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FEATURE ARTICLE

Migratory passage and run size of American Shad and river herring in the Raritan River, New Jersey, USA

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Abstract

Objective: Restoration of many populations of anadromous American Shad *Alosa sapidissima* and river herring (Alewife *A. pseudoharengus* and Blueback Herring *A. aestivalis*) has been hampered by the presence of barriers to their spawning migrations and insufficient monitoring of run size. Here, we describe results of a 10-year (2012–2021) study of American Shad and river herring passage at the Island Farm Weir (IFW), the downstream-most migration barrier on the Raritan River, New Jersey, United States.

Methods: We used passive integrated transponder tags applied to fish that were captured and released downstream of the IFW to estimate passage rates and migration delays associated with upstream movements through an antenna array on a vertical slot fishway within the weir. By combining estimated passage rates with video monitoring of the total numbers of American Shad and river herring transiting the fishway, we estimated the annual run size below the weir.

Result: Results suggest that the fishway on the IFW is moderately effective for American Shad (passage rate = 41%; 95% credible interval [CI] = 21–61%) but ineffective for the smaller-bodied river herring (passage rate = 0.5%, 95% CI = 0–2%; fallback-adjusted passage rate = 1.1%, 95% CI = 0.0–4.5%). The IFW may have also delayed the spawning migrations of those fish that did pass, with total passage times ranging from 0.4 to 20.9 days (mean ± standard deviation = 8.2 ± 5.3 days) for American Shad and 15.0 days for the one river herring that passed within the same year that it was tagged. Run size estimates during the study period ranged from 103 to 2624 individuals for American Shad and from 1486 to 53,334 for river herring.

Conclusion: Restoration of these species in the Raritan River will likely require removal of the IFW or replacement of its current fish passage device with one that increases the passage rates of alosines.

KEYWORDS

Alosidae, dam removal, fish ladder, radio frequency identification

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INTRODUCTION

Anadromous runs of alosines, a subfamily of the Clupeidae that includes American Shad *Alosa sapidissima* and river herring (Alewife *A. pseudoharengus* and Blueback Herring *A. aestivalis*), historically supported important fisheries and were critical forage species in many rivers of the northeastern United States. For example, the total nationwide American Shad harvest reached a peak of 22,408 metric tons in 1814 (Atlantic States Marine Fisheries Commission [ASMFC] 2007), and by the 1840s, overfishing had driven the first of several fishery collapses in the Delaware River (Hardy 1999). Alosines can be an important diet item for piscivorous fishes like the Striped Bass *Morone saxatilis* during these species' spring freshwater spawning migrations (Andrews et al. 2018). Studies of marine-derived nitrogen demonstrate that river herring spawning runs are an important biogeochemical flux from marine to freshwater ecosystems (Walters et al. 2009). These migratory species thus represent substantial sources of ecosystem functions and services to eastern U.S. river ecosystems (Hare et al. 2021).

Despite attempts at restoration, populations of alosines in the northeastern United States have declined to the point at which they are no longer filling their historical economic and ecosystem roles (Limburg and Waldman 2009). American Shad commercial harvest in the Delaware River—once the most productive shad fishery on the U.S. East Coast—is now extremely limited in Delaware, prohibited in Pennsylvania, and restricted to a single haul seine operation (the Lewis Fishery at Lambertville) in New Jersey, which is maintained largely for its value as a long-term monitoring time series. The directed at-sea fishery for American Shad has been closed coastwide since 2005 (ASMFC 2020). River herring have been under a harvest moratorium since 2012 for all U.S. states that lack a sustainable fishery management plan. The most recent stock assessment for the entire coastwide metacomplex of river herring concluded that they are at or near historic lows (ASMFC 2017). River herring were recently considered for listing under the U.S. Endangered Species Act, although a review concluded that they did not currently meet the criteria for listing (National Marine Fisheries Service 2019). Stocking of American Shad in the Raritan River, New Jersey—where they were previously extirpated—resulted in a small but persistent population that supported a modest recreational fishery. This fishery was closed beginning in 2013, when all directed fishing for the species was prohibited in New Jersey except within the main-stem Delaware River (New Jersey Department of Environmental Protection 2013).

Impact statement

Using a combination of electronic tags and video monitoring, we found that a fish passage structure on the Raritan River, New Jersey, works moderately well for the large-bodied American Shad but passes only a small fraction of the smaller-bodied river herring.

One of the major anthropogenic impacts thought to be preventing the recovery of alosines is the loss of access to freshwater spawning habitat due to dams (Savoy and Crecco 1995; Hasselman and Limburg 2012). Globally, we are in the midst of a dam-building boom, with thousands of new dams currently under construction or planned, particularly in South America, Asia, and Africa (Zarfl et al. 2015). However, within the northeastern United States, small mill dams already dotted the landscape as early as the 17th century, and dams in this region continued to grow in numbers and size until the 1980s (Graf 1999). Within the state of New Jersey alone, there are estimated to be over 1700 dams (D. Lima, New Jersey Department of Environmental Protection, personal communication). Although many of the larger dams in the northeastern United States have fish passage devices, these structures are often ineffective at maintaining anadromous fish runs, either because of low passage rates (Brown et al. 2013) or because the passage devices result in migratory delays and thus reduce the energetic condition of migrating fish (Castro-Santos and Letcher 2010). Studies of fish passage are relatively common, but the majority focus on salmoniform fishes (Roscoe and Hinch 2010), and empirical studies of alosine passage are less common (but see Franklin et al. 2012, Raabe et al. 2019, Weaver et al. 2019, and Sullivan et al. 2023).

