USE OF ACOUSTIC TELEMETRY TO IDENTIFY SPAWNING RIVER AND SPAWNING MIGRATION PATTERNS OF AMERICAN SHAD IN THE ALBEMARLE SOUND, NORTH CAROLINA

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Abstract

American Shad *Alosa sapidissima* is an economically, culturally, and ecologically important anadromous species, which undertakes a significant spawning migration, swimming from the ocean into areas far upstream in coastal rivers to reproduce. The species has a large range in the western Atlantic, occurring from Nova Scotia to Florida. However, because American Shad generally return to natal rivers to spawn, each major river likely has its own spawning stock. Fish entering the Albemarle Sound, North Carolina, to spawn primarily ascend one of two rivers at the far western end of the estuary; the Roanoke River or the Chowan River. Determining the current primary spawning river for American shad in the Albemarle Sound would help inform research efforts and resource management decisions to improve stocks. American Shad were captured in Albemarle Sound, tagged with sonic transmitters, and tracked using an array of acoustic receivers. Of 62 fish which made detectable migrations during six study years, 55 ascended the Chowan River, while only 5 ascended the Roanoke River, and 2 entered other rivers. These telemetry results suggest the Chowan River and its tributaries are the major spawning rivers for American Shad in Albemarle Sound.

Introduction

American Shad *Alosa sapidissima* plays an important ecological and economic role in freshwater, estuarine, and marine environments at different points during its anadromous life cycle. American Shad has a relatively wide native range, occurring from St. Lawrence, Canada to the St. Johns River in Florida (Limburg et al. 2003). In the past, when abundances were much higher, the species likely played an important role in ecosystem nutrient and energy cycling among freshwater, estuarine, and marine ecosystems (Hall et al. 2012). The species is also economically important to the commercial and recreational fishing industries along the North American Coast. Spawning migrations begin as water temperatures warm, starting in southern rivers and progressing northward.

Like many anadromous species, American Shad has long been thought to exhibit some degree of natal homing (Hollis 1948), even exhibiting fidelity to specific tributaries (Carscadden and Leggett 1975). Using chemical signals in otoliths, the natal rivers of adult American Shad can be accurately determined (Thorrold et al. 1998). Working in the York River in Virginia, Walther et al. (2008) found that only a small percentage of fish were strays from other rivers (6%), indicating that American Shad largely return to spawn in their natal rivers. However, within the natal river, stray between individual tributaries was more common (Walther et al. 2008). Working in the Lehigh River, a tributary of the Delaware River, Hendricks et al. (2002) found a high percentage of tributary fidelity, and even some evidence of migration route preference. Fish migrating up the Lehigh River were found more frequently on the side of the Delaware River influenced by the Lehigh River (Hendricks et al. 2002).

In North Carolina, American Shad migrations occur in every major coastal river, including the Albemarle Sound and its primary tributaries, the Roanoke and Chowan Rivers. American Shad in this system are considered to be iteroparous (repeat spawners) (Leggett and

Carscaddden 1978; Hasselman et al. 2013). From a fishery management perspective, American Shad in the Albemarle Sound are considered a single population. The Atlantic States Marine Fisheries Commission (ASMFC) assessed that stock as being "low but stable" (ASMFC, 2007), and more recently as "sustainable" and "not overfished" (ASMFC, 2020). However, because American Shad home to their natal rivers, fish migrating up the Roanoke, Chowan, or other rivers that drain into the sound may be distinct populations. Little population genetics work has been conducted in the Albemarle Sound. Genetic analysis of American Shad collected from the Roanoke River and Chowan River tributaries using a suite of 12 microsatellite markers indicated a single genetic population. However, the methods employed may not be sufficient to detect genetic differentiation at such a small geographic scale (Evans and McGrady 2019). No work on natal homing or straying using chemical signals in otoliths has been conducted in the sound. From a conservation perspective, determining which of the Albemarle Sound's major tributaries are primarily used by American Shad is a priority.

The Albemarle Sound is a large, oligohaline estuary located at the confluence of the Chowan and Roanoke rivers, eventually draining into the Atlantic Ocean through Oregon Inlet (Figure 1A). The sound is 88.5 km long, averaging 11.3 km wide, and 5 to 6 m deep (Street 1975). The Chowan River and its tributaries, the Blackwater, Nottoway, and Meherrin rivers, drain about 12,000 km^2 of land in Virginia and North Carolina. The river is formed by the union of the Blackwater and Nottoway rivers at the Virginia-North Carolina border; the Meherrin River enters the Chowan River 18.6 rkm downstream from their confluence. As it enters Albemarle Sound, the Chowan River is 4.4 km wide. The Roanoke River is significantly larger, draining about 25,300 km^2 from the Blue Ridge Mountains in Virginia to the coastal plain in North Carolina. It is only 1 km wide as it enters Albemarle Sound.

The Chowan and its tributaries are relatively unimpeded. Dams limit access to only about 18% of historically available habitat (based on rkm). The Emporia Dam (FERC No. 5998) impounds the Meherrin River 138 rkm upstream from the confluence with the Chowan River. Fish passage has been prescribed and a fish lift is in place at Emporia Dam, but it is generally inefficient for American Shad (E. Brittle, Virginia Department of Game and Inland Fisheries, pers. comm.). Baskerville Millpond Dam impounds the Nottoway River 175 rkm from its confluence with the Chowan. There are no known impoundments on the Blackwater River. In the Chowan River, American Shad spawning occurs upstream of the confluence of the Blackwater and Nottoway rivers in Virginia, as well as portions of the Meherrin River in North Carolina and Virginia (ASMFC 2007).

