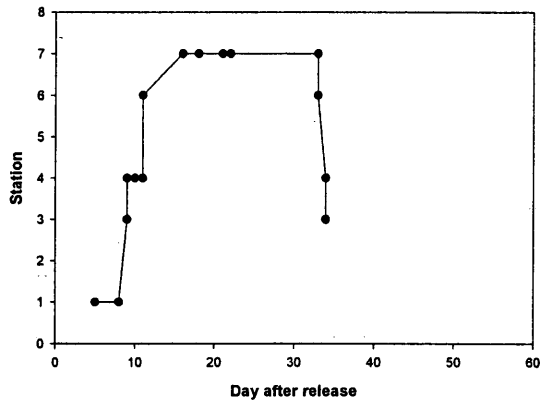


H. Ceased detection on the emigration:

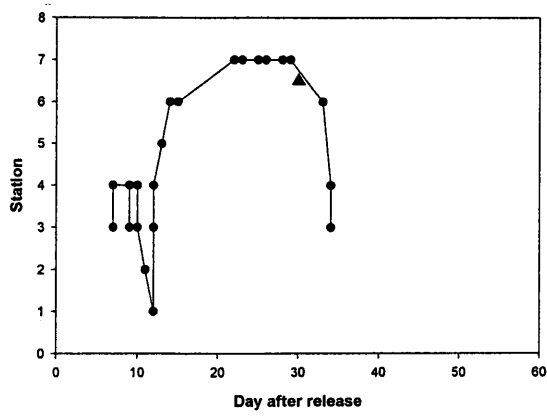
Fish 12



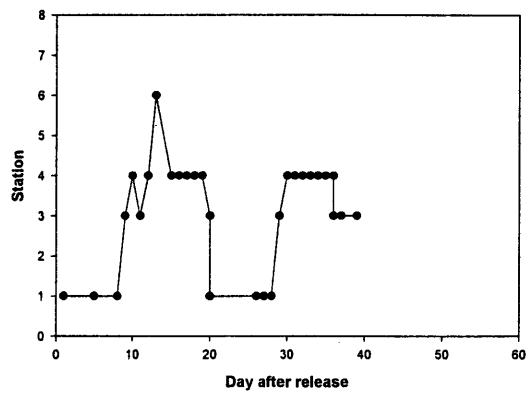
Fish 20



Fish 35



Fish 170



APPENDIX 3

Figures 1 – 5. Residence times, upstream/exit transit and minimum rate of progress times for all American shad (*Alosa sapidissima*) that resided within the James River.

Figure 1. Residence times for all individual American shad (*Alosa sapidissima*) that resided within the James River. Letters denote different migratory patterns defined in Chapter 1.