Here, we use a combination of video monitoring and passive integrated transponder (PIT) tagging to investigate passage rates and estimate run sizes of American Shad and river herring through a fishway located within a coastal plain river in New Jersey: the Raritan River. We ask the following questions: (1) "How effective is the fishway at facilitating upstream passage for American Shad and river herring?"; and (2) "How has the run size for these species changed over the period of video monitoring from 2013 to 2021?" The first question is broken down into two discrete components related to passage rates and migratory delay: (1) "What fraction of tagged fish find the fishway entrance and make their way through it to the exit?"; and (2) "How long does it take for tagged fish to find the entrance to the fishway and make their way to the exit after they first find the entrance?”

METHODS

Study site

Our primary field site was the Island Farm Weir (IFW), located on the Raritan River below its confluence with the Millstone River in Bound Brook, New Jersey, United States (40.543° N, 74.566° W; Figure 1). The IFW, a low-head dam that was built in 1994, maintains the water level for the New Jersey American Water treatment plant, which provides for household water needs in the region. The fish passage structure adjacent to the weir is a vertical slot fishway consisting of eight chambers and a viewing room. Discharge at a U.S. Geological Survey gauging station in Bound Brook (1.8 km below the IFW) averaged 32 m^3/s (standard deviation [SD] = 55 m^3/s) over our study years during the period of peak alosine passage (defined as the period encompassing 90% of individuals tallied on video). We estimated American Shad and river herring passage efficiency through the IFW and the run size for each species by using video monitoring combined with PIT tagging (Table 1).

Video monitoring

From 2013 to 2021 (generally in late March through late June), we monitored the passage of fish through the fishway using a camera system facing a clear polycarbonate viewing window near the exit of the fishway. Video was recorded 24 h/day during the monitoring season. In 2013, we used a closed-circuit television camera and digital video recording system (DYK14G Mini-DVR; Advanced Technology Video) to record passing fish. In 2014, we upgraded the camera system to an infrared-capable security camera (CVC627B Bullet Camera; Speco Technologies) and we installed an infrared, weather-resistant LED light bar (LBIR-850-35; Super Bright LEDs, Inc.) above the fishway near the viewing window to provide better illumination of the water column. All electronics were powered by pairs of 225-ampere-hour, 12-V, deep-cycle marine batteries.

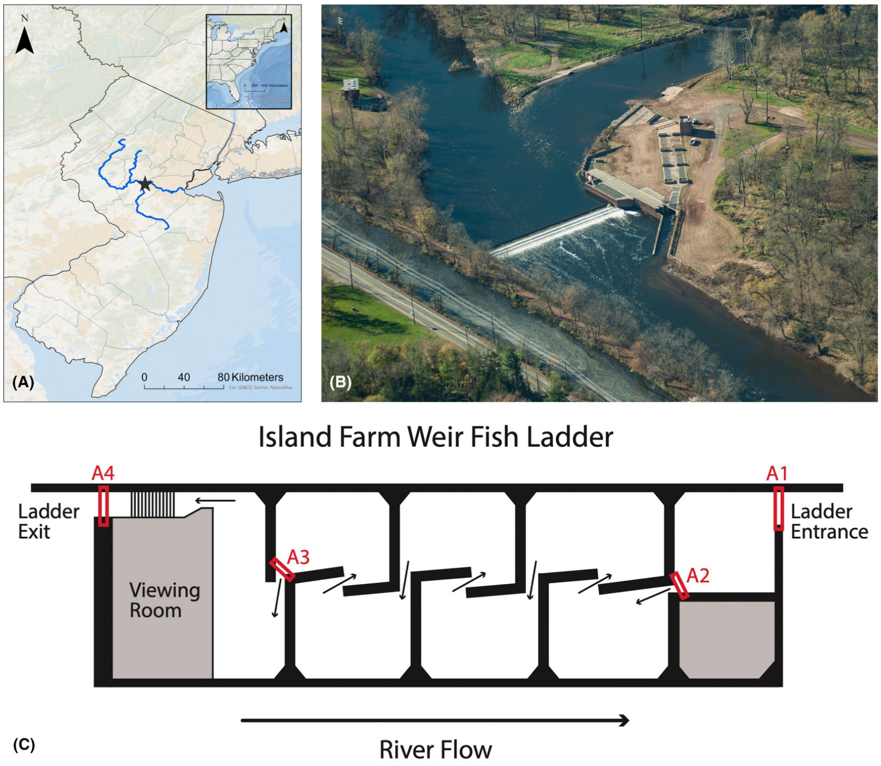

FIGURE 1 (A) Study location map, showing the Island Farm Weir (black star) at the confluence of the Millstone and Raritan rivers (blue lines) in Bound Brook, New Jersey. (B) Aerial view and (C) plan view diagram of the Island Farm Weir and Fishway are shown. In the diagram, red rectangles A1–A4 show locations of the passive integrated transponder tag antennas. The viewing room is near the upstream exit of the fishway. The large arrow at bottom in panel C represents the direction of river flow, and the small arrows within the fishway indicate the direction that a passing fish would swim to move upstream through the fishway. (Photo credit: Jamie Darrow, New Jersey Department of Environmental Protection.)

