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ARTICLE

Upstream Movements of Atlantic Salmon in the Lower Penobscot River, Maine Following Two Dam Removals and Fish Passage Modifications

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Abstract
The Penobscot River Restoration Project (PRRP), to be completed in 2016, involved an extensive plan of dam removal, increases in hydroelectric capacity, and fish passage modifications to increase habitat access for diadromous species. As part of the PRRP, Great Works and Veazie dams were removed, making Milford Dam the first impediment to federally endangered Atlantic Salmon *Salmo salar*. Upstream habitat access for Atlantic Salmon is dependent upon successful and timely passage at Milford Dam because nearly all suitable spawning habitat is located upstream. In 2014 and 2015, a total of 73 adult salmon were radio-tagged to track their upstream movements through the Penobscot River to assess potential delays at (1) the dam remnants, (2) the confluence of the Stillwater Branch and the main stem of the Penobscot River below the impassable Orono Dam, and (3) the Milford Dam fish lift (installed in 2014). Movement rates through the dam remnants and the Stillwater confluence were comparable to open river reaches. Passage efficiency of the fish lift was high in both years (95% and 100%). However, fish experienced long delays at Milford Dam, with approximately one-third of fish taking more than a week to pass in each year, well below the Federal Energy Regulatory Commission passage standard of 95% within 48 h. Telemetry indicates most fish locate the fishway entrance within 5 h of arrival and were observed at the entrance at all hours of the day. These data indicate that overall transit times through the lower river were comparable to reported movement rates prior to changes to the Penobscot River due to the substantial delays seen at Milford Dam. The results of this study show that while adult Atlantic Salmon locate the new fish lift entrance quickly, passage of these fish was significantly delayed under 2014–2015 operations.

Currently, populations of Atlantic Salmon *Salmo salar* in the United States are dramatically below historical levels, with runs declining to 500 to 2,000 fish in all Maine rivers combined by the mid-1990s. This led to the listing of the Gulf of Maine distinct population segment (GOM DPS), which included eight rivers in Maine, as federally

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endangered in 2000 (Fay et al. 2006). The Penobscot River was not included in the original listing because it has the largest return of Atlantic Salmon in the United States; however, after continued declines this run was added to the endangered GOM DPS in 2009. Despite conservation efforts, adult returns have decreased in recent decades and fluctuated at low levels (generally less than 2,000 returning adults). The GOM DPS has been identified as a high priority for recovery by the National Marine Fisheries Service (NMFS) because, although the species is at a high risk of extinction, the primary threats facing Atlantic Salmon are well understood (NMFS 2016).

Multiple factors, including overfishing, habitat loss, dams, and pollution, have contributed to Atlantic Salmon declines (Parrish et al. 1998; NRC 2004). Of these factors, dams have been identified as a major threat because they obstruct the downstream migration of juveniles, as well as the upstream and downstream migrations of iteroparous adults (NRC 2004). A large number of dams have restricted adult salmon access to upstream spawning habitats on the Penobscot River since the 1820s (Opperman et al. 2011). Until recently, 100% of high-quality rearing habitat was located above at least four dams (Fay et al. 2006). The cumulative negative effects of dams on upstream migration and spawning success have been well documented for Atlantic Salmon (Gowans et al. 2003), as well as Pacific salmonids (Naughton et al. 2005; Caudill et al. 2007; Roscoe et al. 2010). As a result, dam removal is being considered as a tool in multiple recovery plans across the United States, including the Elwha River (Wunderlich et al. 1994) and the Klamath River (Gosnell and Kelly 2010). Additionally, NMFS has identified the need to reconnect the Gulf of Maine with headwater streams and reduce the effects of dams that prevent or delay Atlantic Salmon passage as part of the 2016 Atlantic Salmon 5-year action plan for recovery of the species (NMFS 2016).

Over the past decade, steps have been taken in the Penobscot River to decrease the negative impacts of dams on Atlantic Salmon. The Penobscot River Restoration Project (PRRP), set to be completed in 2016, involved an extensive plan of dam removal, increases in hydroelectric capacity, and fish passage modifications. In the summers of 2012 and 2013, the Great Works and Veazie dams, respectively, were removed from the main stem of the Penobscot River (Figure 1). Upstream passage success for Atlantic Salmon at both dams was annually variable and often poor prior to removal (43–100% at Veazie Dam, 12–95% at Great Works Dam; Holbrook et al. 2009), so the demolition of these two dams was anticipated to be a significant step in improving upstream passage for adult salmon in the system.

To offset losses in energy production from the removal of the Great Works Dam and Veazie Dam on the main stem of the Penobscot River, hydropower generation was increased at facilities on the Stillwater Branch, a section of river that moves around a large island in the lower river (Opperman et al. 2011). Generation increases included changes to the Orono Dam, which is located at the confluence of the Stillwater Branch and the main stem of the Penobscot River. A trap was put in place at the base of the Orono Dam to capture upstream migrants entering the Stillwater Branch. Trapped fish would be trucked upstream and released on the main stem of the Penobscot River. This trapping and trucking operation was not designed to handle large numbers of upstream migrants because passage is provided via the Milford Dam fishway on the main stem. Following these changes, adult upstream migrating salmon may be attracted to increased flow coming from the Stillwater Branch, leading adult salmon to the Orono Dam, which lacks an upstream fishway. While the Orono Dam lies close to the confluence (about 200 m upstream), attraction to the area below the dam could cause delay in upstream migration.