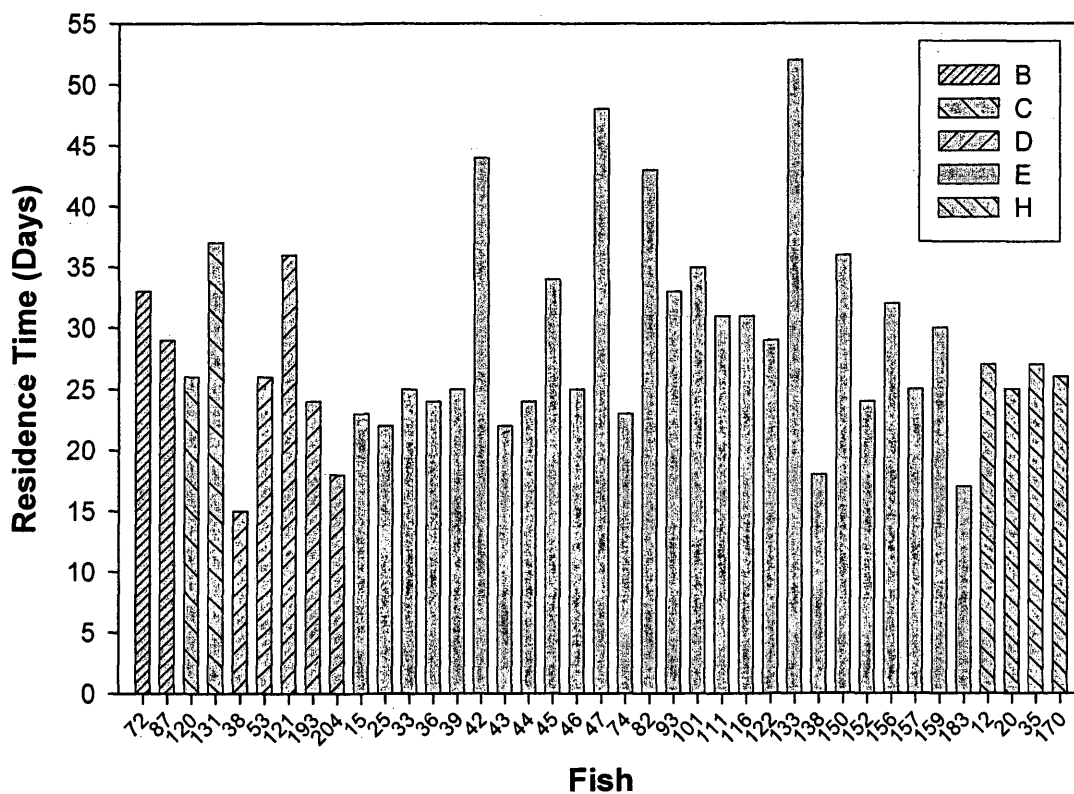


Figure 2. Upriver minimum rates of travel for all individual American shad (*Alosa sapidissima*) that resided within the James River. Letters denote different migratory patterns defined in Chapter 1.

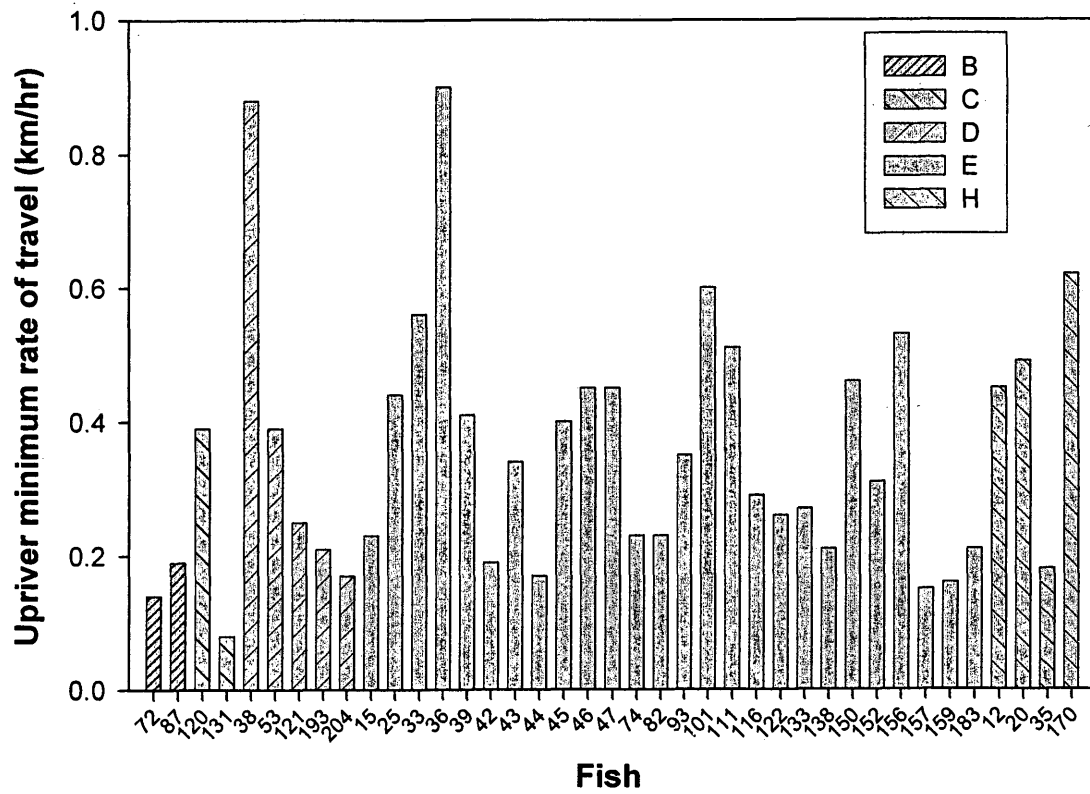


Figure 3. Upriver transit times for all individual American shad (*Alosa sapidissima*) that resided within the James River. Letters denote different migratory patterns defined in Chapter 1.