TABLE 1 Capture and passage efficiency estimation methods[a] that were used to study American Shad and river herring migration at the Island Farm Weir on the Raritan River, New Jersey.

Criterion	American Shad	River herring
Capture method	Angling ($n=40$); seine ($n=10$); gill net ($n=1$); fyke net ($n=0$)	Angling ($n=13$); seine ($n=144$); gill net ($n=0$); fyke net ($n=7$)
Capture location	Immediately below dam ($n=45$); 6.2 km from dam ($n=5$); 14.4 km from dam ($n=1$)	Immediately below dam ($n=17$); 6.2 km from dam ($n=147$)
Release location	Same as capture location	Same as capture location
Timing (relative to peak migration)	Throughout migration season	Throughout migration season
Tagging method and anesthesia	Intracoelomic implantation without anesthesia	Intracoelomic injection without anesthesia
Equipment performance and reliability	Monitored using within-antenna marker tag to verify receiver function (in 94% of study hours, the array had at least one antenna functioning from the date of first tagging until the end of peak passage). Tag read range was checked every 2–4 days. Receivers and video monitoring equipment were removed during high-water events (11.33% of the time that the receiver was present).	The same equipment used for American Shad was used for river herring
Fallback after passage	Not observed (i.e., no tagged fish that passed through the fishway were subsequently recorded again within the fishway)	Not observed (i.e., no tagged fish that passed through the fishway were subsequently recorded again within the fishway)
Fallback (or mortality) before passage	Unknown	Estimated fallback rate of 52% in a second, smaller New Jersey river during a study using similar capture and tagging methods

[a] Efficiency metrics sensu Cooke and Hinch (2013). See also Bunt et al. (2012).

Video footage analysis

We manually reviewed all video footage at 4–16× viewing speed using VLC Media Player (VideoLAN). We counted and identified all fish passing the viewing window, and we recorded the time and date of passage for each identified fish. If an individual was not identifiable due to poor visibility, we marked it as "unidentified." Fish that made an unsuccessful passage attempt were not counted; likewise, fish that passed downstream through the fishway exit were not counted.

PIT tagging

From 2012 to 2019 (generally in late March through late May), we visited sites downstream of the IFW two to four times per week to capture and PIT-tag American Shad and river herring. We captured fish by using a 91-×2-m seine at a site 6.2 km downstream from the weir (40.542° N, 74.514° W) and via hook and line or seine near the base of the weir (40.5431° N, 74.5653° W). In 2012, fish were also captured by using gill nets and fyke nets at the site 6.2 km downstream from the weir. We tagged each captured American Shad and river herring with a uniquely coded half-duplex PIT tag (Oregon RFID; length = 23 mm for American Shad and 12 mm for river herring) that was inserted into the coelomic cavity via a small incision in American Shad or was injected via a sterilized syringe (PIT Tag Injector; Oregon RFID) in river herring. All tagged fish were released at their tagging site.

Antenna array

We detected tagged fish at the fishway by using multi-antenna half-duplex radio frequency identification (RFID) readers (Oregon RFID) powered by pairs of 225-ampere-hour, 12-V, deep-cycle marine batteries and connected to PIT tag antennas within the fishway (placement described below). Antennas were constructed of 5.08-cm polyvinyl chloride (PVC) tubing with two loops of 12-gauge stranded thermoplastic high-heat nylon (THHN) wire separated by corrugated plastic placed inside the PVC tubing. We connected antennas to RFID tuner boxes that allowed for custom antenna sizes. Tuner boxes were connected to the RFID readers by using 20-gauge stranded and shielded twinaxial cable. We fitted antennas with a Marker Tag (Oregon RFID) that electronically "revealed" a PIT tag at 15 min intervals to monitor performance of the PIT tag detection system. Additionally, we verified antenna performance twice weekly using a PIT tag attached to a long piece of PVC pipe that we manually moved through the detection plane of the antenna to check the range and detection of the test tags.

From 2012 to 2014, we maintained two antennas at the fishway: one at the fishway entrance (A1) and one at the fishway exit (A4; Figure 1), generally from late March to late June. From 2015 to 2019, we maintained four antennas in the fishway: one at the fishway entrance (A1), one at the exit of the first (downstream) chamber (A2), one at the entrance to the final (upstream) chamber (A3), and one at the fishway exit (A4; Figure 1). We retrieved PIT tag data, including the times and identities of all marker tags and fish tags that were detected, twice weekly from the field site using a laptop computer, where the data were stored for later analysis.