By contrast, dams limit access to 60% of historically available habitat in the Roanoke River. Roanoke Rapids and Gaston dams (FERC No. 2009) impede upstream movement of American Shad 221 rkm upstream from the mouth of the river. Fish passage has been prescribed at Roanoke Rapids but has not yet been implemented because of concerns about safe and effective downstream passage out of the reservoirs (Harris and Hightower 2011), and failure of the Roanoke River American Shad spawning population to reach the agreed-upon population target to trigger passage. American Shad spawning occurs below the Roanoke Rapids Dam, between 208 and 221 rkm upstream (Sparks and Hightower 1998; Hightower and Sparks 2003). Historically, migrations were reported as far as 321 rkm upstream (Moseley et al. 1877), with a reported upper limit at Salem, Virginia, 557 rkm upstream (McDonald 1878).

As part of the Federal Energy Regulatory Commission's relicensing of the Roanoke Rapids and Gaston dams, a number of studies were conducted on the Roanoke River population of American Shad, including the development of a model to estimate the number of adult females spawning in the Roanoke River. The precise methodology behind this population estimate has changed over the years, and the estimate is itself tremendously variable, however it remains an important tool for resource managers. Those estimates have ranged from 2,500 to 40,000 adult fish spawning in the Roanoke River, depending on the year (Harris and Hightower 2012; Hughes and Hightower 2015; J. McCargo, North Carolina Wildlife Resources Commission pers. comm.). Before dams restricted access, the Roanoke River population of spawning adults was estimated at 797,000 fish, based on the acreage of suitable habitat in the Roanoke and Dan rivers (Hightower and Wong 1997). Comparatively, almost no data exist on the spawning population in the Chowan River and its tributaries.

There are known spawning areas in both the Chowan and Roanoke River basins, but it is unclear if one river hosts a larger spawning population than the other. The objective of this study is to use acoustically-tagged fish and telemetry to determine which river basins are used by adult American Shad during their spawning runs. If substantial numbers of American Shad ascend the Roanoke River to Roanoke Rapids Dam, resource managers may wish to continue prioritizing efforts to rebuild the stock and implement safe and effective passage on the Roanoke River. Alternatively, if more American Shad ascend the Chowan River and then the Meherrin River to Emporia Dam, resource managers should allocate additional efforts to improve fish passage and habitat within the Chowan basin. In addition, these data will be useful to fishery managers in North Carolina and Virginia in guiding future studies aimed at assessing the population status of American Shad in the Chowan basin.

Methods

North Carolina Division of Marine Fisheries (NCDMF) personnel captured, tagged, and released adult American Shad in 2013, 2014, 2016, 2017, 2018, and 2019. Funding was not available in

2015. Typically, tagging was scheduled to take place outside of the commercial fishing season, with the majority of fish being tagged after the season had concluded. Fish were captured using gill nets, but stretch mesh size, net length, and soak time varied between years (Table 1). After the initial year, which had very long soak times and low catch, average soak times ranged from 60 to 154 minutes. In all years of the study, nets were set near the NC Highway 32 Bridge, approximately 12.5 rkm downstream from the confluence of the Chowan and Roanoke rivers (Figure 1A). In 2013 and 2014 nets were set on both the north and south sides of the sound, but the majority of fish were captured on the north side. In 2016, 2017, and 2018, effort was not equal between the north and the south sides of the sound. More nets were set on the north side because of low previous catch in south sets. In 2019, all nets were set on the north side. Mortality data during sampling were not consistently recorded during all years, but in 2013 and 2014 sampling mortality was high, approximately half of all American Shad caught were deceased.

Captured shad were implanted with a VEMCO V9 series 180 kHz coded acoustic transmitter that measured 27.5 mm in length and weighed 2.7 g in water. The VEMCO tags had a 300 m detection range and a battery life of 652 days to document repeat spawning. Tagged fish were measured to the nearest millimeter (fork and total length) and assigned a sex if possible. Tags were inserted carefully through the esophagus into the stomach with a pencil eraser, and the fish were then returned to the water. A total of 266 fish were tagged during the six years of the study.

As part of ongoing studies of Atlantic Sturgeon *Acipenser oxyrinchus*, Striped Bass *Morone saxatilis*, and Largemouth Bass *Micropterus salmoides*, an array of acoustic receivers was already in place at ocean inlets and throughout Albemarle Sound and the Chowan and Roanoke rivers as well as smaller tributary rivers. In 2013, Dominion Energy installed additional receivers in the upper Roanoke River below Roanoke Rapids Dam. In subsequent years, additional receivers were placed at strategic locations in the Meherrin, Nottoway, and Blackwater rivers in the Chowan basin by personnel from the Virginia Department of Game and Inland Fisheries. Purchase, operation, and maintenance of receivers was a collaboration among researchers from NCDMF, North Carolina Wildlife Resources Commission (NCWRC), North Carolina State University (NCSU), Virginia Department of Game and Inland Fisheries (VADGIF), and Dominion Energy. In total, 61 receivers were in place at the conclusion of the study (Figure 1B). While most locations had only one receiver, several sites at wide water bodies (NC 32 Bridge and US 17 Bridge) had multiple receivers. Data were periodically downloaded from the receivers by researchers from NCDMF, NCWRC, VADGIF, and Dominion Energy.