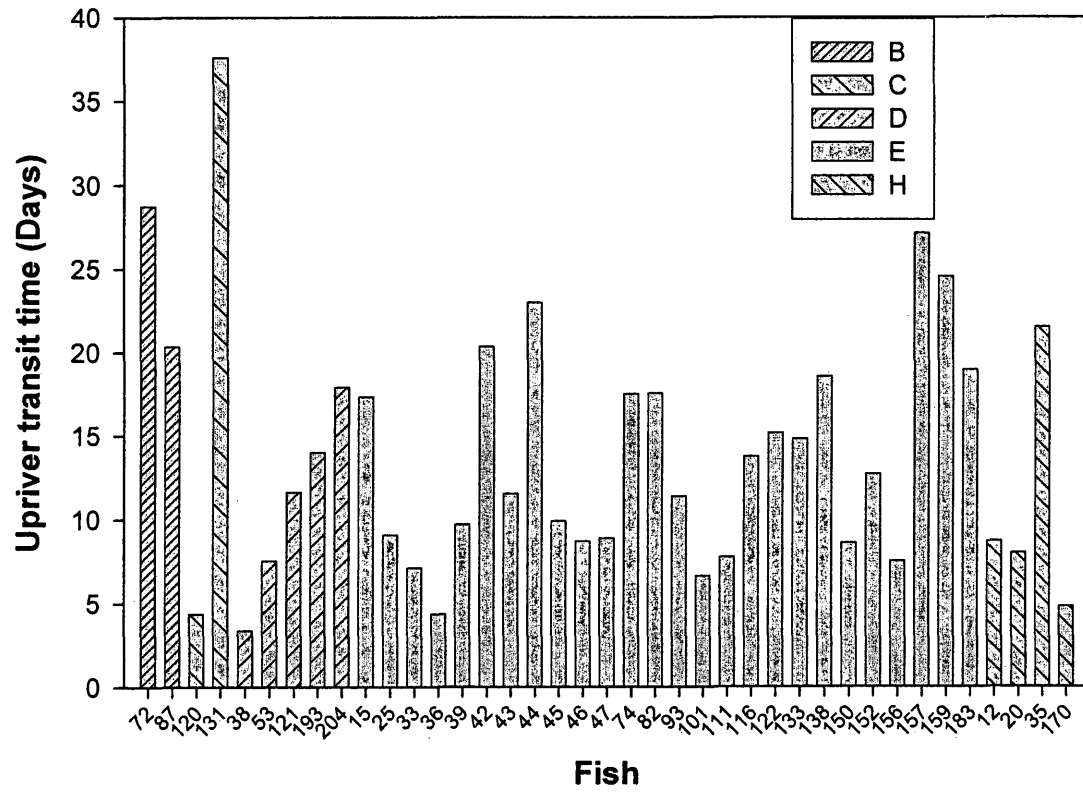


Figure 4. Exit minimum rates of travel for all individual American shad (*Alosa sapidissima*) detected exiting the river at Hog Island after residence within the James River. Letters denote different migratory patterns defined in Chapter 1.