Estimating attraction, staging, and transit times

After compiling all tagging data from the IFW in R (R Core Team 2021), we estimated three metrics related to passage efficiency through the IFW fishway: attraction, staging, and transit times. Following Castro-Santos et al. (1996), we defined attraction time as the length of time between tagging and the first detection at the fishway entrance antenna (A1), staging time as the length of time between the first and last detections at the fishway entrance antenna (A1), and transit time as the length of time between the last detection at the fishway entrance antenna (A1) and the first detection at the fishway exit antenna (A4; i.e., the time to transit through the fishway). Staging and transit times can be viewed as measures of the fish's willingness to enter the fishway and the fish's ability to pass through the fishway, respectively. We further defined "passage time" as the sum of all three metrics, representing the total length of time from tagging until exiting the fishway on the upstream end.

Estimating river herring fallback

The stress of tagging can cause some individuals to abandon their migration, a phenomenon known as "fallback." Therefore, some proportion of tagged fish that failed to reach the fishway likely resulted from fallback and not from an inability to navigate to the fishway. Estimation of fallback after PIT tagging can be done but requires an antenna spanning the entire channel, which was not feasible in the Raritan River.

Here, we estimated the fallback probability for river herring using data from a separate study that took place in 2013 at the Lake Shenandoah Dam (40.086° N, 74.185° W) on the South Branch Metedeconk River in southern New Jersey (J. M. Vasslides, unpublished data). In that study, 139 river herring were tagged and both their upstream and downstream movements were assessed using a three-antenna array. River herring were captured via a modified fyke net approximately 60 m downstream of the fishway entrance and were tagged by using the same 12-mm PIT tags used for river herring on the Raritan River. To track the number of river herring that successfully continued upstream after tagging, a "cross-stream" antenna that spanned the width of the stream, oriented vertically, was placed approximately 2 m downstream from the entrance to the fishway. Additional antennas were located within the fishway entrance and within the fishway exit to assess the fishway attraction and passage efficiencies, respectively. The antennas were constructed as above but with two loops of 10-gauge THHN wire and were attached to an identical RFID system. The detection efficiency of the cross-stream antenna was estimated to be 50% based on the fraction of fish that were detected at the entrance antenna but not at the cross-stream antenna. We estimated the fraction of tagged fish that continued on after tagging (i.e., 1 − fallback probability) as the number recorded at the cross-stream antenna divided by the total number tagged, with the resulting value divided again by 0.5 to adjust for the 50% antenna detection efficiency.

Passage rate, fallback rate, and run size estimation

We fitted a Bayesian hierarchical model to estimate the proportion of individuals that successfully transited the IFW fishway ("passage rate") and therefore were available to be counted in our video surveys. The dependent variable was the count of tagged individuals detected by the fishway exit antenna (A4) in each year (n_i). This count was assumed to be distributed as a binomial random variable, Binomial($n_i|N_i$, θ_i), where N_i is the total number of tagged fish in each year and θ_i is the passage rate parameter to be estimated. We assumed that logit (θ_i) originated from a common normal distribution for each fish species (f) with a mean of logit(p_f) and precision (i.e., variance^{-1}) of τ_f. The hierarchical structure of the model allows estimates from years with sparse tagging data to be informed by the overall mean rate (p_f)

for each species. We estimated the corrected fallback probability for river herring within a similar Bayesian model using data from the South Branch Metedeconk River study, assuming Bernoulli-distributed fallback events with 139 trials. We adjusted the estimated passage rate of river herring from our Raritan River IFW tagging data by dividing the estimate by 1 minus the South Branch Metedeconk River fallback probability, propagating uncertainty from both sources. American Shad passage rates were not adjusted for fallback, as we lacked comparable data for this species. We estimated run size for American Shad and river herring by dividing the video counts by the final posterior distribution for the estimated passage rate. For years in which we had video counts but no tagging data, we used the posterior predictive distribution for the mean passage rate parameter (p_f) for this calculation. We assumed vague priors for all parameters and fitted the models by using JAGS and jagsUI in R (Kellner 2021). We ran three chains of 1,000,000 iterations each, including a burn-in period of 500,000 and keeping every 200th draw. Model convergence was assessed by examining trace plots and Gelman–Rubin statistics ($\hat{r} < 1.1$).

The approach described above makes two implicit assumptions about fish detection at the fishway. The first is that all PIT-tagged fish are detected within the antenna array. The second is that all fish passing through the fishway are correctly identified as they pass the video monitoring station near the upstream exit. In the Results and Discussion, we evaluate the extent to which these assumptions were met and the associated impacts on passage and run size estimates.

RESULTS

Video monitoring performance

From 2013 to 2021, we observed 65,287 fish passing through the IFW fishway, including 3491 American Shad and 708 river herring. We were unable to identify 13,971 fish (21.4%) from our video monitoring due to poor water clarity or poor lighting conditions. We did not review nighttime video in 2013 except for up to about 0.5 h after sunset due to the lack of infrared-capable equipment. However, analysis of passage timing in 2014–2021, when an infrared camera system and infrared spotlight were deployed, showed that 94% of American Shad and river herring passed during daylight hours (from sunrise to 0.5 h after sunset; Figure S1 available in the Supplementary Material in the online version of this article). The video equipment performed well throughout the study, with technical issues compromising only 9 days (1.1%) of video footage out of 847 days over the course of the 9-year study. In addition, we removed the video equipment for 96 days due to high-water events; thus, footage was recorded and available for 742 (87.6%) of the 847 days.