Data from the receivers were compiled by year and used to track fish movement throughout the system. Several fish behaviors were defined based on the telemetry data, including fallback post tagging, and what constituted a likely spawning migration. A fish was considered to have initiated a spawning migration if it was detected by receivers at the mouth of any river and/or was subsequently detected further upriver. To aid in interpretation and discussion, spawning migrations were further classified as being complete, partial, or upstream only, based on the detection record. In a complete migration, the fish was detected moving upstream, back downstream, and was last detected leaving Albemarle Sound past the Manns Harbor, Pirate Cove, or Oregon Inlet receivers (Figure 1B). In a partial migration, the fish was detected moving upstream and began to move back downstream before the last detection. In an upstream only migration, the fish was only detected moving in the upstream direction. We recognize that the latter two categories could be the result of mortality (e.g., spawning, fishing related, delayed tagging, etc.), tag loss, tag failure, or missed detections. Although, the last two causes were unlikely given tag life and the extent and distribution of receivers. For fish with complete and partial detection records, the time spent above the most upstream receiver encountered was calculated. A fish was considered to have exhibited fallback behavior if it was detected by receivers closer to the mouth of the sound than its capture location, indicating that the fish was no longer moving upstream. Given the uncertain nature of passive telemetry tracking, fish mortality was difficult to define accurately.

Statistical comparisons of size and sex distribution were made between fish that were tagged and fish that were detected, between those that exhibited fallback and those that did not, and between fish that made migrations and those that did not. Differences in fish size were analyzed with a two sample t-test, analyzing each sex separately. Differences in sex ratio were analyzed with a two proportions z-test comparing each sex separately. In addition, comparisons of time between first and last detection and time spent at or above the most upstream receiver encountered were made between spawning rivers using analysis of variance.

Results

Between 2013 and 2019, NCDMF captured 366 American Shad and tagged 266. Approximately half of all fish tagged were female, 20% were male, and 30% could not be accurately sexed. Females ranged in size (total length) from 437 to 572 mm with a mean ± SE length of 498 ± 2 mm (Figure 2). Males were typically smaller, ranging from 442 to 549 mm with a mean ± SE length of 487 ± 4 mm. Fish with an unknown sex ranged from 439 to 584 mm with a mean ± SE length of 497 ± 3 mm. Precise capture methods and soak times varied between years of the study (Table 1), making overall catch per unit effort difficult to determine accurately. Of the 266 fish tagged, 212 were subsequently detected by receivers. The 56 fish not detected are presumed to be mortalities. There was no difference in the size (female t = 0.89, df = 42.59, P = 0.37; male t =

-1.58, df = 12.39, P = 0.13; unknown t = 1.15, df = 28.43, P = 0.25) or sex distribution (female $\chi^2 < 0.01$, df = 1, P = 0.92; male $\chi^2 = 0.03$, df = 1, P = 0.85; unknown $\chi^2 = 0.13$, df = 1, P = 0.72) between tagged fish and detected fish.

Fallback behavior was observed in 114 of the 212 fish detected, approximately half of all fish. Typically, fish fell back to the Bluff Point, Laurel Point, or Manns Harbor receivers, between 5.5 and 79.5 rkm downstream from the capture location (Figure 1B). Of the 114 fish that exhibited fallback behavior, 28 subsequently made detectable migrations, resuming upstream movement after a mean ± SE of 11 ± 1 days. In the 86 instances where fish fell back but did not make a detectable migration, fish may have exited the sound and abandoned their spawning run. There was no difference in size (female t = 1.77, df = 98.77, P = 0.08; male t = 0.60, df = 34.34, P = 0.55; unknown t = 0.31, df = 59.96, P = 0.76) between fish that exhibited fallback behavior and fish that did not. There was no difference in the proportion of females ($\chi^2 <$ 0.01, df = 1, P = 0.96) or males ($\chi^2 = 1.11$, df = 1, P = 0.29) that fell back and those that did not, but a significantly lower proportion of fish with unknown sex exhibited fallback behavior ($\chi^2 =$ 4.91, df = 1, P = 0.03).

Over the six years of the study, 62 of the 212 fish detected appear to have made upstream migrations. More than half were female (55%), 15% were male, and 31% were of unknown sex. Females had a mean ± SE length of 495 ± 4 mm. Again, males were typically smaller, with a mean ± SE length of 481 ± 4 mm. Fish with an unknown sex had a mean ± SE length of 493 ± 5 mm. There was no difference in the size (female t = 0.62, df = 63.34, P = 0.53; male t = 1.57, df = 32.53, P = 0.13; unknown t = 0.53, df = 39.70, P = 0.59) or sex distribution (female $\chi^2 = 0.44$, df = 1, P = 0.50; male $\chi^2 = 1.33$, df = 1, P = 0.25; unknown $\chi^2 = 0.01$, df = 1, P = 0.90) between detected fish that made migrations and those that did not. Of the fish that made upstream migrations, 55 entered the Chowan, 5 entered the Roanoke, 1 entered the Alligator River, and 1 entered the Pasquotank River. A single male made a migration up the Chowan River in 2013 and remarkably returned the following year to make another migration, meaning 56 Chowan River migrations were detected and 63 migrations in total (Figure 3).