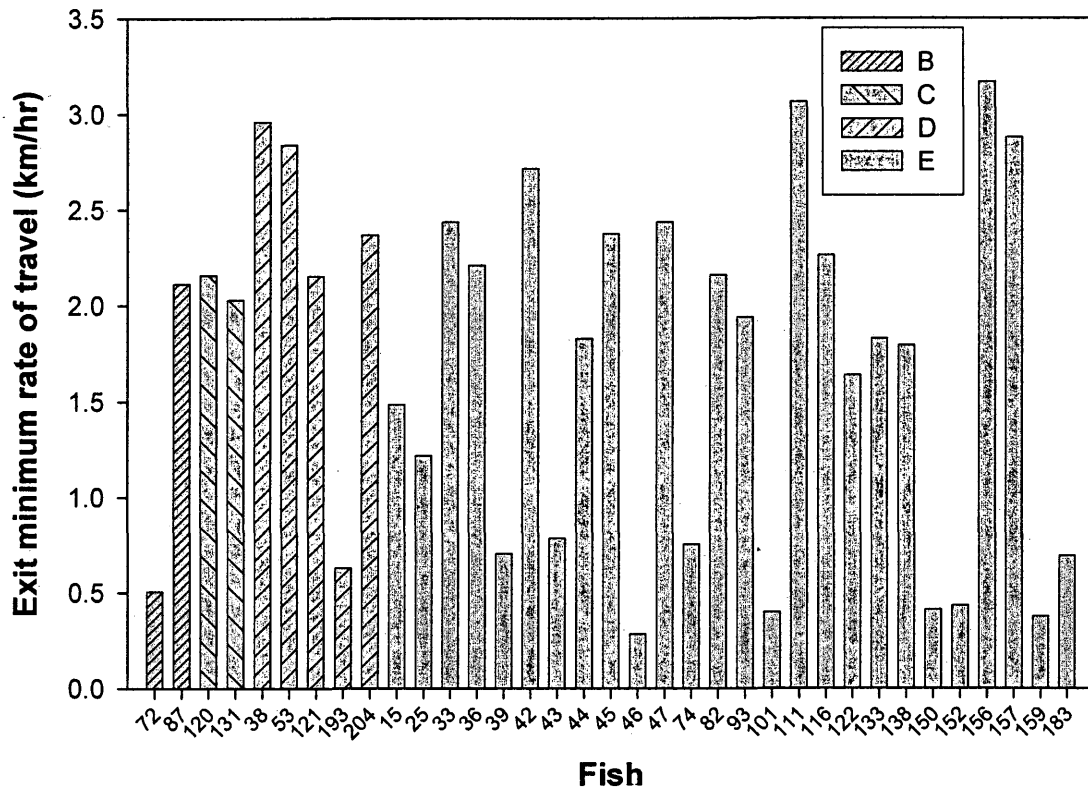
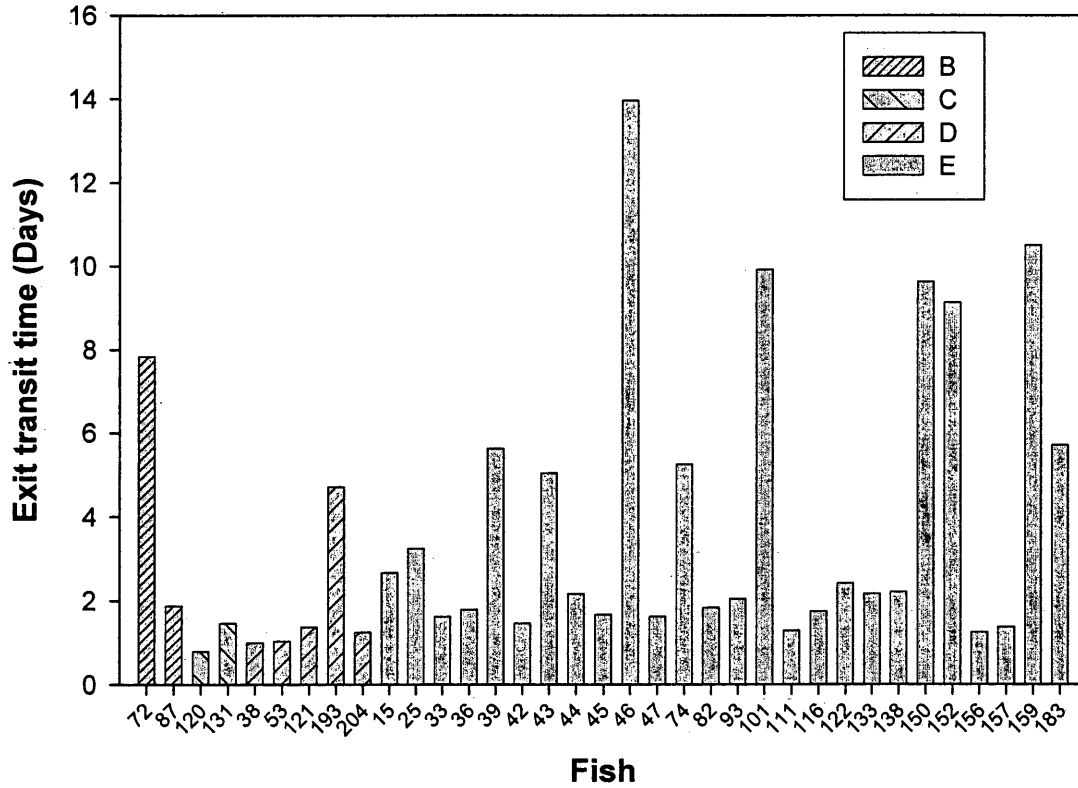