After the removal of the Great Works and Veazie dams, Milford Dam has become the downstream-most dam on the main stem of the Penobscot River, hence, the first barrier for upstream migrating anadromous fish. Passage success at Milford Dam through a Denil fishway was relatively high prior to the PRRP (>80%; Holbrook et al. 2009), and delays were short compared with the other dams in the lower river (Shepard 1989; Holbrook et al. 2009). In April of 2014, a new fish lift and handling facility designed to pass Atlantic Salmon, Sea Lamprey *Petromyzon marinus*, Alewives *Alosa pseudoharengus* and Blueback Herring *A. aestivalis* (collectively referred to as “river herring”), and American Shad *A. sapidissima*, was completed at Milford Dam. With effective passage at the Milford Dam fish lift, as well as a natural bypass set to open at the Howland Dam (about 40 river kilometers [rkm] upstream of Milford Dam) in 2016, Atlantic Salmon are anticipated to have access to 60% of their historical range (Opperman et al. 2011). However, this increase depends on passage success at Milford Dam. Efficient passage at the lift is therefore a critical component of Atlantic Salmon recovery in the Penobscot River.

Upstream migration of adult Atlantic Salmon in unimpounded rivers can be broken down into three phases prior to spawning: (1) steady progress upriver with periods of swimming alternating with periods of rest, (2) searching with movements up and down river close to the spawning area, and finally (3) a long residence period in the spawning area (Økland et al. 2001). In a natural environment, migrating adults face many challenges that may alter their migration patterns, including changes in physiological conditions, changes in water flow (Thorstad et al. 2008), and high temperatures (Shepard 1995). However, dams can have considerable effects on upstream progress. Fishways primarily designed for Atlantic Salmon passage have been installed at many dams in Maine, but adult Atlantic Salmon can experience delays before successful passage despite the addition of fishways (Gowans et al. 1999; Thorstad et al. 2008; Holbrook