PIT tag antenna array performance

From 2012 to 2019, the PIT tag antenna array remained in operation from approximately late March through late June of each year. Due to high-water events, the array was removed for a total of 96 (11.3%) of the 847 days; additionally, there were periods during which individual antennas were not fully operational. However, at least one antenna was confirmed operational at the array during 94% of hours that occurred during the period beginning on the date the first PIT tags were deployed and ending at the end of the peak fish passage period in each year (Figure S2).

Attraction, staging, and transit times

From 2012 to 2019, we detected 26 of 51 tagged American Shad and 5 of 164 tagged river herring at our antenna array. Of the five river herring that were detected, we detected two individuals during the same year in which they were first tagged, whereas three individuals were detected during the year after initial tagging (i.e., 348–363 days later). These interannual individual returns are excluded from our attraction and passage time calculations. Over the course of the study, we documented 21 of 51 tagged American Shad as navigating through the fishway, with fish being detected at the upstream exit antenna (A4). Over the same period, we documented only two river herring that successfully moved upstream of the dam after tagging, and only one of those individuals did so during the year in which it was tagged. Attraction time (the time between tagging and detection at the entrance antenna [A1]) averaged 5.4 ± 4.3 days (±SD) for American Shad (range = 0.1–16.0 days; $n = 25$) and 12.1 ± 2.6 days for river herring (range = 10.2–13.9 days; $n = 2$; Figure 2). Staging time (the time between the first and final detections at the fishway entrance antenna [A1]) averaged 1.7 ± 3.9 days for American Shad (range = 0.0–19.6 days; $n = 25$) and 5.2 ± 5.4 days for river herring (range = 0.0–12.0 days; $n = 5$). Transit time (the time between the final detection at the fishway entrance antenna [A1] and the initial detection at the fishway exit antenna [A4]), averaged 0.1 ± 0.3 days for American Shad (range = 0.005–1.000 days; $n = 20$) and 0.01 ± 0.001 days for river herring (range = 0.010–0.012 days; $n = 2$). The mean total time that elapsed between tagging and full passage through the fishway was 8.2 ± 5.3 days for American Shad (range = 0.4–20.9 days;

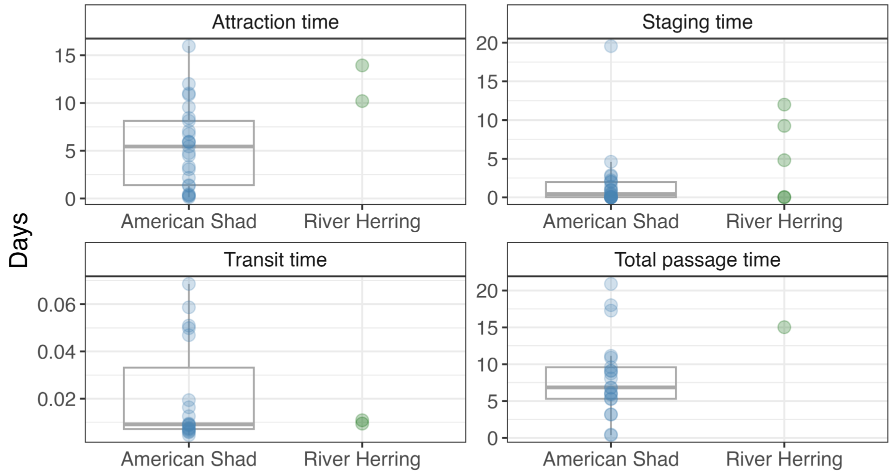

FIGURE 2 Attraction, staging, transit, and total passage times for American Shad and river herring at the Island Farm Weir in central New Jersey. Individual data points are shown as semi-transparent circles, while box-and-whisker plots (American Shad only) show the median, interquartile range, and range of the data. One data point for American Shad (transit time = 1.0 day) is omitted from the plot for clarity.

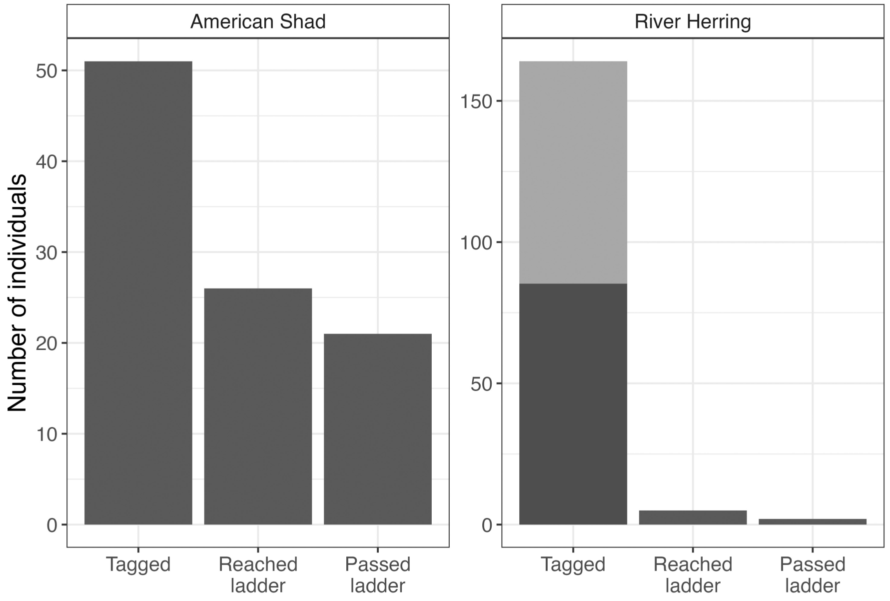

FIGURE 3 The total numbers of American Shad (left panel) and river herring (right panel) that were tagged, reached the fishway entrance, and successfully passed through the fishway exit at the Island Farm Weir. Lighter gray shading for tagged river herring represents the fraction of fish that were estimated to have abandoned migration after tagging based on fallback estimates.