Figure 5. Exit transit times for all individual American shad (*Alosa sapidissima*) detected exiting the river at Hog Island after residence within the James River. Letters denote different migratory patterns defined in Chapter 1.



APPENDIX 4

Sampling date, gear type, location, number of eggs and larvae, and physical data for all
American shad (*Alosa sapidissima*) ichthyoplankton samples collected in the James
River, 2005.

Date	Gear	rkm	Eggs	Yolksac	Post yolk-sac	Water temp °C	Tidal stage	Conductivity	DO mg/ml	pH
4/28/2005	Bongo	91.5	0	0	0	16.50	Ebb	0.144	7.70	7.86
4/21/2005	Bongo	93.5	0	0	0		Ebb			
4/28/2005	Bongo	96.5	0	0	1	16.51	Ebb	0.148	7.57	7.65
4/21/2005	Bongo	99.5	0	0	0		Ebb			
4/21/2005	Bongo	100.5	0	0	1		Ebb			
4/28/2005	Bongo	102.5	0	0	1	16.25	Ebb	0.157	8.00	7.69
4/21/2005	Bongo	105.5	0	0	0		Ebb			
4/28/2005	Bongo	109.5	0	0	1	16.33	Ebb	0.162	8.44	7.77
4/21/2005	Bongo	110.5	0	0	0		Slack			
4/28/2005	Bongo	111.5	0	0	0	16.67	Ebb	0.163	8.83	7.91
4/21/2005	Bongo	118.5	0	0	0		Flood			
4/28/2005	Bongo	119.5	0	0	0	17.10	Ebb	0.158	9.44	7.90
4/28/2005	Bongo	124.5	1	4	1	17.10	Ebb	0.162	9.48	7.94
4/28/2005	Bongo	127.5	0	7	5	17.39	Ebb	0.171	9.17	7.98
4/28/2005	Bongo	132.5	3	21	5	17.10	Ebb	0.190	9.11	7.97
4/26/2005	Bongo	133.5	1	20	2	17.80	Ebb	0.163	9.09	8.15
5/5/2005	Bongo	133.5	0	8	1	16.53	Ebb	0.142	8.95	7.92
4/12/2005	Bongo	134.5	0	8	0		Ebb			
4/20/2005	Bongo	135.5	0	122	1		Flood			
4/28/2005	Bongo	137.5	5	17	1	17.80	Ebb	0.189	9.21	8.36
4/26/2005	Bongo	138.5	0	35	2		Ebb			
4/12/2005	Bongo	139.5	5	2	0		Ebb			
5/5/2005	Bongo	139.5	1	11	0	15.91	Ebb	0.152	9.51	7.98
5/5/2005	Bongo	141.5	0	3	0	16.25	Flood	0.149	9.57	8.13
4/26/2005	Bongo	142.5	2	56	1		Ebb			
4/28/2005	Bongo	142.5	0	9	0	17.01	Ebb	0.190	9.05	8.09
4/12/2005	Bongo	143.5	6	0	0		Ebb			
4/20/2005	Bongo	143.5	0	110	0		Flood			
4/12/2005	Bongo	146.5	0	1	0		Ebb			
5/5/2005	Bongo	146.5	0	6	0	15.75	Slack	0.159	9.71	8.03
4/28/2005	Bongo	147.5	0	6	0	16.30	Ebb	0.183	9.28	8.07
4/20/2005	Bongo	149.5	0	93	0		Slack			
4/26/2005	Bongo	149.5	0	11	1		Ebb			
4/28/2005	Bongo	152.5	1	1	0	17.08	Ebb	0.184	9.65	8.30
4/12/2005	Bongo	154.5	0	0	0		Ebb			
4/20/2005	Bongo	154.5	1	53	0		Ebb			
4/26/2005	Bongo	154.5	0	0	0		Ebb			
5/5/2005	Bongo	154.5	0	5	0	15.68	Ebb	0.150	10.21	8.30