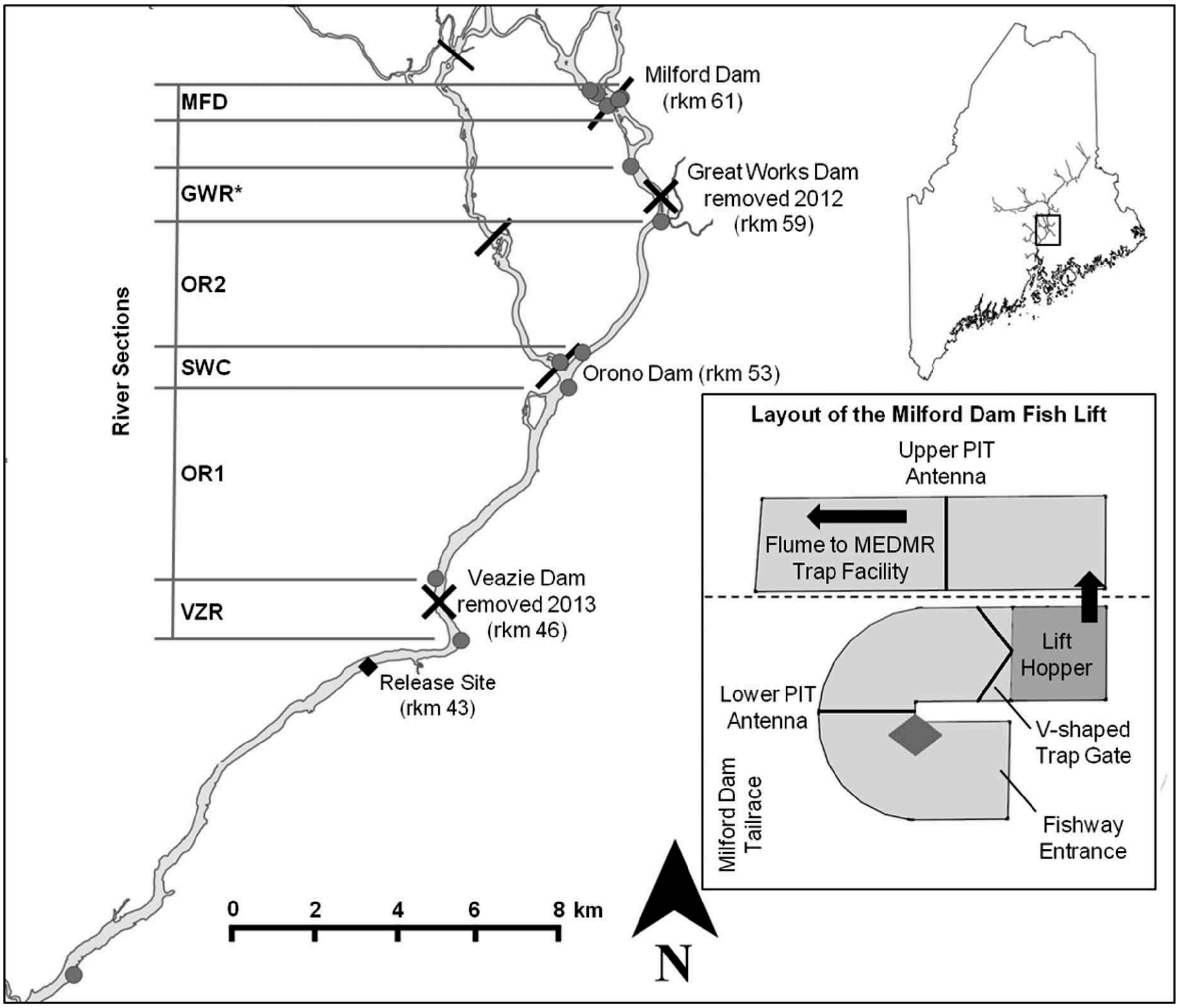

FIGURE 1. Map of the Atlantic Salmon study area on the lower Penobscot River, Maine. Stationary radio receivers indicated by gray circles, and release site for tagged fish indicated by a black diamond. River sections used in upstream movement calculations shown as VZR (Veazie Dam remnants), OR1 (open river 1), SWC (Stillwater confluence), OR2 (open river 2), GWR (Great Works remnants), and MFD (Milford Dam). Inset shows a schematic of the Milford Dam fish lift (fishway is 3.05 m across). Gray diamond represents the location of the dropper antenna. Note: upstream receiver in GWR added in 2015, upstream movement speed calculations in 2014 included unlabeled section between GWR and MFD.

et al. 2009). Substantial delays at fishways can lead to decreased energy reserves, which can cause decreases in reproductive success and survival (Dauble and Mueller 1993; Geist et al. 2000). For this reason, the Federal Energy Regulatory Commission (FERC) licensing regulations include both passage and delay criteria. These criteria are set in coordination with the state and federal regulatory fisheries agencies and specify that 95% of adult salmon must pass Milford Dam within 48 h after coming within 200 m of the dam (NMFS 2012).

The goals of this study were to investigate movements of adult Atlantic Salmon in the lower Penobscot River after the dam removals and fish lift installation. Specifically, we sought to determine if migrating adults were being delayed at (1) the remnants of the Veazie Dam and the Great Works Dam, (2) the confluence of the Stillwater Branch and the main stem of the Penobscot River below the Orono Dam, and (3) the Milford Dam fish lift (installed in 2014), both overall and in the context of FERC licensing requirements. Last, we use this assessment of current movements to compare transit times of adult Atlantic Salmon in the lower Penobscot River before and after the dam removals and addition of the Milford Dam fish lift.

STUDY AREA

The Penobscot River watershed is the largest in Maine and drains an area of approximately 22,200 km^2 throughout the state (Opperman et al. 2011). The river contains multiple dams that impede the migrations of Atlantic Salmon and other diadromous species. The Great Works Dam, which was located at rkm 59 and was removed in 2012, included two Denil fishways for upstream passage. The Veazie Dam at rkm 46 was removed in 2013; it included a vertical slot fishway (FERC 2009). Adult Atlantic Salmon upstream passage at both dams was annually variable (43–100% at Veazie Dam, 12–95% at Great Works Dam; Holbrook et al. 2009) prior to removal. Milford Dam (rkm 61), now the downstream-most dam on the main stem of the Penobscot River, is approximately 6.1 m high and included a Denil fishway for upstream passage, which is located on the western side of the powerhouse (NMFS 2012). As part of the PRRP, a new fish lift was installed on the eastern shore and the Denil fishway was left intact to be used on occasion during scheduled shut downs or lift failures. The lift became operational in April of 2014 and includes a horseshoe-shaped entrance (3.05 m across), which leads to a V-shaped gate that traps fish in a lift hopper (Figure 1). After being lifted, migrants are dumped into an upper flume, which leads to the trap and handling facility operated by the Maine Department of Marine Resources (MEDMR). The lift operates on a 30-min cycle (greater frequency during the peak of the alosine runs) from 0400 to 2200 hours from mid-April to mid-November.

The Orono Dam (rkm 53) is just upstream of the confluence of the Stillwater Branch and the main stem of the Penobscot River. The dam is 7.6 m high and previously contained four turbines with a total hydroelectric capacity of 2.3 MW. A new powerhouse with three additional turbines was added to the project as part of the PRRP, increasing the total capacity to 6.0 MW. While no upstream passage for anadromous species exists at the Orono Dam, a fish trap was installed at the base of the dam to capture upstream migrants (including Atlantic Salmon, Sea Lamprey, American Shad, and river herring) that are transported to the main stem of the river above the Milford Dam (NMFS 2012). Before the restoration project, up to 30% of total discharge in the lower Penobscot River was directed through the Stillwater Branch. With the addition of new powerhouses on the Stillwater Branch at both the Orono Dam and the Stillwater Dam (rkm 60), that percentage can be increased to 40% of total river discharge (FERC 2004). This study focused on the lower section of the Penobscot River (Figure 1), from Orrington (rkm 32) to Milford (rkm 61), which includes the Orono and Milford dams, and the remnants of the former Veazie and Great Works dams.

METHODS

Tagging and release.—Adult Atlantic Salmon were collected from either the trap and handling facility at Milford Dam (operated by MEDMR, n = 71) or the trap at the base of the Orono Dam (rkm 53, operated by Brookfield Renewable Energy, n = 2). Fork length and sex (as determined by morphology) were recorded at time of capture. When possible, sex was validated after recapture closer to spawning at U.S. Fish and Wildlife Service Craig Brook National Fish Hatchery. A total of 22 multi-sea-winter (MSW, >63 cm) adult salmon were tagged in 2014 from May 24 to June 30, and one additional salmon was tagged on September 19. In 2015, 46 MSW fish and 4 one-sea-winter (1SW) fish (grilse, ≤63 cm) were tagged from May 6 to June 19 (Table 1). In both years tagging was halted when river temperature reached 23°C as a condition of permitting.