Fish that underwent migrations typically lingered in the sound post capture, then rapidly swam upstream, halted upstream movement for a variable amount of time (presumably to spawn), then moved rapidly downstream and exited the sound. The mean ± SE time between first and last detection was 34 ± 3 days. Nineteen fish had a complete detection record (i.e., made a migration and were detected leaving the sound), 20 had a partial detection record, and 24 were only detected during the upstream portion of their migration. Typical movements were best demonstrated by fish with a complete detection record (Figure 4), for which the mean ± SE time between first and last detection was 40 ± 3 days. Fish with a complete or partial detection record (i.e., that presumably spawned) spent a mean ± SE of 20 ± 2 days (n = 39) at or above the most upstream receiver encountered.

Of the 56 Chowan River migrations, 39 remained in the upper Chowan River, 8 entered the Meherrin River, and 9 entered the Nottoway River. None utilized the Blackwater River. For fish that had a complete detection record, there was not a significant difference (ANOVA: F = 1.553, df = 2, P = 0.244) in mean ± SE time between first and last detection between rivers: 48 ± 7 days (n = 7) for the Meherrin River, 34 ± 4 days (n = 5) for the Nottoway River, 36 ± 5 days (n = 6) for the Chowan River. For fish with a complete or partial detection record, time spent at or above the most upstream receiver encountered did not differ (ANOVA: F = 0.048, df = 2, P = 0.953) between fish that entered tributaries or remained in the Chowan River. The fish that remained in the Chowan River typically reached the area above the Meherrin River, but below the confluence of the Nottoway and Blackwater rivers, between rkm 67 and 77. Fish remained in this area for a mean ± SE of 20 ± 3 days (n = 19). Fish that ascended the Meherrin River spent an average of 20 ± 3 days (n = 8) above the most upstream receiver encountered, typically reaching at least as far upstream as the Boones Bridge receiver, 47 rkm from the confluence with the Chowan River. One fish passed the Branches Bridge receiver, an additional 26 rkm upstream. Fish that ascended the Nottoway River passed at least as far upstream as the Upper Nottoway receiver, 12 rkm from the confluence with the Chowan River, and remained there for an average of 19 ± 3 days (n = 9). A single fish passed the Highway 95 receiver 122 rkm from the confluence with the Chowan River.

Five fish migrated up the Roanoke River, more than ten times fewer than migrated up the Chowan River and its tributaries. Only one fish had a complete detection record; the time between first and last detection was 35 days. Two fish ascended as far as the Weldon Ramp receiver at rkm 205, but were not detected at the Roanoke Rapids Dam. One remained for 3 days, the other for 33 days. Only one fish ascended as far as the Roanoke Rapids Dam at rkm 221 where it remained for 51 days. Two fish did not migrate up the Chowan or Roanoke rivers. One was detected entering the Alligator River (Figure 1A) where it remained for 70 days before again being detected leaving the river. Another fish was detected near the mouth of the Pasquotank River (Figure 1A) where it spent four days.

Discussion

American Shad were tracked in North Carolina's Albemarle Sound using passive acoustic telemetry to determine which river basins, primarily the Chowan or Roanoke, are used for spawning. Six years of tracking data indicated the majority of the 62 acoustically-tagged American Shad that made apparent spawning runs during spring migrations ascended the

Chowan River and its tributaries, specifically the Meherrin and Nottoway rivers. Only 8% of the fish detected making upriver migrations ascended the Roanoke River. Because migrating adults typically return to their natal rivers, these results suggest American Shad entering the Albemarle Sound are disproportionately spawning in the Chowan River Basin, and that basin may host a larger population. There are some differences between the Chowan and Roanoke basins that may help explain this result. Additionally, it is possible that the Roanoke River population of American Shad may be disproportionately depleted compared to the Chowan Basin. Finally, these findings have significant implications for fishery managers and highlight the need for further information about the relative population size and genetic relatedness of American Shad in the Chowan and Roanoke Rivers.

Fish tracking through passive acoustic telemetry is imperfect by nature. It is not possible to track every fish with complete certainty; fish may abandon their migration post capture and routinely pass receivers undetected. In this study, 20% of tagged fish were never detected and are presumed to be tagging mortalities. This rate is higher than other American Shad tracking efforts where between 2% and 3% of tagged fish went undetected (Aunins and Olney 2009, Harris and Hightower 2012), although Hightower and Sparks (2003) reported 18% of fish undetected. Only 22% of the fish tagged were ultimately detected making migrations. That leaves a lot of uncertainty, and it is likely that fish bypassed individual receivers. Given the extensive receiver array, it is unlikely fish made entire migrations undetected. In addition, during sampling, more nets were set on north than the south side of the sound. If fish follow specific migration routes in the sound based on destination, it is possible sampling was not representative. Sampling effort was focused on the north side of the sound because of low catch on the south side during early study years. Only five fish tagged on the south side were detected making migrations, four made

Chowan River migrations and one made a Roanoke River migration. The remaining four Roanoke River migrations were made by fish captured on the north side, which would indicate that there was not a relationship between side of capture and river entered.

