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ARTICLE

Acoustic-tagged American Shad utilize historic habitat following dam removal in northern Delaware

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Abstract

Objective: The anadromous American Shad *Alosa sapidissima*, a once commercially important species in the mid-Atlantic region, experienced population declines due to overfishing, poor water quality, and impediments to accessing freshwater spawning habitat. Efforts at the regional and national scale substantially addressed the former two obstacles to facilitate population growth, but dam modifications or removal are still ongoing. In 2019, the state of Delaware removed the first barrier to anadromous fish passage on the Brandywine River (a tributary of the Delaware River), Dam 1.

Methods: A total of 24 American Shad were surgically tagged with acoustic transmitters from 2021 to 2022 above recently removed Dam 1 and tracked in the Delaware River estuary and coastal waters of the Atlantic Ocean.

Result: The length of available habitat increased by 1.3 km, and 75.0% of surgically tagged American Shad used historic spawning grounds in the Brandywine River following dam removal. Nine individuals exhibited long-term residency in the Brandywine River from May to June, demonstrating the importance of this newly available habitat to spawning adults. Additionally, one fish returned to the Brandywine River between years, displaying interannual spawning site fidelity and iteroparity. We also observed exploratory behavior of three additional American Shad that exited and returned to the Brandywine River within the same year.

Conclusion: Overall, we document a successful collaborative network via receiver array maintenance to answer questions regarding anadromous fish migration and habitat use following dam removal.

KEYWORDS

American Shad, anadromous species, dams, fallback response, migration, telemetry

INTRODUCTION

Anthropogenic modifications to natural channels have enabled major societal developments by creating navigable waterways, establishing drinking water supplies, and allowing for waste removal. However, extensive damming in pursuit of these developments has greatly reduced the ability of fishes to access historic habitat (Larinier 2000), contributing to population declines and loss of freshwater biodiversity (Zhong and Power 1996). Habitat fragmentation is especially critical for anadromous fishes, which depend on freshwater habitat for spawning migrations and often exhibit spawning site fidelity. The absence of anadromous fishes due to population decline or damming also restricts ecosystem connectivity and decreases marine-derived nutrient availability in freshwater systems (Walters et al. 2009; Zydlewski et al. 2021). Removal of dams has the potential to restore the linkage between these systems (Tonra et al. 2015) and predam natural migration and spawning behaviors (Duda et al. 2021; Huang et al. 2023). Restoration of these habitats and successful management of anadromous species is dependent on knowledge of the species' in-river distribution, residence and occupancy times, and habitat use (Gahagan and Bailey 2020). Further, understanding the temporal dynamics associated with recolonization and habitat use is needed to better document the beneficial impacts of dam removal.

The anadromous American Shad *Alosa sapidissima* is native to the northwestern Atlantic Ocean, from Nova Scotia to the east coast of Florida, and demonstrates high site fidelity (e.g., >90%) to natal rivers, often characterized by genetically distinct subpopulations (Leim 1924; Dadswell et al. 1987; Brown et al. 1999; Walther et al. 2008; Poulet et al. 2023). American Shad once supported economically important fisheries but experienced a notable collapse, with native populations declining over the past century due to anthropogenic stressors such as overfishing, high rates of bycatch, degraded water quality, and physical obstructions (Atlantic States Marine Fisheries Commission 2007, 2020; Limburg and Waldman 2009). As a consequence of these compounding stressors, there is a low abundance of American Shad in many systems, with some management entities actively stocking fish to augment wild production (Chittenden 1974; Brown and St. Pierre 2001). However, stocking in some systems has proven to be unsuccessful in rebounding populations to historic levels due to diminishing returns from density-dependent mortality (McGrath et al. 2022). Additionally, stocking interferes with historic genetic structure of subpopulations and may only act as a replacement of wild stock, rather than a supplement; dam removal and habitat restoration, in addition to strict harvest regulations, are therefore proposed as a more effective means to aid in population recovery (Aunins et al. 2014). The removal of abandoned, obsolete, or breached dams, even low-head ones (<3 m), will improve connectivity and production as American Shad access suitable and potentially preferable habitat that may contain higher diversity substrate and often contains fewer predators (Raabe and Hightower 2014a).

Impact statement

Dams prevent many fish from accessing habitat that is essential to their survival. Following dam removal, we investigated the movement patterns of American Shad to determine if access to essential spawning habitat was restored. Not only was the habitat used, it was also preferred by the shad in this area. This will potentially help restore failing or stagnated fish populations that used to be popular commercial and recreational fisheries.

The Delaware River basin is a tidal estuary important for many economically important species, serves as a key spawning ground for American Shad in the mid-Atlantic region, and hosted the largest fishery in the nation at the peak of American Shad harvest (Hardy 1999; Limburg et al. 2003). In the 1890s, American Shad landings in the Delaware River basin alone were estimated to be 15 million pounds (~7000 metric tons), which rapidly fell to less than one million pounds (~450 metric tons) by 1920 (Chittenden 1974). In addition to overharvest, the rapid urbanization and industrialization of the tidal system between Trenton, New Jersey (river kilometer [rkm] 215 Delaware River, measuring from the mouth of the Delaware Bay), and Wilmington, Delaware (rkm 113, Delaware River), led to inadequately managed waste products and water pollution, which resulted in hypoxia and poor water quality (Sharp 2010). These conditions disrupted the migration and spatial distribution of American Shad by preventing northward travel during migration runs as American Shad are oxygen-sensitive species (Chittenden 1971; Stoklosa et al. 2018). Despite the main stem of the Delaware River remaining undammed since the removal of the Lackawaxen dam in 1890 (rkm 445, Delaware River), damming of major tributaries such as the Schuylkill River (entrance at rkm 148, Delaware River) and other smaller tributaries also restricted the range American Shad were able to travel and reproduce, thus fragmenting historic spawning habitats (Hardy 1999; Delaware River Basin Fish and Wildlife Management Cooperative 2014). Though water quality dramatically improved in the latter 20th century, physical barriers such as dams remained in place, decreasing the available area for spawning, and American Shad landings remained low compared to historic averages (Sullivan 1994).

In northern Delaware, the Brandywine River intersects the Christina River less than 4 km from the confluence of the Christina and Delaware rivers (rkm 113, Delaware River) and runs through the city of Wilmington. In the Brandywine River, 11 dams were identified as obstructions to fish passage (Brandywine Conservancy 2005; Kauffman 2015). The lowermost dam, dam 1 (also referred to as the West Street Dam), previously located at West Street, Wilmington, Delaware (rkm 3.8, Brandywine River), was removed in 2019, immediately granting American Shad access to 1.3 km of historic habitat. The Brandywine River currently supports a targeted recreational American Shad fishery, though little is known about the status of American Shad in these areas (Atlantic States Marine Fisheries Commission 2020). Angler landings and seine surveys in 2020 indicated that American Shad were completing passage throughout this area and reproducing (E. A. Hale, unpublished data), yet spatial–temporal occupancy patterns remained unclear.