Fish were held in tanks of ambient river water prior to tagging and were not anesthetized. Salmon were tagged with gastrically implanted coded radio transmitters (Lotek Wireless, Inc. Newmarket, Ontario). Tags used for MSW fish were 16 × 73 mm and weighed 25.0 g in air (11.0 g in water; Lotek MCFT2-3L). Tags used for 1SW fish were 14 × 53 mm and weighed 10.0 g in air (4.3 g in water; Lotek MCFT2-3EM). Weights were not recorded for tagged fish; however, using the length–weight relationship in Lear and May (1972), we calculated that tags weighed less than 1% of the body weight of our smallest fish in both age-classes. Both tag types were set to a 2.5-s burst rate. Each tag was wrapped with one livestock castration band (Ideal Instruments, Inc., Schiller Park, Illinois) to decrease the risk of regurgitation (R. Spencer, MEDMR, personal communication; Keefer et al. 2004b). Each salmon also received a 23-mm passive integrated transponder (PIT) tag (Biomark, Boise, Idaho), implanted in the dorsal muscle, which was used to track the fish on the existing PIT array in the Penobscot River (Gorsky et al. 2009; Sigourney et al. 2015). During the gastric tagging procedure, two experienced salmon handlers held the fish upside down against the side of the tank while the tagger opened the mouth of the fish to insert the tag (via flexible

TABLE 1. Summary of radio-tagging data, including number, tagging date, location, median fork length, life stage (multi sea winter [MSW] or one sea winter [1SW]), and sex (as determined by morphology) in the Penobscot River in 2014 and 2015.

			Tagging location			Life stage		Sex	
Year	n	Tagging date	Milford	Orono	FL (cm, range)	MSW	1SW	M	F
2014	23	May 24–Sep19	21	2	77.0 (67–89)	23	0	16	7
2015	50	May 6–Jun19	50	0	74.5 (52–81)	46	4	29	21

plastic tubing) into the esophagus of the fish. Total handling time for tagging and measurements was less than 2 min, with fish out of water for no more than 30 s during tagging. After tagging, fish were moved to an aerated tank of ambient river water and transported 18 km downstream to the release point at the Brewer boat launch (rkm 43). Total transit time was less than 30 min.

*Stationary and active radiotelemetry.—*An array of 11 shore-based stationary radio receivers (Lotek SRX400 or SRX-DL) was maintained in the lower Penobscot River from May through October of 2014 (Figure 1). In 2015, two additional stationary receivers (Lotek SRX800), located in the middle of Milford Dam and above the Great Works Dam remnants, were added to the array, which was in operation from May to October. Most receivers were connected to one Yagi antenna. The east side of Milford Dam had two antennas, one facing into the tailrace and the other facing downstream. In the second year of the study (2015), one dropper antenna (Normandeau Associates and Gomez and Sullivan Engineers 2011) was added into the Milford Dam fishway, and two Yagi antennas were added on the west side of the powerhouse. The underwater dropper antenna was able to detect fish within the lower flume of the fishway, as well as fish within 3 m of the fishway entrance. Based on locations of stationary receivers, the lower river was divided into six sections that were assessed for upstream movement rates. Potential delay regions included the Veazie Dam remnants (VZR), the area of the Stillwater confluence (SWC), the Great Works Dam remnants (GWR), and the area below Milford Dam (MFD). Two open river sections were located between potential delay reaches (Figure 1).

In addition to stationary sites, tagged salmon were monitored by active tracking using a portable radio receiver (Lotek SRX400). Fish were not tracked above Milford Dam because 67 out of 73 of the study fish were recaptured at Milford Dam and taken to Craig Brook National Fish Hatchery for use as sea-run broodstock for the Penobscot River. Active tracking surveys were conducted one to three times per week from May until all fish had either been recaptured or left the study system. The majority of active tracking took place by car and on shore, augmented with trips by canoe in the upper section of the study site (Milford, rkm 61, to Brewer, rkm 43) and by boat in the lower section (Brewer to Orrington, rkm 32). Active tracking utilized both omnidirectional and Yagi antennas to locate tagged salmon.

*Environmental data.—*In 2014, temperature at the Milford fish lift was obtained from MEDMR. In 2015, a temperature logger was placed in the lower flume at the Milford fish lift. Discharge from the U.S. Geological Survey gauge at West Enfield (rkm 100) was used as a proxy for discharge in the lower portions of the river.

*Lower river movements.—*Positions from both stationary and active tracking detections were plotted for each individual fish to look for patterns in movement throughout the study season. In addition, upstream movements were used to investigate whether fish were moving through the lower river while the Milford Dam fish lift was not operational (2200 hours to 0400 hours). Upstream movements were assessed from the last detection on a downstream receiver to the first detection on an upstream receiver. Upstream movements through the dam remnants and open river sections (VZR, GWR, OR1, and OR2; Figure 1) were classified into three groups based on period of initiation and period of completion: (1) night-initiated and completed movements ("night" being 2200 to 0400 hours), (2) night-initiated movements that were completed during daytime hours, and (3) daytime initiated and completed movements. If both the last detection downstream and the first detection upstream were during daytime hours but the interval contained a night, the fish was classified as daytime-only movement because it is possible that it could have ceased movement at night.