$n = 21$). The only river herring to successfully navigate the entire fishway during the same year that it was tagged had a total passage time of 15.0 days.

Passage rate, fallback rate, and run size estimation

Between 2012 and 2019, we found that after tagging, 21 of 51 American Shad and 1 of 164 river herring successfully moved upstream of the dam during the same year in which they were tagged (Figures 3 and 4). Annually, our model estimated that passage rates ranged from 31% to 48% per year for American Shad (Figure 4; mean = 41%; 95% credible interval [CI] = 21–61%) and from 0.0% to 0.9% for river herring (mean = 0.5%; 95% CI = 0–2%). Across all years, approximately half (mean = 49%; 95% CI = 20–76%) of tagged American Shad were detected at the fishway entrance antenna (Figure S3) and 82% (95% CI = 63–97%) of those individuals continued through the fishway and were detected at the fishway exit antenna (Figure S4). For river herring across all years, only two tagged individuals were detected at the fishway entrance antenna, resulting in an average attraction rate of 0.8% (95% CI = 0.0–2.8%; Figure S3).

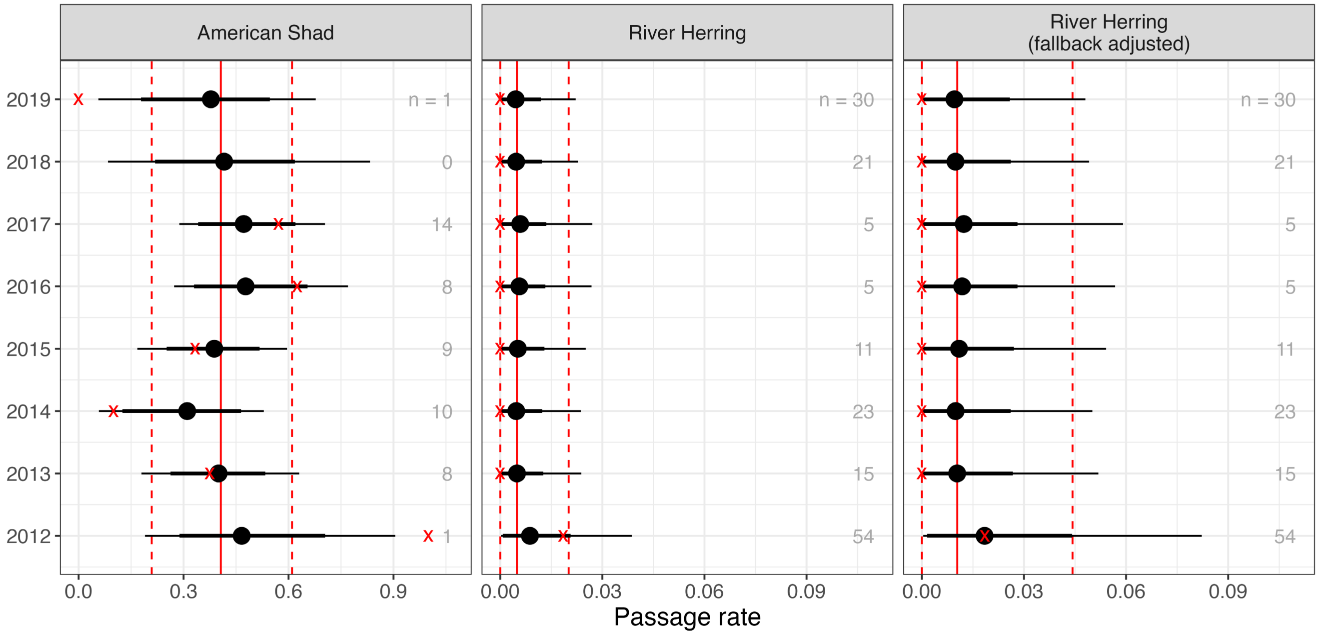

FIGURE 4 Passage rates of American Shad (left panel) and river herring without (center panel) and with (right panel) correction for fallback at the Island Farm Weir on the Raritan River as estimated via a Bayesian hierarchical model fitted to tagging data. Black circles represent the point estimate for each year, with thick and thin lines representing 80% and 95% credible intervals, respectively. Red × symbols show the observed proportion of tagged fish that passed successfully each year, while the numbers to the right show the sample size of tagged fish in each year. The vertical red lines represent the overall mean estimate (solid line) with 95% credible intervals (dashed lines).