Acoustic telemetry is a well-established method for studying movement and habitat connectivity in diadromous fishes (Hussey et al. 2015; Crossin et al. 2017). A network of acoustic receivers presently exists along the Delaware River estuary and Atlantic Ocean. However, tributaries in northern Delaware have remained virtually unexplored despite the fact that this includes important habitat for diadromous fishes such as American Shad. Our study aimed to characterize the occupancy of tagged American Shad in the Brandywine River using acoustic telemetry, following the removal of the furthest downstream dam. The spatial ecology of American Shad in this river system has been previously unexplored using acoustic telemetry, and results from this geographic location can be used to assess the impacts of future dam removal or stream restoration in northern Delaware. We hypothesized American Shad used newly available habitat after the removal of a low-head dam. We were able to characterize the movement of American Shad between spawning and migrating locations, which will allow for more informed conservation of this imperiled, yet culturally and economically important species.

METHODS

Study site

The Christina River is a 56-km-long major tributary of the Delaware River and drains into the Delaware River at rkm 113 (Figure 1A). The Brandywine River is a 32.8-km, sixth-order stream that empties into the Christina River in Wilmington, Delaware, at rkm 3.5 (Figure 1B). The Brandywine River watershed encompasses 847 km^2 of drainage area located throughout northern Delaware and southeastern Pennsylvania (Senior and Koerkle 2003). The most downstream low-head dam (dam 1, also known as West Street Dam) was removed in 2019. This dam was 0.9 m tall and 53.6 m wide (Brandywine Conservancy 2005). The next upstream impediment, dam 2 (Broom Street Dam), is located 1.3 km from dam 1 and is 2.4 m tall (Brandywine Conservancy 2005), rendering it most likely impassable for adult American Shad except in extreme flood events (U.S. Fish and Wildlife Service 2004). The bottom habitat between dam 1 and dam 2 is characterized by sandy gravel and soft sediment, with large boulders present, creating rapids of fast-flowing water. The area downstream of dam 1 is characterized by deeper, slower water with steep banks and sandy substrate. The Brandywine River has historically served as habitat for additional diadromous fishes, including river herring (Alewife *Alosa pseudoharengus* and Blueback Herring *A. aestivalis*), American Eel *Anguilla rostrata*, and Striped Bass *Morone saxatilis* (Seagraves and Cole 1989; Maynard 2014; Park 2017).

Fish sampling and tagging

American Shad were caught opportunistically by rod and reel on May 11, 2022, and by electrofishing on May 10, 2022, downstream from dam 2, in Brandywine Park, Wilmington, Delaware. American Shad were captured in the restored section of the river due to lack of entry points downstream of dam 1. Fish were measured for total length and fork length before undergoing tagging procedures (AUP# 1371). Sex was not confidently determined for each fish and was therefore omitted. Each fish was given a unique identification number from 1 to 26, corresponding to a unique transmitter identification number (Table 1). We surgically ($n = 24$; Park 2022) inserted 69-kHz VEMCO (Now Innovasea Systems, Nova Scotia) V9-2x and V9A-2x transmitters, emitting at 146 and 151 dB. To enhance battery life, these tags have a two-stage pattern of sound emission with a high-frequency burst (70–110-s delays) for the first 180 days followed by a low-frequency period emission for another 180 days (180–240-s delays). The weight of the V9 and V9A transmitters in air is 5.0 and 5.3 g, respectively. Tags did not exceed 2% of the fish's body weight (Bolland et al. 2019). Though the wet weight of the fish was not recorded, previous studies in the mid-Atlantic region indicated that American Shad larger than 300 mm in total length would weigh more than 25.0 g