*Upstream movement speeds.—*Upstream movement speeds based on stationary receiver detections were calculated as

$$\frac{D - 1.0}{t_{\text{first upstream}} - t_{\text{last downstream}}},$$

where D represents the distance between two receivers (in rkm) and t indicates time of detection (h). These calculations represent a minimum upstream movement speed. Subtraction of 1.0 rkm was added to account for the range of the tags (about 0.5 km from the receiver, based on range testing conducted for this study). Speeds through the Stillwater confluence were calculated based on the first detection at the downstream receiver and last detection at the upstream receiver, along with a +1.0 rkm correction, due to the two receivers being <1 rkm apart. For the purpose of this analysis, the lower river was divided into six sections (Figure 1). Movement speeds from the release point (rkm 43) to the first upstream stationary receiver (Eddington Bend, rkm 46) were not included in analysis because movement up to Eddington Bend was taken as reinitiation of migration following tagging and transport.

Due to small sample sizes and nonnormal distributions, nonparametric methods were used for statistical analysis throughout this study, and central tendencies are reported as medians. A paired sample Wilcoxon signed rank test was used to test for differences in upstream movement speeds among potential delay reaches (VZR, SWC, GWR, MFD) and unobstructed reaches (OR1 and OR2). All possible pairwise comparisons, with a Bonferroni correction included to account for multiple comparisons, were performed on sections of the lower river. If a fish made multiple movements upstream after dropping downstream, only the initial upstream attempt was used in movement speed comparisons. Significance for all tests was set at $\alpha = 0.05$. Statistical analyses were performed using R (R Core Team 2015).

*Milford Dam delays.—*Overall delay times at Milford Dam were calculated as the time from the first detection on any of the antennas in the Milford Dam array until successful passage, which is defined as when the fish was recaptured at the trap and handling facility at the top of the Milford Dam flume. This was used as a measure of successful passage because tagged fish were taken to the Craig Brook National Fish Hatchery after recapture and did not continue upstream after passing Milford Dam. In addition, delay times were calculated in terms of the FERC passage standard for the Milford project, which specifies that 95% of adult Atlantic Salmon that come within 200 m of the face of the dam must utilize the lift within 48 h (NMFS 2012). For the FERC standard, successful passage is defined as when the fish has used the lift and been moved to the upper flume. This measure of successful passage ignores the amount of time that salmon spend in the upper flume because this is influenced by the operation of the Milford Dam trap and handling facility and not the fish lift. Delay times in terms of the FERC passage standard were not calculated for fish that were first detected at Milford Dam during either a lift shutdown or when temperatures were greater than or equal to 23°C (the legal limit for assessment, based on the thermal tolerance of Atlantic Salmon; Johnson and Johnson 2009) so that estimates reflect only a fully functioning system.

We used a conservative estimate to look at delay times in terms of the FERC passage standard because tag strength and noise from the hydropower project made it difficult to determine when a fish was 200 m from Milford Dam. In 2014, these delays were calculated based on first detection in the tailrace to the last detection in the tailrace (about 50 m range) before being recaptured. In 2015, the addition of a PIT antenna in the upper flume allowed for detection of fish immediately or shortly after they exited the lift hopper. Delays in 2015 were calculated from the first detection on the dropper antenna at the fishway entrance to the first detection on the PIT antenna in the upper flume. If a detection on the upper PIT antenna was not available, delays were calculated based on the last detection on the dropper antenna before recapture, indicating when the fish had left the lower flume, as a conservative estimate.

Fishway visits.—The addition of a dropper radio antenna in the Milford fishway in 2015 allowed for investigation of fish use of the lower entrance. Number and duration of visits to the fishway entrance were calculated for each fish detected at the entrance. A visit was defined as multiple detections that occurred until a fish left the area for more than 30 min. If a fish was not detected at the entrance for 30 min, a new visit began when the fish returned. Additionally, if a single detection occurred both 30 min after the last detection and 30 min prior to the next detection, that observation was excluded from analysis of fishway visits. The interval of 30 min was chosen due to the operation of the fish lift, which was operated on a 30-min cycle. An absence time of 30 min would represent when a fish had missed at least one lifting of the hopper. Based on these visit calculations (number and duration), the proportion of time individual fish spent near the fishway was calculated for each day. Spearman's rank correlation was used to investigate relationships between the proportion of time spent near the fishway and mean daily flow and mean daily temperature.

To investigate diel patterns of detections at the fishway entrance, detections on the dropper antenna for each individual fish during its entire period spent near Milford Dam were binned into hourly observations. If multiple detections occurred during an hourly bin, the fish was considered present during that hour of the day. The frequency of hours present at the fishway, on a 24-h cycle, was calculated for each fish and then standardized to proportion to determine whether fish were approaching the fishway while the lift was not operational. A Kruskal–Wallis multiple comparisons test (R package: asbio, Aho 2015) was used to test for differences among hours of the day.

Before and after transit times.—Data previously collected via the PIT array in the Penobscot River from 2002 to 2004 (Gorsky et al. 2009) and 2010–2012 (Sigourney et al. 2015) allowed for comparisons between transit times (d) of adult Atlantic Salmon before and after changes to the lower river. The Penobscot River PIT array included PIT tag antennas constructed in the fishway entrances and exits at each hydroelectric dam (Gorsky et al. 2009; Sigourney et al. 2015). Prior to the dam removals, adult salmon were PIT-tagged after capture at the top of the Veazie Dam fishway and released into the head pond following tagging. Transit times from Veazie Dam to Milford Dam were calculated from release into the Veazie Dam head pond to detection exiting the Milford Dam fishway, indicating successful passage at Milford Dam. Transit times from Great Works Dam to Milford Dam were calculated from detection exiting one of the Great Works Dam fishways to detection exiting the Milford Dam fishway. In comparing transit times from Great Works Dam to Milford Dam, 2010, 2011, and 2012 were not included in analysis because the PIT array was not operating at Great Works Dam in those years.