Despite American Shad in the Albemarle Sound system being considered iteroparous, we detected only a single fish that made a repeat migration. We purchased transmitters with a long battery life to cover two migration seasons in an attempt to document this behavior. Initial results were encouraging as one of seven fish tagged in 2013 returned in 2014 and followed the same route up the Chowan River in April of both years. Unfortunately, this was the only observation of a fish returning a second year. This may be because of the relatively low sample size of our study, and because tags were inserted into the stomach, likely impacting fish survival after completing their migration. Most acoustic telemetry studies for American Shad and other alosines have used a gastric insertion method (Acolas et al. 2004). It has been suggested that American Shad are "fragile" (Hendricks 2003) and that the gastric implantation technique may result in low tagging mortality and limited behavioral effects during the spawning migration since American Shad feed little in fresh water (Walter and Olney 2003; Harris and McBride 2009). However, a gastric tag could interfere with feeding or be excreted; thus, a gastric tag may reduce the number of American Shad detected to repeat spawn. Recent research suggests the potential to use surgical implantation to study repeat spawning and the marine phase of American Shad (Gahagan and Bailey 2020).

In addition to migration river use, this study also observed fallback behavior in approximately half of detected fish. This is a common American Shad behavior post capture and is routinely reported in fish telemetry studies (Frank et al. 2009). Other efforts tracking American Shad using radio telemetry reported similar or higher fallback rates to those observed in the

Albemarle Sound. Hightower and Sparks (2003) reported fallback in 58% of fish in the Roanoke River, closely matching our findings in the same system. Bailey et al. (2004) saw fallback in 80% of fish with movements up to 30 rkm over seven days. Working in the estuarine portion of the nearby York River, Aunins and Olney (2009) reported fallback in over 90% of fish. Comparatively, we saw fallback in only 54%, but the fish tracked in our study fell back further distances for longer time periods than previously reported. This may have been because our sampling occurred in the sound and not further upriver and the wide geographic range of our receivers. Fallback behavior may explain why detectable migrations were only seen in 62 of the 212 fish, however, it is impossible to distinguish fish that abandoned their migrations from fish that experienced post-release mortality.

Two fish did not migrate up the Chowan or Roanoke rivers. One was detected entering and leaving the Alligator River, where it is possible, but unlikely, that this fish spawned. The detection record may be the result of the fish moving out of the Albemarle Sound system or using the Intercostal Waterway to enter the Pamlico Sound, via the Alligator River. Another possibility is that fish was preyed upon by a large Blue Catfish *Ictalurus furcatus*, which are common in the Albemarle Sound. A second fish was detected near the mouth of the Pasquotank River. Because many other fish with more complete detection records were also detected near this receiver, it is unlikely that this fish made a migration up the Pasquotank River. Rather, the area of the sound near the mouth of the Pasquotank River may be a part of the migration route American Shad take up the Albemarle Sound.

The observed higher use of the Chowan River over the Roanoke River for spring spawning migrations could partially be the result of differences between the two river basins. There are some obvious physical differences between the two rivers. The Roanoke River Basin drains a much larger area, and discharge from the Roanoke is typically greater than that from the Chowan River. However, while the Chowan River and its tributaries drain a smaller area than the Roanoke River, they offer significantly more unimpeded river kilometers. A fish entering the Chowan Basin has access to 982 rkm of river, compared to only 344 rkm in the Roanoke Basin. It may be that we observed more fish ascending the Chowan River because the American Shad population homing there is larger, owing to the greater availability of spawning habitat.

Another possible explanation of the observed migration river use is that the population of American Shad homing to the Roanoke River may be depleted compared to those homing to the Chowan River. The Roanoke River has been consistently impounded by the Roanoke Rapids and Gaston dams since the 1950s, impeding access to historically used upstream habitat. Resource managers have put significant effort towards restoring the Roanoke River spawning population, including stocking hatchery-reared fry. Studies monitoring the stocking operations have indicated that approximately 70% of the returning adult population are from hatchery origins (Evans and McGrady 2019), supporting the idea that lack of access to spawning habitat has contributed to depleting America Shad numbers in the Roanoke River. Notable too, is that none of the 89 genetically-sequenced fish from the Chowan River tributaries were of hatchery origin, supporting the theory of high spawning river fidelity (Evans and McGrady 2019).

It is likely multiple factors play a role in determining American Shad migrations. Natal homing, the physical conditions and discharge of rivers, and the size of the extant fish populations all contribute to which river basin a fish may ultimately ascend to spawn. From a resource management perspective, determining the cause of these results is important, as it is essential to contextualize the knowledge that more tagged fish migrated up the Chowan River. That river may also be seen as a more valuable target for restoration and conservation resources, if our study results are reflective of the population at large entering Albemarle Sound. Based on the results of this study, resource managers may wish to consider reallocating efforts to improve fish passage within the Chowan Basin, such as making passage at the Emporia Dam more efficient. In addition, developing a population model for that basin is needed to better enable comparisons to the Roanoke River.