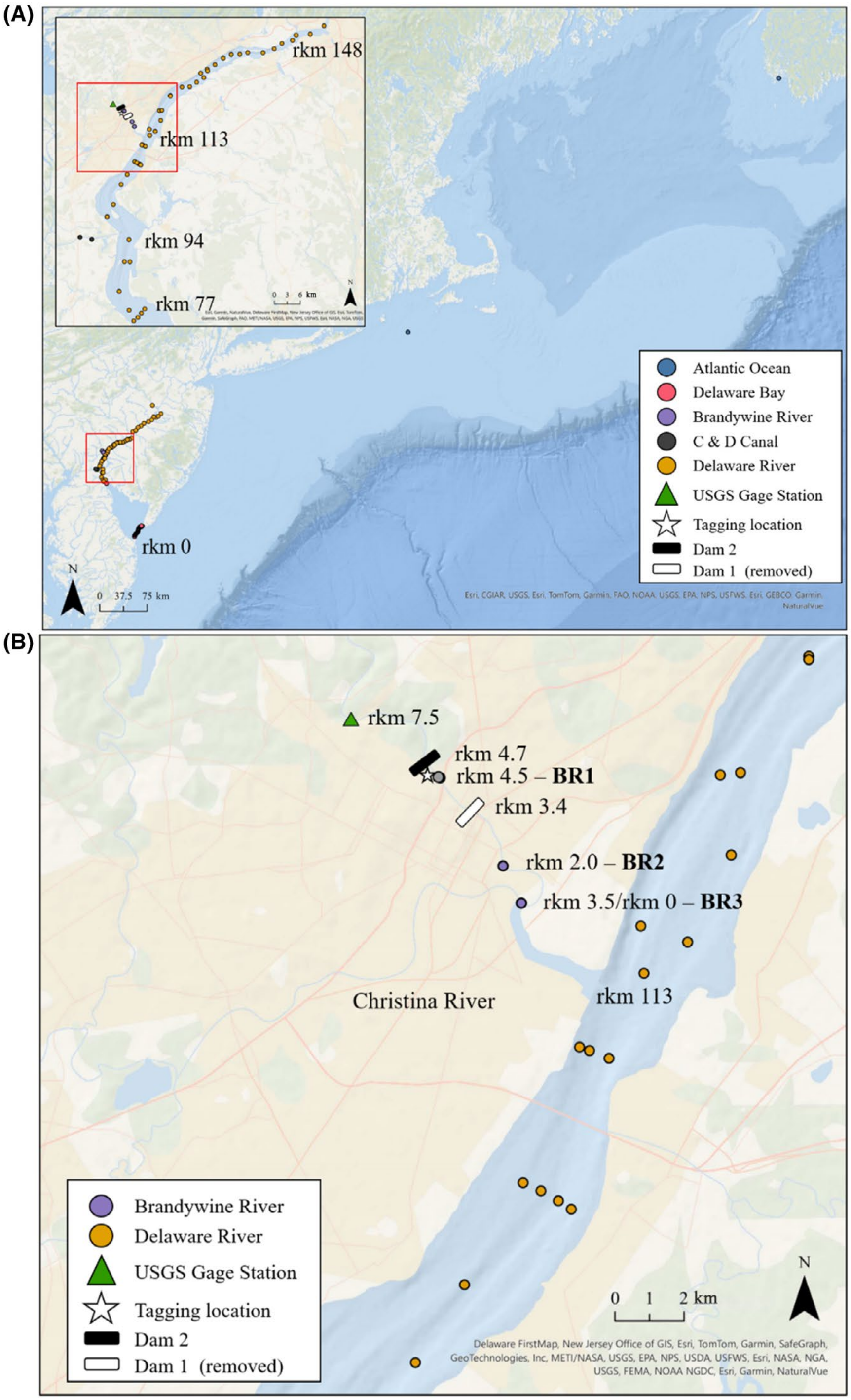

FIGURE 1 (A) A map of the northwestern Atlantic Ocean. Circles denote acoustic receivers within the Delaware State University–Delaware Division of Fish and Wildlife–University of Delaware network and detections reported by Ocean Tracking Network receivers ($n = 92$). The Delaware River begins at rkm 0, between Cape May, New Jersey, and Lewes, Delaware. (B) A map of northern Delaware, including the Christina River and Brandywine River. The receivers BR1 (rkm 4.5) and BR2 (rkm 2.0) were deployed in 2021 and are up- and downstream, respectively, of deconstructed dam 1 (rkm 3.4) in Brandywine River, Delaware. The receiver BR3 (rkm 3.5/rkm 0) was deployed prior to this study and is located at the confluence of the Brandywine and Christina rivers. BR, Brandywine River; C & D Canal, Chesapeake and Delaware Canal; USGS, U.S. Geological Survey.

(Upton et al. 2012). Therefore, fish smaller than 300 mm were excluded. Following electronarcosis and tagging, American Shad were held in river for observation and released after displaying normal swimming behaviors and exhibiting a strong swim-away response. Fish were released within 100 m of their capture site in reasonable spawning habitat, and total handling time did not exceed 3 min.

TABLE 1 Tagging information for American Shad in 2021 and 2022. Fish 1 through 12 were caught by rod and reel, and fish 15 through 26 were caught by electrofishing. Transmitters with code spaces beginning in A69-9007 are V9A tags with accelerometers, and all other transmitters are standard V9s. Estimated tag life provided by the manufacturer is given in days. Tag IDs with asterisks indicate fish that were removed from analyses. Fish impacted with various handling stress are indicated as "Effects." "Days at large" are the number of days a fish spent from the tagging date to its last detection.

Year	Tag ID	Fish ID	Tag life (day)	FL (mm)	TL (mm)	Procedure	Effects	Days at large
2021	A69-9007 15557	1	520	420	472	Surgical		361.8
2021	A69-9007 15558	2	520	437	493	Surgical		5.5
2021	A69-1602 49176	3	850	450	593	Surgical		2.9
2021	A69-1602 49177	4	850	443	484	Surgical		23.7
2021	A69-1602 49178	5	850	468	522	Surgical		12.1
2021	A69-1602 49179	6	850	437	493	Surgical		75.0
2021	A69-1602 49180	7	850	420	475	Surgical	Fallback	29.4
2021	A69-1602 49181	8	850	460	517	Surgical		33.8
2021	A69-1602 49182	9	850	398	446	Surgical		66.1
2021	A69-1602 49183	10	850	480	540	Surgical		35.2
2021	A69-1602 49184*	11	850	458	521	Surgical	<5 detections	5.8
2021	A69-1602 49185	12	850	468	525	Surgical		13.7
2022	A69-1604 32457*	13	887	440	495	Gastric		30.7
2022	A69-1604 32458*	14	887	470	540	Gastric		0.1
2022	A69-1604 32459	15	887	490	540	Surgical		20.1
2022	A69-1604 32460	16	887	510	545	Surgical		13.8
2022	A69-1604 32461*	17	887	445	495	Surgical	Handling related mortality	0.0
2022	A69-1604 32462	18	887	450	495	Surgical		13.5
2022	A69-1604 32463*	19	887	495	550	Surgical	<5 detections and handling related mortality	0.0
2022	A69-1604 32464	20	887	460	520	Surgical		30.2
2022	A69-1604 32465	21	887	425	465	Surgical		10.6
2022	A69-1604 32466	22	887	480	530	Surgical	Fallback	77.0
2022	A69-1604 32467*	23	887	470	515	Surgical	<5 detections	0.0
2022	A69-1604 32468	24	887	490	555	Surgical	Handling related mortality and fallback	0.5
2022	A69-1604 32469	25	887	445	490	Surgical		57.1
2022	A69-1604 32470	26	887	420	455	Surgical		25.9

In 2021, we surgically tagged 12 American Shad with 10 standard V9-2x transmitters and two V9A-2x transmitters that contained accelerometers (Table 1). Accelerometer data was not formally evaluated in our analyses due to low sample size ($n=2$) and poor spatial coverage. However, novel acceleration rates were reported (Figure S1 in the Supplement available separately online; maximum rate = 3.5 m/s^2, mean rates = 1.7 and 2.4 m/s^2). Additionally, we implanted two American Shad with V9-2x tags with the same tag specifications using gastric insertion methods (Smith et al. 2009) as a proof of concept for short-term in situ tag retention in this watershed (Table 1). In 2022, we tagged 12 American Shad with V9-2x transmitters using surgical procedures only (Park 2022).

Acoustic telemetry

An array of three VEMCO–Innovasea VR2Tx receivers were deployed on the Brandywine River in 2021 and 2022 (Figure 1B), with Brandywine River 1 (BR1; rkm 4.5, Brandywine River) located upstream of removed dam 1 (rkm 3.4, Brandywine River) and Brandywine River 2 (BR2; rkm 2.0, Brandywine River) located downstream of dam 1. Brandywine River 3 (BR3), located at the confluence of the Brandywine and Christina rivers (rkm 3.5, Christina River/rkm 0, Brandywine River), was deployed prior to this study by the Delaware Division of Fish and Wildlife. Additional receivers in the Delaware River and Delaware Bay are maintained by the

Delaware Division of Fish and Wildlife and Delaware State University (Figure 1). Detections in the marine environment were collected and reported by members of the Atlantic Cooperative Telemetry Network and the Ocean Tracking Network (Figure 1A; G. Reid, Centre for Marine Applied Research, personal communication; S. Van Parijs, National Oceanic and Atmospheric Administration, personal communication). The locations of acoustic receivers were categorized into four regional categories: Atlantic Ocean (before rkm 0, Delaware River), Delaware River (also containing the Chesapeake and Delaware Canal; rkm 77–530, Delaware River), Delaware Bay (rkm 0–76, Delaware River), and Brandywine River (rkm 0.0–4.7, Brandywine River). Receivers in the Brandywine River (BR1, BR2, BR3) were further distinguished to better discriminate river occupancy and direction of travel of telemetered American Shad. The majority of receivers ($n = 85$) were located within the Delaware River and Delaware Bay, but two receivers were located off the coast of Rhode Island and Nova Scotia. Receivers are owned and maintained by various agencies and are therefore deployed at variable depths (0.5–18.6 m) and undergo maintenance at different intervals. Additionally, receiver coverage varied between years but was approximately $n = 90$ between the 2 years.