Transit times for this study from the former Veazie Dam to Milford Dam were calculated from first detection on the radio receiver located in the area of the former Veazie Dam head pond to time the fish was handled at the trap and handling facility at Milford Dam because this would approximate successful passage at Milford Dam. For consistency between years, transit times from the former Great Works Dam to Milford Dam were calculated from the last detection on the receiver located right below the Great Works remnants to successful passage at Milford Dam because a receiver was not located in the Great Works head pond in 2014 (Figure 1). We felt this would not influence the transit time comparisons because movement between the two Great Works receivers in 2015 often occurred in less than 2 h. Transit times were compared among years for each reach using a Kruskal–

Wallis multiple comparisons test (R package: asbio, Aho 2015).

RESULTS

Lower River Movements

After release in 2014, 22 of 23 salmon were detected by the stationary antenna array in multiple locations. One fish probably regurgitated its radio tag soon after release and was later recaptured without a radio tag at the trap at the base of the Orono Dam. It is unknown if this fish ever approached Milford Dam. All other fish were detected approaching Milford Dam. Tag retention in 2014 was 83% (four tags regurgitated). In 2015 all 50 radio-tagged salmon were detected on multiple stationary radio receivers, and tag retention was 100% for the duration of the study. All fish were detected approaching Milford Dam in 2015.

Tagged salmon displayed three general movement patterns (Figure 2) during the two study years: (1) directed upstream movement followed by holding in the area below Milford Dam for more than 48 h, (2) directed upstream movement followed by rapid passage at Milford Dam (within 48 h), or (3) fallback of greater than 4 rkm from Milford Dam followed by upstream and downstream movements greater than 4 rkm. The threshold of 4 rkm was chosen due to the placement of stationary receivers and represents when fish had dropped back past the next receiver downstream of Milford Dam. Fish that displayed the third movement pattern either eventually returned to Milford Dam to successfully pass or moved downstream and left the system. For both years (n = 72), the most common movement pattern was holding in the area below Milford Dam for more than 48 h (58.3%), whereas 33.3% of tagged fish passed Milford Dam quickly (<48 h). A small subset of fish (8.3%) made downstream and upstream movements after reaching Milford Dam. Most fish were moving upstream during the hours that the Milford fish lift was operational; however, a small percentage completed upstream movements between 2200 and 0400 hours (GWR = 10.9%, VZR = 2.3%, OR1 = 2.4%, OR2 = 5.4%). Additionally, some fish initiated upstream movement during these hours (GWR = 9.1%, VZR = 0.0%, OR1 = 2.4%, OR2 = 1.8%)

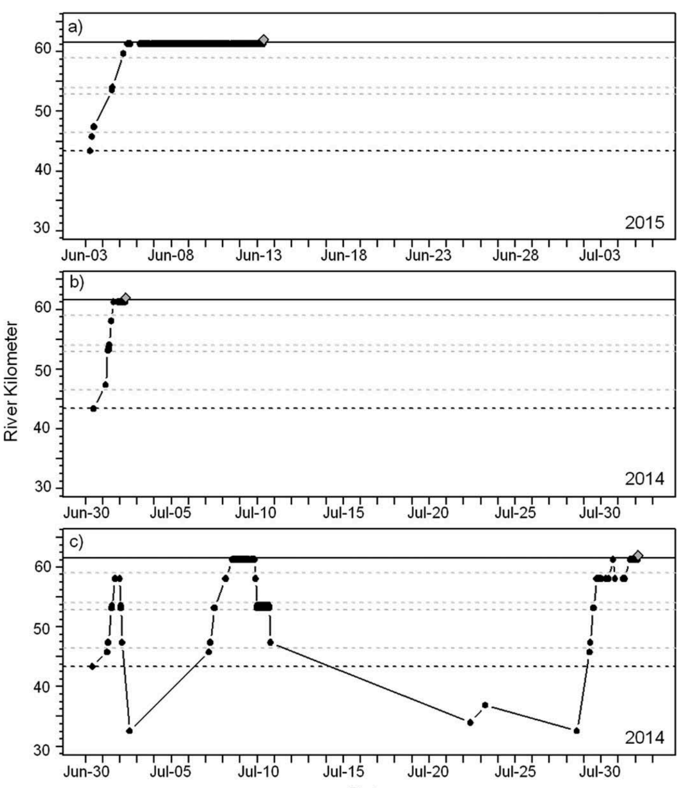

FIGURE 2. Characteristic migration tracks of radio-tagged Atlantic Salmon throughout the study: **(a)** fish holding below Milford Dam, **(b)** fish passing Milford Dam in less than 48 h, and **(c)** fish making upstream and downstream movements after reaching Milford Dam. Dashed gray lines represent the former Veazie Dam (rkm 46), the Stillwater confluence (rkm 53), and the former Great Works Dam (rkm 59). The dashed black line represents the release point (rkm 43), and the solid line represents Milford Dam (rkm 61). Successful passage is indicated by a gray diamond.