The current consensus is that upstream passage at Roanoke Rapids to above J. Kerr Dam (the third dam on the river) may not be best for the population at the present time (Harris and Hightower 2012). They constructed a matrix model to predict possible population-level effects of transporting American Shad to habitats above the dams on the Roanoke River. Their model predicted that transport would only benefit the current American Shad population if effective fecundity and survival rates were optimal. Harris and Hightower (2011) moved 1,161 adult American Shad above the three dams but found no American Shad eggs in weekly sampling in the upper basin and only 1 of the 227 sonic-tagged adult American Shad migrated successfully downstream through all three dams. In addition, outmigration success of oxytetracycline-marked American Shad fry released in the upper river above J. Kerr Dam was much lower than that for marked fry released in the lower river below Roanoke Rapids Dam.

The scope and scale of our study were relatively small, relying on acoustically-tagged fish and telemetry to examine habitat use in a single system. However the findings may be useful to fishery managers and stakeholders in other systems. Especially in planning similar acoustic telemetry studies or identifying research needs. The importance of representative sampling should be addressed in future studies. If American Shad migrating through Albemarle Sound follow specific routes, our sampling may not have been representative. Our results were also constrained by avoiding the commercial fishing season, and thus may have not represented the entire spawning season. We also stress the importance of sharing receivers among fishery managers and stakeholders for multiple studies and of receiver placement. Interpretation of our results is constrained by receiver placement, which purposefully was non-random, and could have led to migrations going undetected into other tributary rivers in Albemarle Sound as only the Roanoke and Chowan rivers had stationary receivers.

Our study also highlights a number of data needs in the Albemarle Sound system that may be relevant in tracking movement of alosines in other systems. As discussed, developing a population estimate for American Shad spawning in the Chowan River is essential to enabling comparisons to the population using the Roanoke River. There is also a need to determine if fish spawning in the two rivers are genetically distinct stocks, and how much straying occurs between fish homing to natal spawning grounds. Based on the limited work, a high return of hatchery fish in the Roanoke, and lack of hatchery fish in Chowan tributaries indicates straying is minimal.

Analysis of American Shad movements in the Albemarle Sound indicated that more fish ascended the Chowan River to spawn, compared to the Roanoke River. The exact reason is unknown, but the Chowan River offers access to more unimpeded habitat, and the spawning population in the Roanoke River may be disproportionately depleted. Resource managers should recognize that more fish may be using the Chowan River and its tributaries for spawning and passage, and restoration efforts in those systems (such as improving water quality) may benefit a higher proportion of the Albemarle Sound population of American Shad. However, improving water and habitat quality and rebuilding the spawning population in the Roanoke River should remain a priority, especially if that population is disproportionately depleted.

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Tables and Figures

Table 1. Summary of effort, catch, detections, and migrations during each of the six years of the study. In 2014 a single fish tagged the previous year returned, and is indicated by the *.

Year	Trips	Net Sets	Net Length (yd)	Stretch Mesh (in)	Total Soak Time (Minutes)	Captured	Tagged	Detected	Migrations
2013	14	37	480 - 1000	5.0 - 6.5	10260	26	7	4	1
2014	8	38	500 - 540	4.5 - 6.0	5880	103	53	41	10 *
2016	8	42	200 - 480	4.0 - 5.5	2549	57	55	43	2
2017	8	52	600	5.0 - 6.0	4320	83	74	57	26
2018	9	68	600	4.5 - 5.5	5696	54	46	40	13
2019	5	40	600	4.5 - 5.5	2997	43	31	27	10
Total:	52	237			31702	366	266	212	63