During the 2013 tagging fallback study in the South Branch Metedeconk River, 33 (24%) of 139 tagged river herring were observed to continue upstream after tagging. Based on these data, our modeled estimate for the continuation probability (i.e., 1 – fallback) after correcting for a 50% observed detection efficiency was 48%, with a 95% CI of 35–63%.

From 2013 to 2021, raw visual counts based on the video data ranged from 47 to 1207 individuals for American Shad and from 7 to 267 individuals for river herring (Figure 5). Modeled run size below the IFW, adjusted for the estimated fraction that did not reach the video camera, ranged from 103 (95% CI = 61–175) to 2624 (95% CI = 1686–4237) for American Shad and from 1486 (lower bound of 95% CI = 157) to 53,334 (lower bound of 95% CI = 4164) for river herring (Figure 5). We did not attempt to estimate the upper bounds of run size for river herring because the lower bounds of the 95% CIs for annual passage rate estimates were very close to zero in some cases (e.g., minimum = 2×10^{-16}%), leading to very large (and implausible) adjusted run size estimates.

DISCUSSION

Understanding how dams affect migratory fish passage and measuring the effectiveness of fish passage structures are pressing needs globally as the construction of new dams and new passage structures accelerates. We reported on the passage efficiency and estimated the run size for migratory fish, American Shad and river herring, which are of high cultural and economic significance in the eastern United States. The estimated passage rate for American Shad (41%) falls within the typical range for the species as reported in the literature, with rates of 10–20% considered “common” and a rate of 50% considered “excellent” (Larinier and Travade 2002). However, even the best constructed passage structures can hinder restoration efforts for shads, as passage rates for this group are low compared with other taxa (e.g., salmonids, with up to 95–100% passage; Larinier and Travade 2002). Our estimated mean passage rate for American Shad falls below the mean passage rate from a meta-analysis of nonsalmonid fish at vertical slot fishways (51%; Bunt et al. 2016) but is above the mean rate estimated for all structures combined (21%; Noonan et al. 2012).

In contrast, the passage rate we estimated for river herring is exceptionally low (0.5%), even after attempting to account for fallback (1.1%). Passage rates appear to be highly variable for this group in the literature, possibly due to variation in structural characteristics of the fishways. For example, one study found a similarly low (5.6%) passage rate for Alewife at a pool-and-weir fishway (Landsman et al. 2020), while another found relatively high passage rates (63–64%) at a Denil fishway (Sullivan et al. 2023). Even subtle differences in spillway design

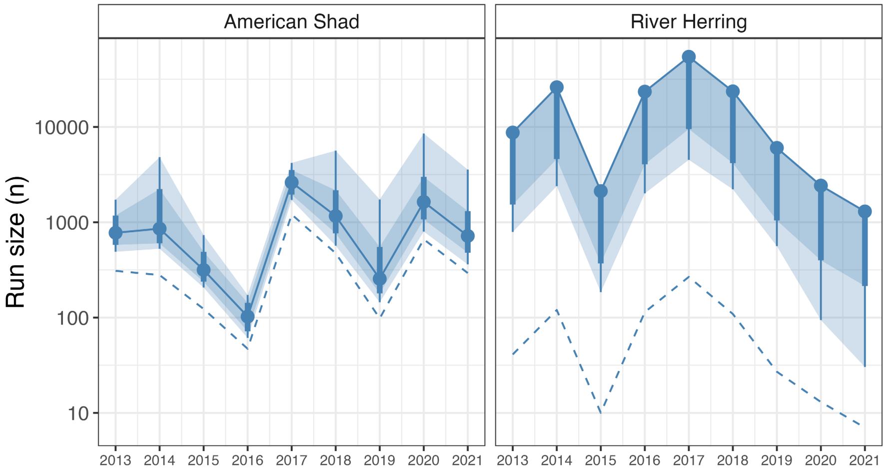

FIGURE 5 Run size estimates for American Shad and river herring at the Island Farm Weir on the Raritan River, New Jersey. Dashed lines represent observed counts for American Shad (left panel) and river herring (right panel) based on video observations. The solid lines and circles represent the estimated run size, corrected for modeled fishway passage (both species) as well as tagging fallback rates (river herring only). Shading and error bars show 80% and 95% credible intervals. Upper credible intervals are not shown for river herring due to exceptionally high values resulting from uncertainty in passage rates.

influence American Shad passage (Mulligan et al. 2019). The smaller size of Alewife and Blueback Herring relative to American Shad likely contributed to the poorer passage rates observed for river herring in our study. Even within Alewife, larger individuals are more likely to pass a fishway successfully (Nau et al. 2017; Sullivan et al. 2023). Regardless of the cause, the IFW in the Raritan River appears to be acting as a near-total obstruction to river herring migration in its current form and is therefore functioning as an impediment to restoration efforts for these species.