Upstream Movement Speeds

Upstream movement speeds in 2014 in the reaches downstream of Milford Dam were variable, ranging from 0.04 to 2.4 km/h (1.0 to 57.1 km/d; median = 1.0 km/h). Salmon moved at speeds from 0.02 to 2.0 km/h (0.5 to 47.0 km/d) before reaching Milford Dam (median = 0.5 km/h) in 2015. In both years, speeds through the potential delay reaches of the Veazie and Great Works dam remnants as well as the Stillwater confluence were comparable to speeds through unobstructed reaches of river (Figure 3). While no differences were detected in upstream movement through the Stillwater confluence, an increase in detections was observed in 2014 from July 8 to July 11, when two tagged fish were consistently detected below the Orono Dam. Main-stem temperatures during this period (20–23°C) were in the upper critical range for Atlantic Salmon (Jonsson and Jonsson 2009). Although salmon moved through dam remnants and open river sections at similar speeds, movement through Milford Dam was often more than 100 times slower than both unobstructed and potential delay river sections, and median upstream speed in the area of Milford Dam was only 0.006 km/h (0.001 to 0.096 km/h) in 2014 and 0.005 km/h (0.001 to 0.050 km/h) in 2015.

Milford Dam Passage Success and Delays

In 2014, 95.5% (21/22) of tagged fish that were detected on the Milford array successfully passed Milford Dam. The one fish that was not able to pass was detected on the PIT antenna inside the fishway entrance on July 1, and the tag was recovered on July 22 in the mouth of Sedgeunkedunk Stream (rkm 35). Of the fish that successfully passed Milford Dam, all used the new fish lift except for one, which may have passed over

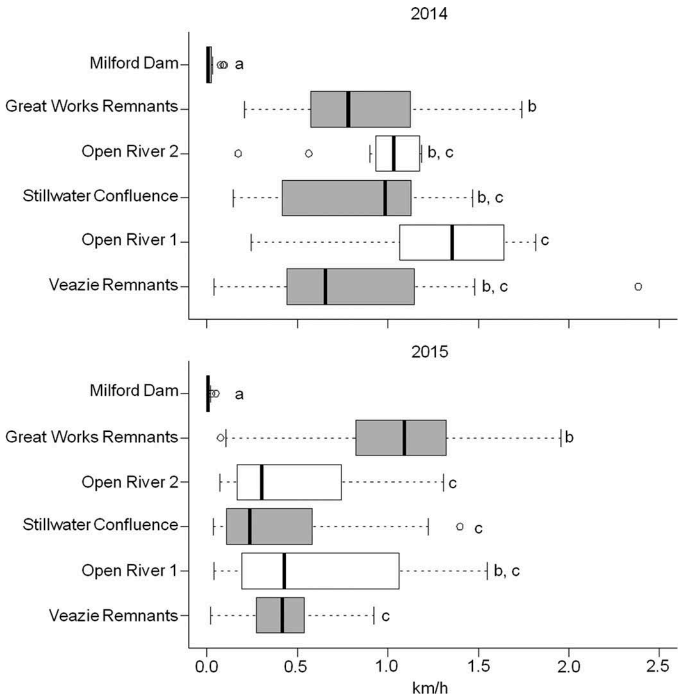

FIGURE 3. Upstream movement speeds of radio-tagged Atlantic Salmon through unimpounded (open) and potential delay (gray) reaches of the lower Penobscot River. Significant differences (Wilcoxon signed rank test with multiple comparisons) denoted by different lowercase letters.

the spillway before the flash boards were installed. Delay times from first detection on the Milford antenna array to recapture at Milford Dam ranged from 0.03 to 78.4 d (median = 3.0 d). After reaching Milford Dam, 36% (8/22) of fish dropped back more than 3 rkm, four of those fish falling back past the release site at rkm 43. After being detected downstream of Milford Dam (about 500 m), 67% of fish were detected in the tailrace in less than 24 h, and 71% in less than 48 h. Despite this, only 55% passed within 48 h of being detected in the tailrace.

In 2015, 100% of tagged fish successfully passed Milford Dam, all using the fish lift. One radio-tagged salmon did fall back after using the Milford fish lift, possibly through a tube at the back of the upper flume as it was never seen at the trap and handling facility. The initial approach of this fish was used in FERC passage standard delay calculations (h), although it was continually tracked through the summer until successfully passing Milford Dam at the beginning of October before falling back a second time. This fish was not included in general delay time calculations (d) since it was never recaptured or seen at the MEDMR trap and handling facility when it was initially lifted in June. Delay times ranged from 0.4 to 26.9 d (median = 4.3 d) from first detection on the Milford array to recapture. As in 2014, some fish displayed small downstream movements after reaching Milford Dam, 26% (13/50) dropping back more than 3 rkm and 2% (1 fish) dropping back past the release site at rkm 43. The addition of the dropper antenna indicated that 78% of fish were approaching the entrance to the fishway within 5 h of being detected on the Milford array. All fish that were detected on the dropper antenna (n = 49) had approached the fishway entrance within 24 h of detection elsewhere on the Milford array. One fish was not detected on the dropper antenna due to an antenna malfunction later in the season.