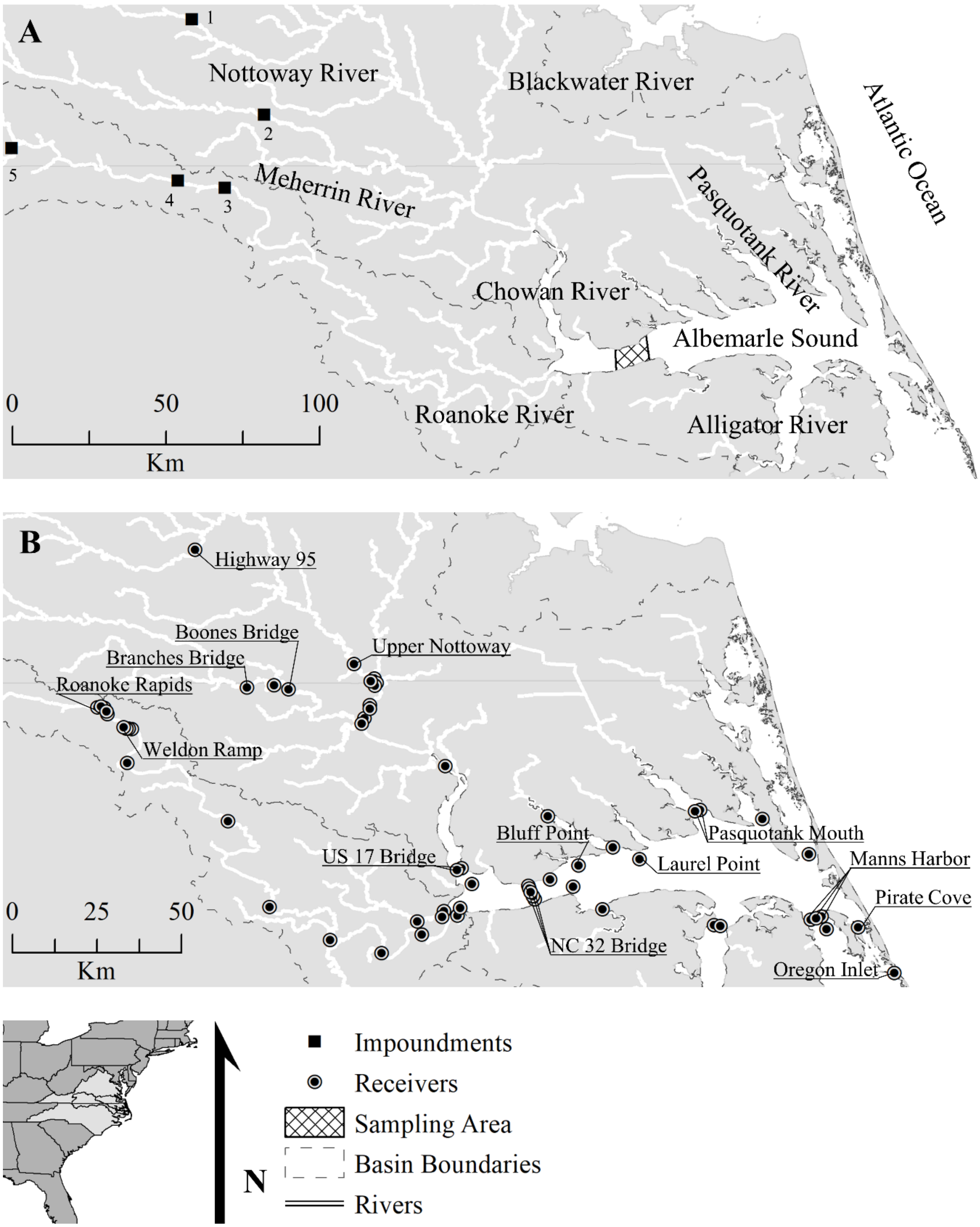

FIGURE 1. Maps of the study area on the Virginia-North Carolina border. **(A)** The Albemarle Sound and its tributaries indicating names of major water bodies, major impoundments, and our sampling area. The number next to each impoundment corresponds to the following project names: 1 Baskerville, 2 Emporia, 3 Roanoke Rapids, 4 Gaston, 5 Kerr. **(B)** Locations of receivers used to track the movements of acoustically-tagged American Shad, with significant receivers labeled.

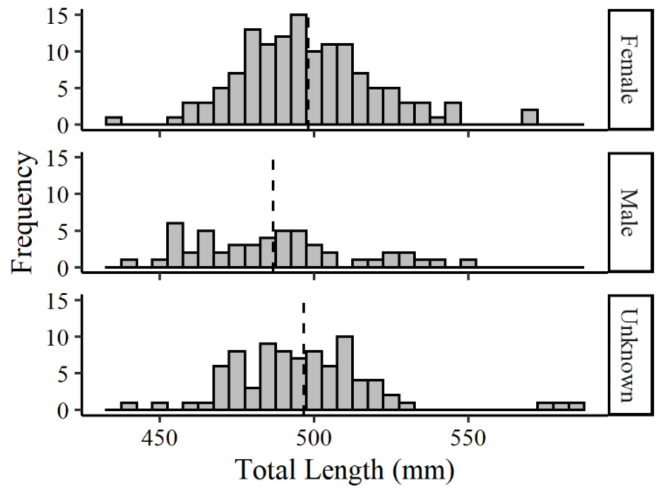

FIGURE 2. Length-frequency distributions of female, male, and unknown sex American Shad that were acoustically tagged during the six years of the study. Each bar represents a count of fish representing a size range of 5mm. Vertical dashed lines represent the mean total length.