A line of receivers at rkm 0 was in place at the beginning of the Delaware Bay from Cape May, New Jersey, to Lewes, Delaware, and is referred to as the Delaware Bay Gate. A similar line of receivers at rkm 77, known as the Delaware River Gate, demarcates the mouth of the Delaware River, as established by Delaware and New Jersey states. Receivers owned by Ocean Tracking Network members off the coast of Rhode Island and Nova Scotia were given an approximate distance of −400 and −1000 km, respectively.

Data analysis

The two fish tagged with acoustic transmitters using gastric insertion (Smith et al. 2009) were excluded from all analyses due to low sample size (Table 1). We compared fish fork length using Welch's t-test to determine if tagging size was consistent between years (R Core Team 2023). Before calculating t-scores, data were tested for normality using a Shapiro–Wilk normality test and homoscedasticity using Levene's test of equality of variances. For statistical tests, p-values <0.05 were considered significant. The fork length was normally distributed across years, and there was no significant difference in fork length between years (Welch's t-test: $p = 0.077$).

We removed any fish from further analysis that had perceived mortality, including fish with fewer than five detections or fish that failed to be detected after a 5-day latent mortality window, except for one fish that displayed fallback behavior. We categorized fish as displaying fallback behavior when consecutive downstream travel out of the Brandywine River was initiated within 24 h of tagging (McCartin et al. 2019). Fallback is loosely defined as the spontaneous downstream movement away from targeted spawning grounds (Moser and Ross 1993), typically during upstream migration and after periods of stress (i.e., handling or tagging). "Fallback" is not a standardized term (Frank et al. 2009) and offers no concrete suggestion on distance or duration required to classify a fish as displaying fallback behavior. To standardize this qualifying behavior, Eakin (2017) further classified fallback as "terminal" or "non-terminal," indicating if a fish went on to complete spawning migration or exited the system completely.

To calculate occupancy, detections were condensed into unique detection events using the "detection_events" function in the GLATOS package, using the four regional categories as the location (Holbrook et al. 2017; R Core Team 2023). This function calculates the time gap between the first and final occurrence in a particular location. We also calculated occupancy time within the Brandywine River at BR1, BR2, and BR3. Total occupancy, using tagged fish as replicates, was compared across regions using a Friedman rank-sum test after testing for normality and skew using a Shapiro–Wilk normality test and Levene's test of equality of variances. Occupancy in the Atlantic Ocean was excluded for this test, and p-values <0.05 were considered significant.

Environmental data

Water data (including temperature, discharge, dissolved oxygen, pH, and gauge height) were extracted from a U.S. Geological Survey gauging station located in the Brandywine River using the DATARETRIEVAL package (DeCicco et al. 2023; R Core Team 2023). Station 01481500 is located on the Brandywine River 2.8 km upstream of dam 2 (Figure 1B). We averaged water physical parameters per hour and calculated the frequency of American Shad detections at Brandywine River receivers for each hour. We then ran cross correlation analyses between water quality parameters and American Shad detections to explore associations of fish presence to changing water conditions using the "ccf" function in the stats package (R Core Team 2023). Significance was determined if correlations crossed critical values at the 5% level.

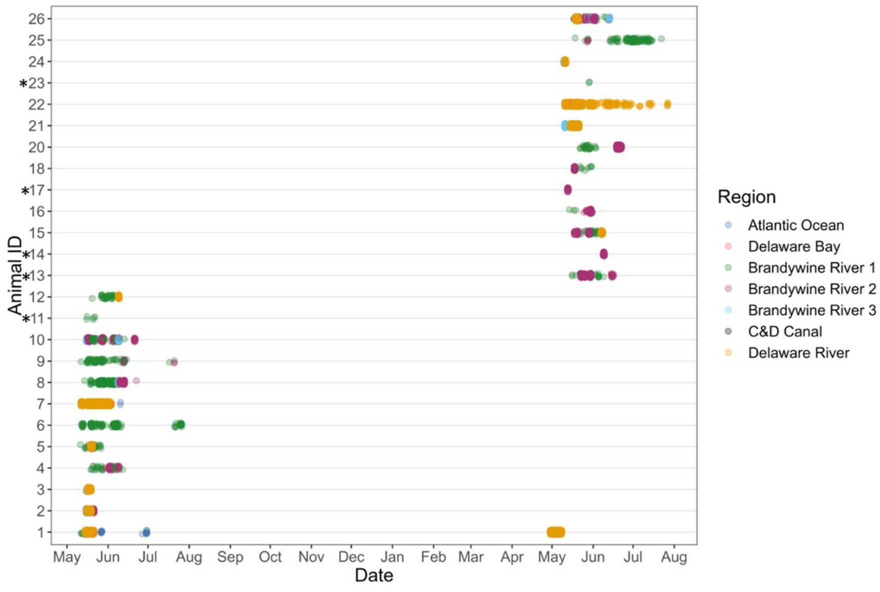

FIGURE 2 Abacus plot for 25 out of 26 American Shad tagged in 2021 and 2022, with vertically jittered detections from May 2021 to August 2022. Fish 19 produced zero detections. Fish 13 and 14 were tagged gastrically. Colors refer to regions assigned to each receiver. Asterisks represent fish removed from analyses: fish 11, 13, 14, 17, and 23. The Chesapeake and Delaware Canal is abbreviated as C&D Canal.

RESULTS

American Shad were present above removed dam 1 following capture and tagging procedures. Tagged fish provided over 13,000 combined detections at 64 receivers (Figure 1). Three fish exhibited apparent mortality (fish 17, 19, and 24), all of which were tagged in 2022 (Figure 2). Fish 17 exhibited handling-related mortality within a 5-day latent mortality window as well as fish 19, which produced zero detections. Fish 11 and 23 were detected fewer than five times during the study and removed for quality control (Table 1). Fish 24 disappeared 20 h posttagging but exhibited complex fallback behaviors, discussed below, and was therefore included in our analyses. However, we did consider fish 24 to exhibit a tagging-related response. Fish 11, 17, 19, and 23 were removed from all analyses, and the remaining 20 American Shad were used in subsequent analyses (Table 1). In total, three fish (12.5%) exhibited handling-related mortality within the 5-day window (fish 17, 19, and 24).

In 2021, five individuals did not exit the Brandywine River before detections ceased (fish 4, 6, 8, 9, and 10; Figure 3). In 2022, an additional four fish stayed within the Brandywine River for all tagging events (fish 16, 18, 20, and 25; Figure 4). These nine American Shad were classified as Brandywine River spawning season residents, often staying until mid to late June, while the other 11 fish displayed complex movement patterns. Four fish exited and re-entered the Brandywine River after initial tagging (fish 1, 2, 5, 26). Each of these fish departed the Brandywine River and explored several kilometers of the Delaware River before reentering the Brandywine River. Fish 1 exited the Brandywine River in 2021 and returned in the successive year, displaying site fidelity across years and potential iteroparity. The other seven fish (7/20 or 35%) that displayed more complex behaviors left the Brandywine eventually and did not return.