The length of time that it takes a fish to find and navigate a fishway can provide insight into potential energetic costs and into the general significance of the structure as a barrier to movement. For American Shad at the IFW, the time between tagging and first detection at the fishway entrance (attraction time) was highest, with a mean of 5 days. Meanwhile, the time to actually pass through the fishway (transit time) was much shorter on average, with a median time of 13 min. The mean transit time (101 min) was heavily influenced by a single individual with an extremely long 24-h transit time. A similar pattern was observed for river herring, with mean attraction and transit times of 12 days and 14 min, respectively. However, sample sizes were much smaller for the river herring ($n=2$ and 3, respectively). Comparisons of attraction time between American Shad and river herring are confounded by the fact that most American Shad (45 of 51) were tagged immediately below the fishway, while most river herring (147 of 164) were tagged at a location 6.2 km downstream of the fishway (Table 1). Little information on attraction and transit times is available in the literature; however, American Shad have been noted to have difficulty navigating some fishways in which they “milled in schools” (Ice Harbor-type fishway; Haro and Kynard 1997), a behavior that was also noted below a dam with a vertical slot fishway (Grote et al. 2014). On the other hand, Haro et al. (1999) found relatively quick passage times (generally <30 s) for both American Shad and Blueback Herring at a Denil fishway. In comparison, the relatively long median transit times that we observed (13–14 min for American Shad and river herring) may suggest difficulties in navigating the IFW fishway.

A substantial challenge in the interpretation of data on fish passage from tagging studies is the potential for “fallback,” or downstream movement after tagging. Fallback can occur naturally but may also be a result of handling stress. Fallback has previously been estimated for alosines by using tagging methods that allow for spatially continuous geolocation. For example, radio tag (Hightower and Sparks 2003) and acoustic tag (Aunins and Olney 2009) studies of American Shad have observed fallback in a substantial portion of tagged fish, with many individuals abandoning their migrations entirely. Here, we were able to estimate fallback for river herring based on a study using identical tagging methods in a smaller river where a cross-channel antenna could be constructed. However, we could not estimate fallback of American Shad. The fraction of individuals exhibiting fallback in studies of American Shad tagged with radio and acoustic tags varies widely from as low as 10% to as much as 100% (Smith et al. 2009). The prevalence of fallback behavior emphasizes the importance of short handling times and minimally invasive procedures. The use of PIT tags in this study is likely to be a significant advantage in this respect, as they can be quickly injected using a hypodermic needle and are little more than 1% of the weight of telemetry tags (0.1 g for PIT tags versus 9 g for typical telemetry tags).

Another challenge in PIT tag studies of fish passage using fixed antennas is maintaining continuous antenna coverage of the fish passage device. Antennas must be powered continuously and retuned occasionally to ensure that they reliably detect tagged fish. Occasional high-water events were the greatest obstacle to maintaining continuous antenna coverage in this study. We were forced to temporarily remove all monitoring equipment, including antennas, readers, the video camera, and memory cards, when high water was forecasted, as floods occasionally reached levels that would have destroyed the equipment. Nevertheless, at least one antenna was confirmed operational at the array during 94% of hours that occurred in the period from the first tag deployment to the end of peak fish passage in each year (Figure S2). Despite this high rate of antenna coverage, at least one American Shad likely made it through the entrance antenna without detection in 2014. This individual was detected at the exit antenna but not at the entrance antenna during a day when the entrance antenna was being replaced and retuned. Although the detection efficiency in our study was high, it was not 100%, and missed detections of tagged fish would cause attraction and passage estimates to be biased low and run size estimates to be biased high.

Similarly, not all fish could be identified from the video monitoring near the upstream exit of the fishway. Unidentifiable fish represented 21.4% of the total. In the (implausible) extreme case that all of these unidentifiable fish were either American Shad or river herring, this would mean that the true run size was 21.4% higher than our estimates. Allocating these 21.4% of individuals proportionally to the identified species is not justifiable, as the unidentified fish tended to be smaller bodied.

Restoration efforts targeting American Shad and river herring on the Raritan River have focused on removing small low-head dams. One dam on the main-stem Raritan River below the IFW was removed in 2011 before this study began. An additional three dams above the IFW were removed during the study period: the Robert Street and Nevius Street dams on the main stem were removed in 2012 and 2013, respectively; and the Weston Mill Dam on the Millstone River was removed in 2017. Although the limited sample size before and after each of these events precludes any statistical analysis, the run size estimates for American Shad and river herring show no evidence of a rapid population recovery after the removal of these dams. In fact, the number of river herring passing above the IFW peaked in 2017 (267 individuals), declining each year thereafter despite the Millstone River spawning habitat that was made available by dam removal upstream of the IFW. The exceptionally low passage rates of river herring at the IFW suggest that their recovery may continue to be hampered without either removal of the IFW or installation of a more effective fish passage device. There is some capacity to increase attraction water velocity at the downstream entrance of the IFW fishway, and a review of passage studies suggests that this may increase passage efficiency (Noonan et al. 2012). However, even if the threefold increase in passage efficiency with increased water velocity seen in that study could be achieved for river herring attempting to pass through the IFW, the resulting passage rate would still be under 5%. Benefits to American Shad from removal of the IFW or modification of the fishway may be more limited, as this species currently has a higher passage rate and there is relatively little of the main-stem spawning habitat that they prefer above the IFW.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code for this study are available at https://github.com/mikeallen-eco/fish_pass.

ETHICS STATEMENT

This work was conducted under approval from the Rutgers University Institutional Animal Care and Use Committee (Protocol Number 11-013).

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