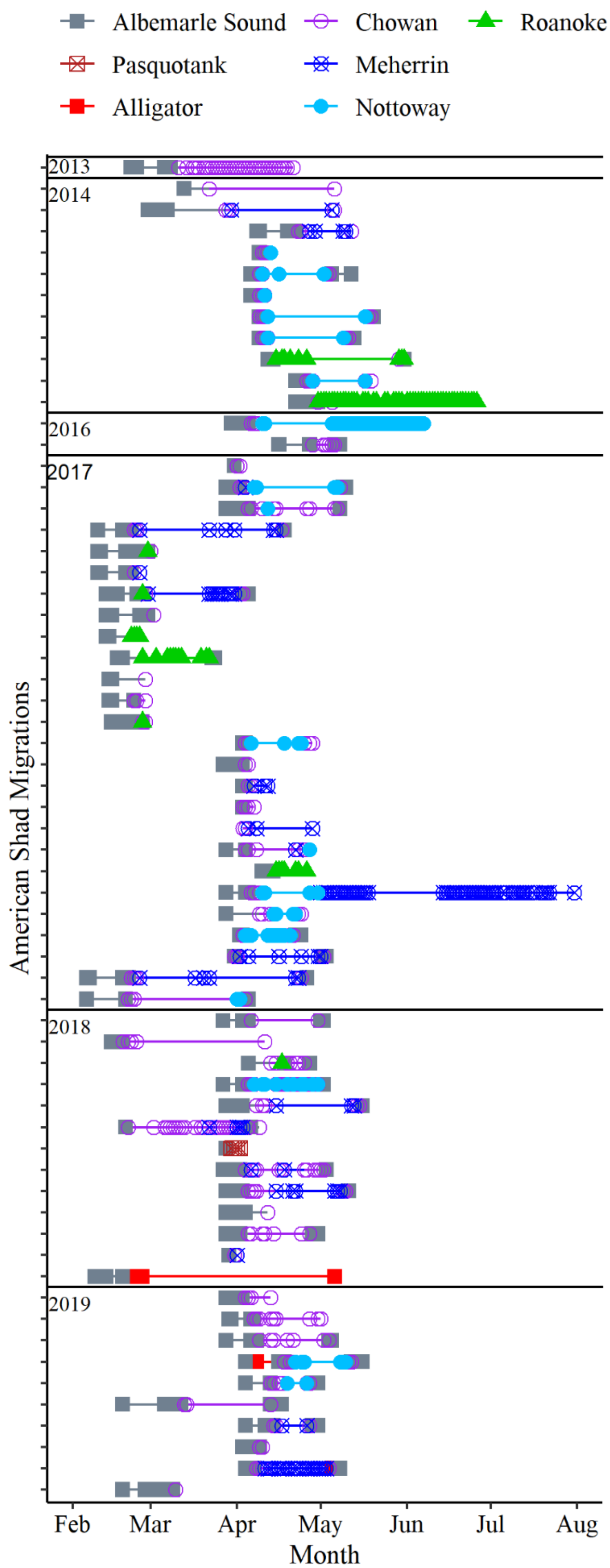

FIGURE 3. Plot illustrating the general river position and timing of the 63 American Shad migrations detected during the six years of the study. Each fish is represented by an individual horizontal line with points indicating detections. The shape and color of points and lines distinguish between the major bodies of water encountered.

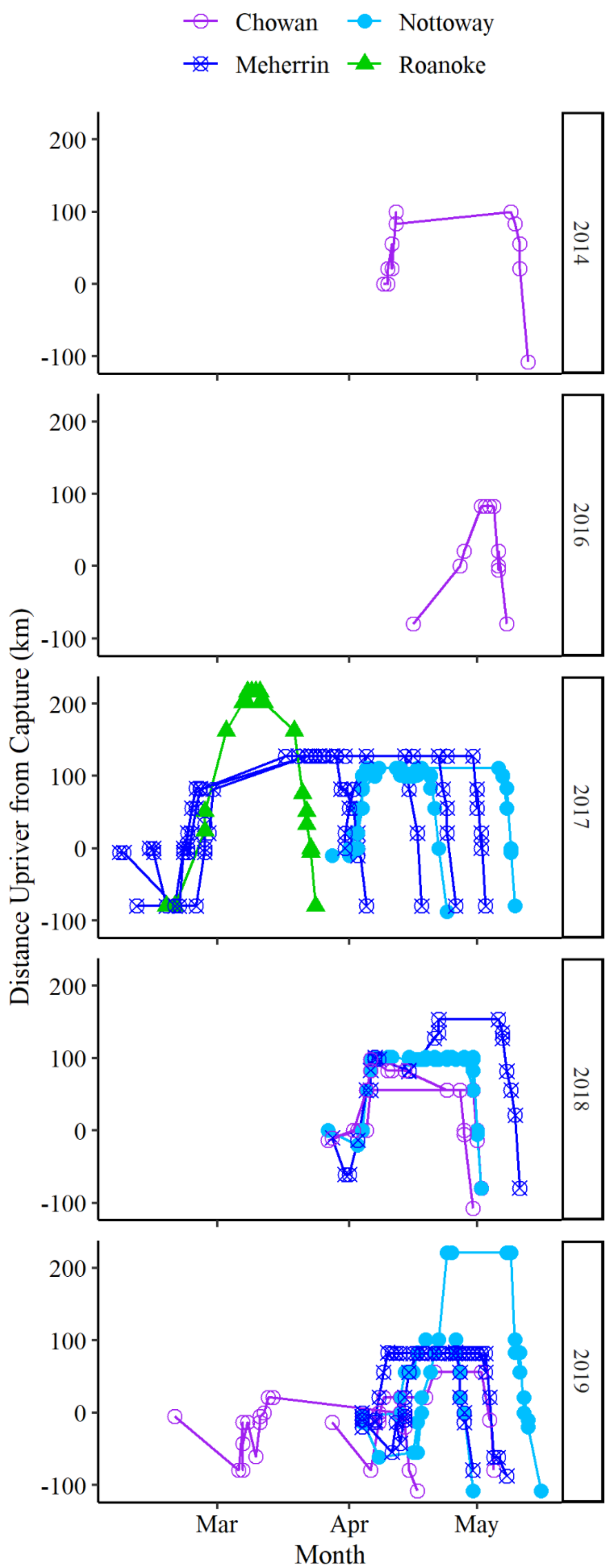

FIGURE 4. Plot tracking the 19 American Shad for which a complete migration was detected by receivers through the six study years. Each fish is represented by an individual line (2014 n = 1, 2016 n = 2, 2017 n = 7, 2018 n = 4, 2019 n = 6). Each point represents the fish's distance from the capture location (y axis) and time it was detected (x axis). Positive distances indicate movement upstream of the capture location and negative distances indicate movement downstream of the capture location. The shape and color of points and lines distinguish between the rivers each fish ultimately ascended to spawn. Fish typically lingered in the sound post capture, then rapidly swam upstream, halted upstream movement for a variable amount of time, then moved rapidly downstream and exited the sound.