We identified two fish in 2022 that exhibited fallback behaviors within 24 h posttagging (fish 22 and 24; Table 1). Fish 22 exited the Brandywine River, entered the Delaware River at rkm 113, and immediately swam to the Delaware River Gate (rkm 77, Delaware River) within 48 h, with a rate of transport of 0.92 km/h or 0.25 m/s. Fish 22 then immediately reversed course and swam upstream to the confluence of the Christina and Delaware rivers (rkm 113, Delaware River) and swam downstream again, where it remained near rkm 110 for nearly 2 months. Fish 24 exited the Brandywine River and traveled as far downstream as rkm 106 within 10 h of tagging before exhibiting mortality, at a rate of 1.5 km/h or 0.42 m/s. Overall, 33% (4/12) of fish (fish 17, 19, 22, and 24) in 2022 experienced handling effects (mortality and fallback) compared with 0% (0/12) in 2021.

Occupancy was defined by unique detection events: the summed total time one particular fish spent near receivers within a given region. American Shad tagged in the Brandywine River spent a higher proportion of their time in the Brandywine River compared to the Delaware River, Delaware Bay, and the Atlantic Ocean (Figure 5A). On average, American Shad spent 67% of their time in the

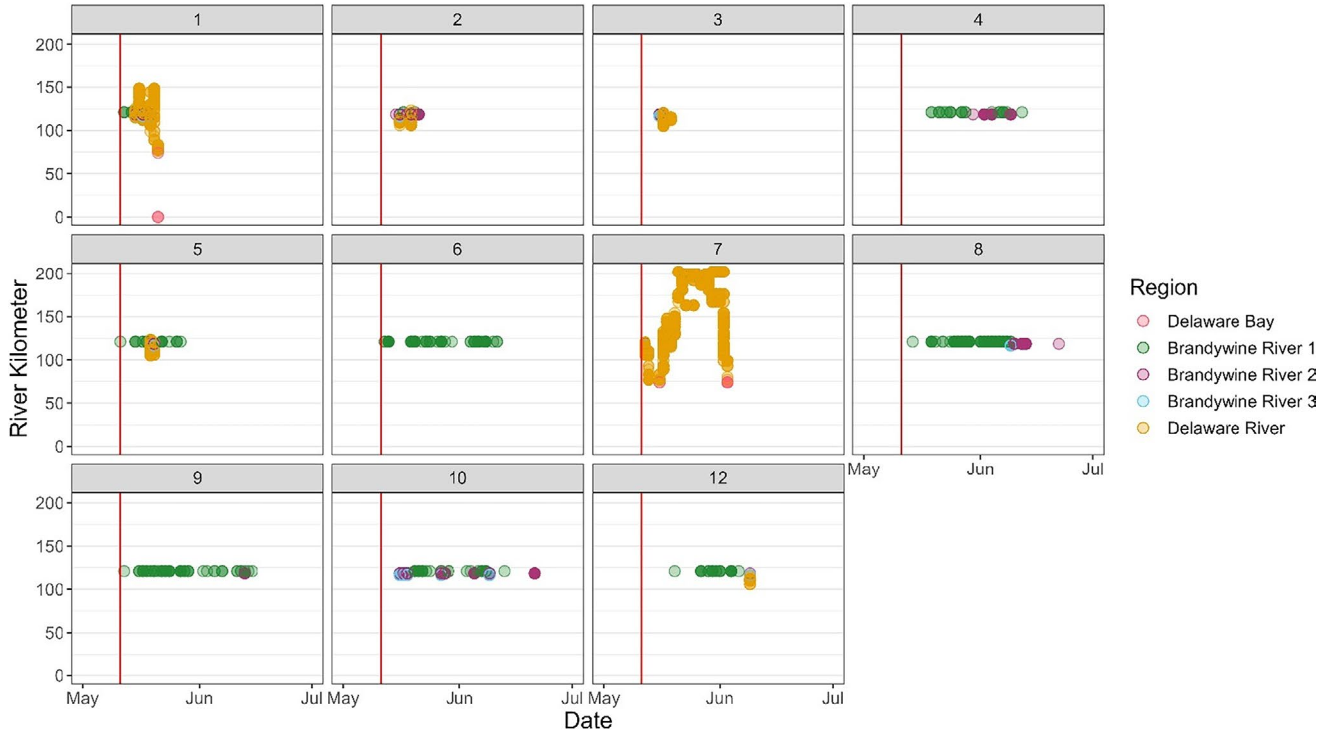

FIGURE 3 American Shad detections in the Delaware Bay basin for fish 1 to 10 and fish 12 in 2021. The red vertical line indicates the tagging date at Brandywine River 1. Colors correspond to geographic region. Detections from fish 1 and 7 in the Atlantic Ocean were excluded for scaling purposes. River kilometer 0 is located at the entrance to the Delaware Bay.

Brandywine River, and within the Brandywine, more time was spent at BR1, located upstream of removed dam 1, compared to BR2 or BR3 (Figure 5B). When we excluded detections in the Atlantic Ocean to compare occupancy within the Delaware River basin, we found that American Shad spent significantly more time in the Brandywine River compared to the Delaware River or Delaware Bay in both 2021 and 2022 (Friedman rank-sum test: $p < 0.0001$; Figure 6). However, time spent in the Brandywine River was lower in 2022 compared to 2021 and higher in the Delaware River in 2022. When total occupancy in each system is normalized to the number of fish detected there, the relative time spent in the Atlantic Ocean, Brandywine River, Delaware Bay, and Delaware River was 2.4 weeks, 2.5 weeks, 0.4 days, and 1.4 weeks, respectively.

American Shad on average traveled 407.5 km (range = 0–3299) and spent an average of 6.5 weeks (0–52) in our study area (Figure S2). Movement averages were skewed by fish 1 and 7, which traveled outside of the Delaware River estuary (Figure S3). Both of these individuals were detected off the coast of Rhode Island, and fish 1 was also detected in Nova Scotia, Canada. Additionally, fish 1 was the only fish to have returned in a successive year, for a total return rate of 9.0% from individuals in 2021. This individual returned to the Brandywine River in 2022, 2 days after entering the study system, displaying high site fidelity, but also made complex forays to the confluence of the Schuylkill and Delaware rivers 35 km upstream at rkm 148 (Delaware River). When fish 1 and 7 are removed from analyses, the average distance traveled and average time spent in the study decreases to 89.7 km and 4.1 weeks, respectively.

The frequency of American Shad detections within the Brandywine River were calculated per day and compared to hourly averages of water quality parameters in the Brandywine River using a cross-correlation function to determine temporal windows of impact. No significant patterns were observed for dissolved oxygen or gauge height, but water temperature was negatively correlated to frequency of American Shad detections 0–35 h prior to detection hour (Figure S4A). Similarly, flow rate was positively correlated to detection frequency approximately 12 h before detection and negatively correlated 30 h before detection, and pH was negatively correlated 0–35 h before detection (Figure S4B and S4C).