Date	Gear	rkm	Eggs	Yolksac	Post yolk-sac	Water temp °C	Tidal stage	Conductivity	DO mg/ml	pH
4/20/2005	Bongo	158	0	141	0	19.56	Ebb	0.148	10.73	9.21
4/26/2005	Bongo	158	0	0	0	15.01	Ebb	0.148	9.98	8.12
4/28/2005	Bongo	158	0	8	0	18.24	Ebb	0.181	9.96	9.05
5/5/2005	Bongo	158	0	12	0	16.32	Slack	0.151	10.51	8.84
4/21/2005	Anchored	90.5	0	0	0	16.66	Flood	0.127	10.58	8.25
4/21/2005	Anchored	95.5	0	0	2	16.79	Flood	0.131	11.17	8.57
4/21/2005	Anchored	100.5	0	0	1	17.13	Flood	0.134	11.11	8.57
4/21/2005	Anchored	105.5	0	0	0	18.06	Flood	0.141	12.62	9.11
4/21/2005	Anchored	110.5	0	0	0	18.73	Flood	0.143	13.36	9.32
4/21/2005	Anchored	115.5	0	0	2	19.20	Flood	0.145	13.68	9.38
4/12/2005	Anchored	124.5	0	0	0	15.89	Ebb	0.120	9.08	8.23
4/12/2005	Anchored	129.5	0	0	0	16.28	Ebb	0.126	7.88	7.88
4/12/2005	Anchored	135.5	1	0	0	16.64	Ebb	0.132	9.31	7.95
4/20/2005	Anchored	135.5	0	0	0	17.20	Flood	0.159	9.12	8.16
4/26/2005	Anchored	135.5	0	1	1	16.31	Ebb	0.149	9.62	8.21
4/12/2005	Anchored	140.5	0	0	0	16.91	Ebb	0.137	9.39	8.06
4/20/2005	Anchored	140.5	0	0	0	17.38	Flood	0.167	9.41	8.06
4/26/2005	Anchored	140.5	1	0	0	15.50	Ebb	0.146	9.53	8.02
4/12/2005	Anchored	145.5	71	0	0	15.45	Ebb	0.134	9.73	8.07
4/20/2005	Anchored	145.5	0	0	0	19.13	Flood	0.159	9.01	8.57
4/26/2005	Anchored	145.5	0	1	0	14.98	Ebb	0.160	9.50	8.00
4/12/2005	Anchored	150.5	3	0	0	15.62	Ebb	0.135	9.69	8.04
4/20/2005	Anchored	150.5	0	0	0	17.74	Ebb	0.149	9.07	7.97
4/26/2005	Anchored	150.5	0	0	0	14.87	Ebb	0.144	9.74	8.05
4/12/2005	Anchored	155.5	0	0	0	16.33	Ebb	0.136	9.67	8.20
4/20/2005	Anchored	155.5	0	1	0	19.00	Ebb	0.146	9.47	8.66
4/26/2005	Anchored	155.5	0	0	0	15.01	Ebb	0.146	9.83	8.10

VITA

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Born in Richmond, Virginia, 20 September 1978. Graduated from Meadowbrook High School in 1996. Earned a B.A. in Biology from the University of Richmond in 2001. Entered the master's program in College of William and Mary, School of Marine Science in 2003.