DISCUSSION

American Shad tagged in the Brandywine River above removed dam 1 displayed wide differences in in-river distributions, residence and occupancy times, and habitat use. We hypothesized that American Shad would use newly available habitat after dam removal and found

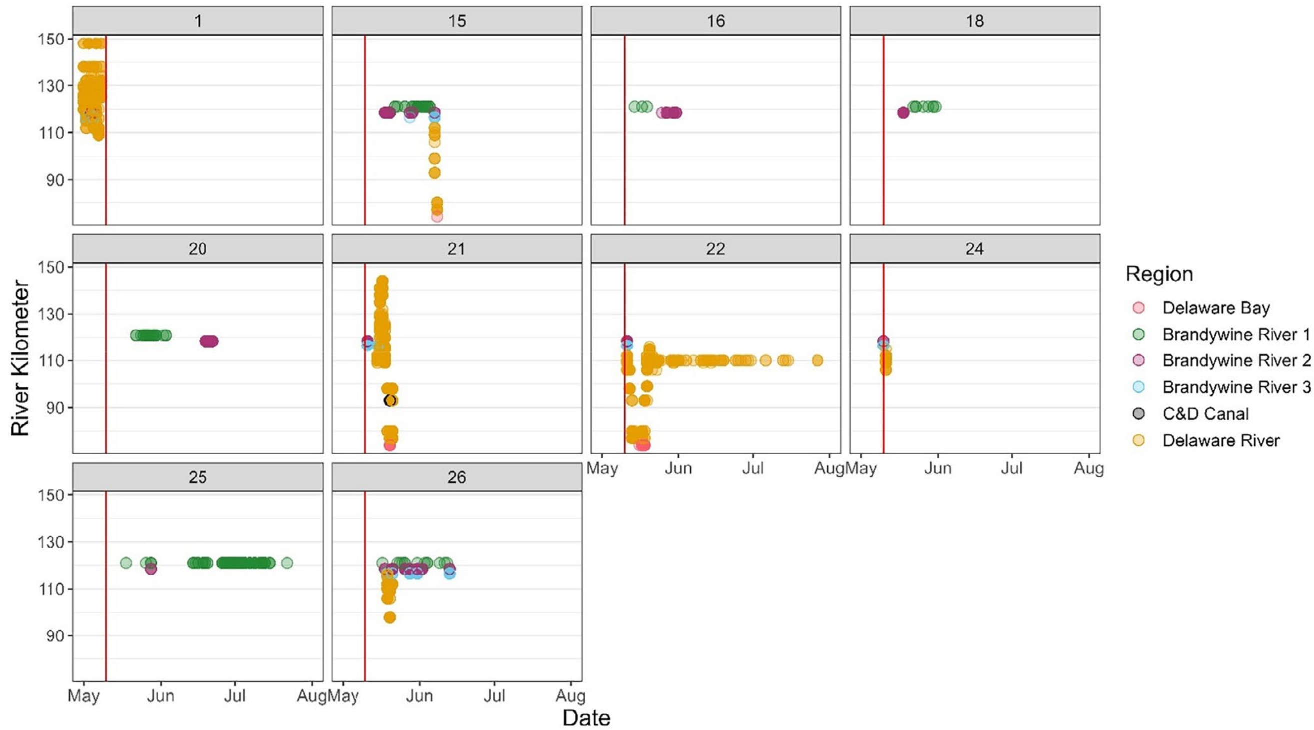

FIGURE 4 American Shad detections for fish 1, 15, 16, 18, 20–22, and 24–26 in 2022. Fish 17, 19, and 23 have been removed due to perceived mortality. The red vertical line indicates the tagging date at Brandywine River 1. Colors correspond to geographic region. River kilometer 0 is located at the entrance to the Delaware Bay.

that not only did tagged fish continue to use this habitat, they also preferentially spent time there. American Shad telemetered above breached or removed dams in North Carolina similarly spent time in newly available habitat and the upper reaches of available habitat (Raabe and Hightower 2014b).

After initial capture and tagging above the dam 1 removal site, the vast majority (15/20 or 75.0%) of surgically tagged American Shad that survived the tagging process continued to be observed upstream from dam 1 at BR1 (or moved downstream and returned). This clearly demonstrates the reestablishment and expansion of range in American Shad in northern Delaware tributaries less than 2 years after dam removal. Raabe and Hightower (2014b) tagged American Shad at downstream locations of a removed dam in North Carolina and found that 24–31% of tagged American Shad migrated above the dam removal site. We do not have proportional return rate data from our study that are directly comparable to their numbers, but it is evident that the restored section of river in our study is important, as the fish we tagged were caught within the restored section and multiple (4/20 or 20%) American Shad demonstrated fidelity to this stretch of the river after leaving the river entirely. Additionally, substantially more time was spent at BR1 compared to BR2, which is habitat characterized by fast-flowing water, large boulders, and sandy gravel; this is habitat ideal for spawning. In comparison, BR2 is in deeper water with slower flow and a notable absence of riffles.

This habitat use suggests that American Shad use the maximum extent of the Brandywine River and would continue using habitat upstream of dam 2, were the dam to be modified to allow passage. Other studies corroborate the ability of river restoration to reestablish American Shad (Trinko Lake et al. 2012) and river herring populations (Huang et al. 2023; Ogburn et al. 2023). The use of this historic habitat by American Shad suggests that other diadromous fishes, such as river herring and Striped Bass, may also exhibit successful recolonization.

Aside from within-year fidelity during exploratory movements, we also document interannual site fidelity and potential iteroparity in the Brandywine River from the one American Shad that returned to the receiver array in a successive year. Fish 1 was detected off the coast of Rhode Island in May 2021, continued offshore to the coast of Nova Scotia in late June 2021, and returned to the Brandywine River in May 2022. The precision of homing by American Shad has previously been summarized (Walburg and Nichols 1967; Limburg et al. 2003). Despite using transmitters with long battery lives, small sample sizes in 2021 ($n=12$) and potential skip spawning in this region (20% repeat spawners in early 2000s; Limburg et al. 2003) most likely prevented us from observing additional American Shad returns in 2022. Fish 7 was also

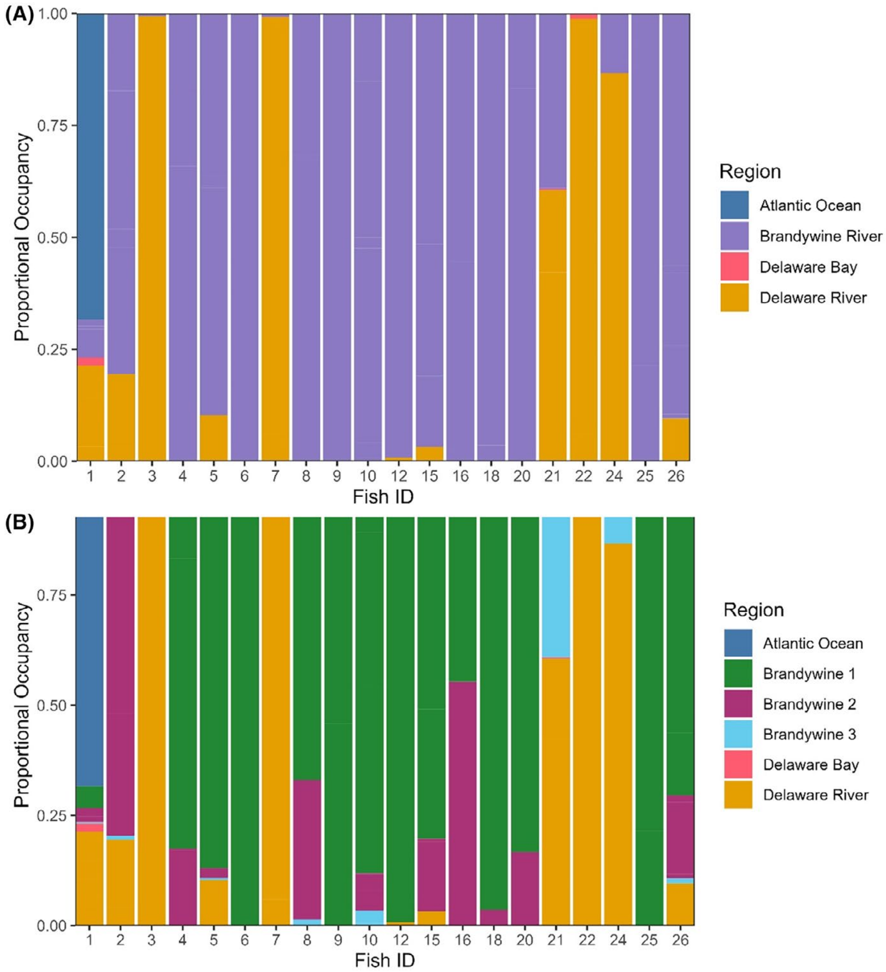

FIGURE 5 Proportion of time spent within a given water system for each fish as calculated by unique detection events. "Delaware River" indicates detection events in the Delaware River and Chesapeake and Delaware Canal. Occupancy in (A) the Brandywine River as a whole is shown in purple, and occupancy in (B) BR1–BR3 is shown in green, magenta, and blue, respectively.

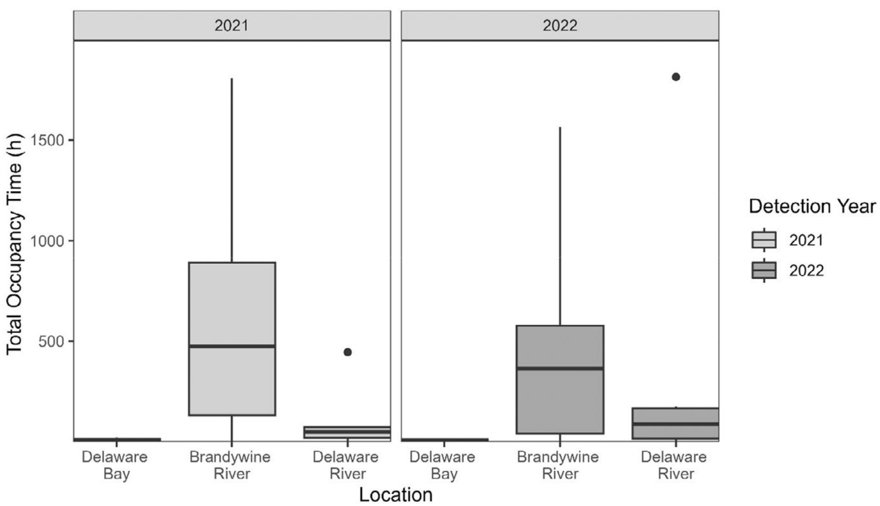

FIGURE 6 Total occupation time in hours for each American Shad in each region in 2021 and 2022. The horizontal line in each box indicates the median, the box dimensions represent the 25th to 75th percentile ranges, and whiskers show the 10th to 90th percentile ranges. Black dots indicate outliers that have been included to show the range of habitat use. Detections in the Atlantic Ocean have been excluded due to low sample size. There is a significant relationship between habitats in both years (Friedman rank-sum test, $p < 0.05$).

observed off the coast of Rhode Island in 2021, 2 weeks after fish 1. These two individuals plausibly congregated with distinct groups, as American Shad are known to form offshore aggregations in three discrete locations: on the Scotian Shelf, in the Middle Atlantic Bight, and off Florida (Dadswell et al. 1987). Specifically in the Bay of Fundy, American Shad will appear in maximum numbers in late June and July during this region's spawning run, which is when fish 1 was observed in this area.

Fish 1 and 7 may have also foraged outside of the Atlantic Cooperative Telemetry Network–Ocean Tracking Network receiver array, increasing the diversity of habitat used and the total distance traveled. We were able to calculate estimates of total distance traveled for each fish, but these are conservative estimates for fish 1 and 7 since the spatial resolution of acoustic receivers remains poor in the Atlantic Ocean along the shelf. Total distances traveled for other American Shad in the Brandywine River and Delaware River are also not precisely accurate, as detection probability depends on the strength of the transmitter signal, a match in timing between transmitter and receiver, and receiver detection range. The range of detection can vary with water quality, salinity, current speed, temperature, tide cycle, time of day (due to compounding noise interference), seasonality, and episodic weather events (Mathies et al. 2014), making accurate distance calculations even more difficult and unreliable. Additionally, the placement of BR1 in the Brandywine River probably resulted in variable detection efficiency due to intermediate noise interference from the dam and strong riffles. One range test on BR1 resulted in a maximum detectable range of 20 m at 27°C, which is a conservative estimate due to high turbidity in the area. Therefore, total distance traveled is more of a gross estimate and detections within wide streams or near noisy perturbations act as a "leaky" gate of fish passage rather than a sphere of likely occurrence in a water column. Similarly, occupancy is dependent on a fish remaining in location and being detected on those receivers; low spatial resolution, such as in the Delaware Bay (Figure 1A), or poor detection efficiency can overestimate occupancy and residence times.

Of the 20 analyzed American Shad, 15 were detected upstream of removed dam 1 at BR1 and 18 were detected at BR2. Detections in the Brandywine River provide insights into seasonal river utilization by American Shad within tributaries of the Delaware River basin. For example, fish 10 was detected in the Brandywine River from May to July. Similarly, nine fish were only ever detected in the Brandywine River (BR1, BR2, and BR3), and residence times were as high as 2 months. It is unlikely that this trend would deviate with changes in receiver density or range detection or that the fish were simply faster than the intervals of transmitter pulses. For example, of all 11 fish that exited the Brandywine River (and the three that returned), BR3 was detected on the way out or way back in for every instance except once. What is more likely is that fish with a final detection at BR3 continued upstream in the Christina River, where there is an absence of acoustic receivers, before extraction or postspawning mortality occurred. American Shad last detected at BR1 may have also experienced postspawning mortality, and it is unlikely that American Shad were trapped above dam 2, even during large flood events that occurred during our study, as detections at BR1 continue after discharge and gauge heights return to baseline conditions (Figure S5). Occupancy durations in the Brandywine River of up to 2 months is similar to residency reported in Aunins and Olney (2009), who reported that American Shad remained at upstream spawning locations for weeks in the James River, Virginia. Several of the Brandywine River resident American Shad also had short residence times, either only appearing for a small window of time (fish 16 and 18; 115 and 8 h) or appearing and then reappearing later for a short period (fish 20; 160 h). Other Brandywine residents (fish 6, 8, 9, and 25) had much higher residence times (1782, 577, 1574, and 749 h, respectively). Duration within a receiver array may be highly variable across individuals and constitute natural diversity of movements (Frank et al. 2009).

Mortality was highly context dependent and was attributed to either natural mortality, fishing pressure, or tagging-related stress. American Shad that exited the Brandywine River and migrated downstream, but were never detected at the Delaware Bay Gate receivers (in addition to Brandywine River residents that failed to exit this river), were assumed extractions or mortalities at the end of their detection window or to have passed the Delaware Bay Gate undetected and perished in the Atlantic Ocean. One additional cause of detection cessation is tag expulsion, but this is unlikely for American Shad detected for weeks on the receiver array. Additionally, mortality specifically attributed to tagging stress was considered only within 120 h posttagging. This latent mortality window was arbitrarily determined but is important to address as failure to identify any source of mortality may misinterpret fish behavior (Klinard and Matley 2020). We place large assumptions that mortalities occurring several weeks after tagging were not related to chronic stress that may have developed because of tagging stress. However, such mortalities appear to be common; other acoustic studies using alosines have reported the disappearance of fish during the spawning period or study season (Frank et al. 2009; Eakin 2017; Mack et al. 2021), and a review of 600+ acoustic telemetry papers reported an average of 11% animal mortality or tag expulsion (Klinard and Matley 2020). Of the 24 tagged American Shad in our study, three fish exhibited potential mortality within the

5-day window, for a total of 12.5% (fish 17, 19, and 24). Fish 19 produced zero detections and is an example of a fish that may have expunged the transmitter or immediately perished after tagging.

Handling effects also included instances of fallback. Fish 22 and 24 exhibited nonterminal fallback within 24 h of tagging. The distance traveled and changes in trajectory by fish 22 and 24 during fallback are likely not attributed to spawning season timing or water temperature, as their movement in mid-May and >15°C water contradicts trends observed in other American Shad performing fallback (Moser and Ross 1993). The two fish that displayed fallback behavior were caught by means of electrofishing in 2022, which suggests that there may have been more stress associated with this method of capture or that the year-class that was tagged in 2022 was more susceptible to handling stress. However, Hickory Shad *Alosa mediocris* in the Chesapeake Bay experienced no difference in mortality between electrofishing and angling (Matsche et al. 2017). In 2022, four fish exhibited a handling response (mortality or fallback) compared to no fish in 2021. In the future, we suggest that seine-net or hook-and-line capture be used before electrofishing, if possible, to minimize handling stress and any corresponding mortality or sublethal behavioral changes. Additionally, we would recommend the use of gastric tagging to minimize handling time and stress for American Shad, depending on the study objectives. In river herring, gastrically tagged individuals significantly retained tags and displayed no adverse impacts (Smith et al. 2009). However, similar studies that followed the same protocol of gastric insertion in American Shad reported 92.5% fallback (Aunins and Olney 2009) or 44.8% handling impacts (Olney et al. 2006). Of the two gastrically tagged American Shad, one (fish 14) suffered mortality and the other (fish 13) spent 2 months in the Brandywine River (Figure S6). While the impacts of insertion method are not clearly understood in American Shad, fallback may still impact dam passage or reproductive success but may be unavoidable in biotelemetry studies no matter the method of tag insertion. Fallback behaviors may also be acute rather than chronic. For example, Twaite Shad *A. fallax* that returned to a river system the following year had higher passage rates at weirs than recently tagged Twaite Shad (Davies et al. 2023). We similarly observed more exploratory behavior in 2022 by fish 1 when it returned for its second year. These complex reactions to handling and tagging must be considered when investigating questions concerning "typical" behavior.

Additional variation in spatial distribution and swimming patterns in American Shad is likely attributed to a range of factors, including natal homing, time of day, maturity, and physical water properties, such as temperature, river discharge, and tidal cycle (Moser and Ross 1994; Aunins and Olney 2009). Determining the factors that play the most influential roles on American Shad distributions and behavior are important to inform management. We investigated water temperature, dissolved oxygen, pH, discharge, and gauge height and found evidence to suggest that temperature, discharge, and pH are significantly correlated to the frequency of American Shad detections within the Brandywine River, up to 35 h before detection. Temperature typically determines the timing of American Shad migrations and reproduction, and peak spawning temperature ranges from 14°C to 20°C (Stier and Crance 1985), but American Shad will reproduce anywhere from 8°C to 26°C (Walburg and Nichols 1967). In the Brandywine River at U.S. Geological Survey gauging station 01481500, the minimum temperature reported from May to August was 10.9°C and the maximum was 30.3°C, with average monthly temperatures ranging from 17.6°C to 25.8°C (Figure S5). It is possible that higher temperatures in June (>20°C) influenced the departure of fish 1, 7, 15, and 21 from the Brandywine River, as American Shad typically follow isotherms during migration (Leggett and Whitney 1972). While river discharge remained mostly stable (May–August monthly averages = 5.5–25.8 m^3/s), high pulses of water during flood events peaked at 235.5 m^3/s. Raabe (2012) similarly found significant association between river discharge and American Shad captures and detection frequency following dam removal. The pH remained in a range typical of freshwater (May–August monthly averages = 7.86–8.32), but peaks often exceeded 9.00, were as high as 9.40, and likely contributed to the negative relationship observed. Though an upper pH physiological tolerance is not established for adult American Shad, it is probable that adults would not reproduce in conditions unsuitable for their eggs and larvae, as a pH of 9.0 was determined as the upper limit for larval hatching and growth at 12°C (Leim 1924) and a pH of 7.5 was determined as the optimal pH for larval production (Leach and Houde 1999).

Overall, we found that our hypothesis was supported; American Shad in the Delaware River basin use habitat upstream of removed dams for an extended period, indicating the capability of river restoration to expand the range of American Shad spawning habitat. We additionally describe within-year and between-year site fidelity in the restored section of the Brandywine River and behavioral responses (fallback) to surgical tagging via electrofishing in 2022. These results are useful for informing future restoration projects that promote diadromous fish passage. Despite historical knowledge on the Delaware River American Shad stock status, little is known about their habitat use and residency in tributaries of the Delaware River. Our results indicate that the Brandywine River serves as an important habitat and is beneficial for successful survival and reproduction. Future research should focus on the best methods to obtain this data and other spatial ecology tools to assess habitat use and ecological function for multiple life history stages.

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CONFLICT OF INTEREST STATEMENT

The authors declare there are no competing interests.

DATA AVAILABILITY STATEMENT

Data generated or analyzed during this study are available from the corresponding author upon reasonable request. All code for analysis can be found on the GitHub repository: https://github.com/rroday/AmericanShad2021-2022.

ETHICS STATEMENT

All procedures were performed in compliance with relevant laws and institutional guidelines under Institutional Animal Care and Use Committee Protocol #1371-2021-1 developed in conjunction with the Delaware Division of Fish and Wildlife and the University of Delaware.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.