Delays and the FERC Standard

In 2014, the lift was shut down from June 15 to 26, as well as from September 21 to 29. Two tagged fish arrived at Milford Dam during these shutdowns and are not included in the FERC delay time analysis. Additionally, main-stem river temperatures reached 23°C on July 1. The eight tagged fish that arrived at Milford Dam on this date or the day before are also not included in the FERC delay analysis since these temperatures are the legal limit for assessment. Removing these fish left 10 tagged salmon that were detected in the tailrace before passing Milford Dam. Two of these tagged fish were present at Milford Dam during the June lift shutdown; however, they had arrived more than 48 h prior, so they had already failed to meet the standard. Of these 10 fish, 50% passed within the 48-h window. Delay times ranged from 1.2 h to 76 d, with 70% of tagged fish passing Milford Dam within 1 week. Tagged fish were not affected by lift shutdowns or high river temperatures in 2015. Delay times ranged from 7.4 h to 26 d, with 34.7% of fish passing within the 48-h window and 63.2% passing within 1 week (Figure 4).

Fishway Visits

Based on our criteria for a visit described above, individual fish made between 1 and 47 visits to the entrance of the Milford Dam fishway (median = 11) in 2015 before passing; fish that spent more days at Milford Dam made the most visits overall. More than half (53%) of these visits lasted less than 90 min. Across all days of the study season, individual tagged fish averaged 27% of a day (6.5 h) visiting the fishway (0.1% to 84%). The proportion of time fish spent near the fishway entrance in a day was not significantly correlated with mean daily flow (Spearman's rank correlation; p = 0.23) or mean daily temperature (p = 0.22). The number of visits that an individual fish made per day ranged from 1 to 12 (median = 2). Tagged fish were detected on the dropper antenna at all hours of the day, and no diel patterns were observed in fishway approach (Figure 5). This observation was supported by the results of the Kruskal–Wallis multiple comparisons test, which failed to detect differences between hours for all but the following pairs: 1400 and 0100 hours, 1400 and 0200 hours, 1400 and 2100 hours, 1400 and 2200 hours, 1400 and 2300 hours, and 1600 and 0200 hours.

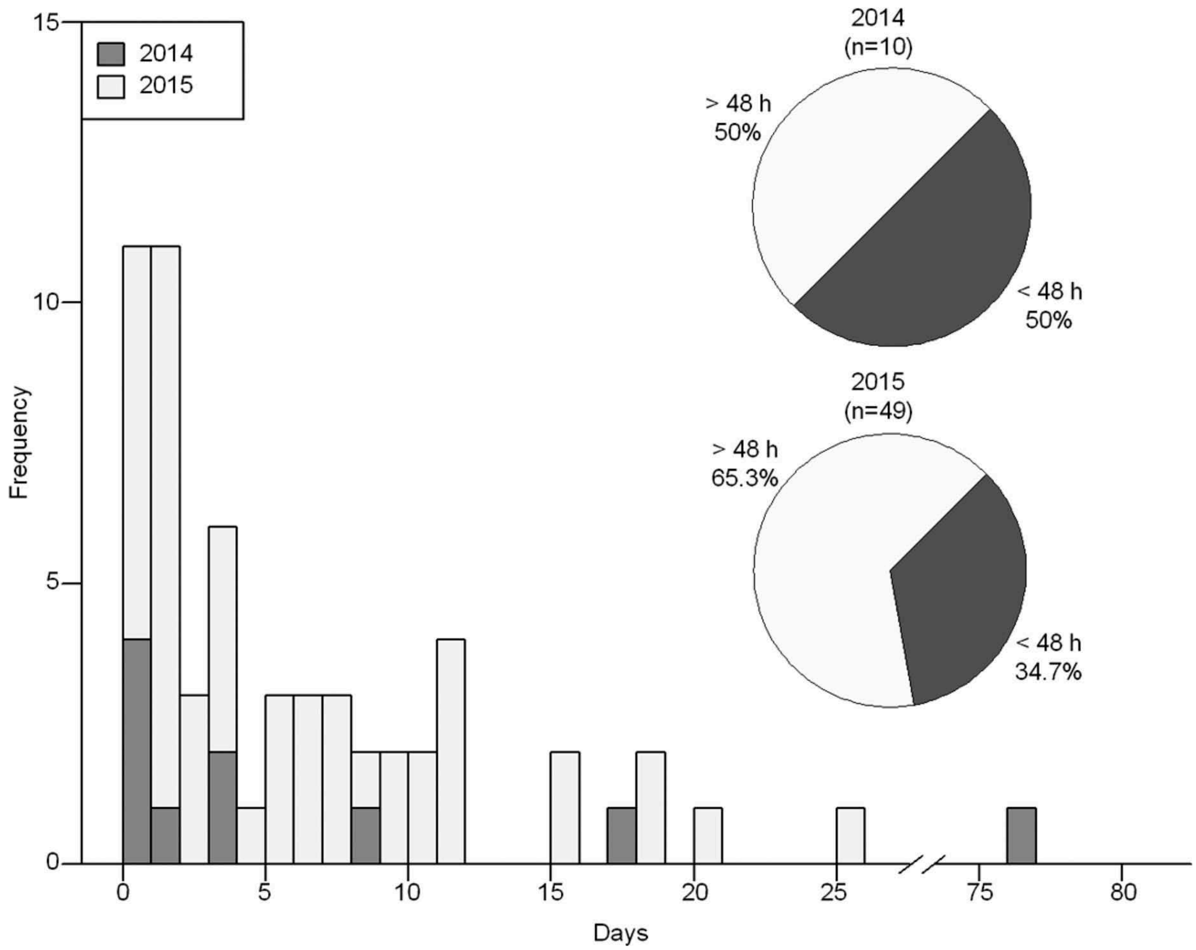

FIGURE 4. Histogram of Federal Energy Regulatory Commission delay times of Atlantic Salmon approaching Milford Dam in 2014 and 2015. Pie charts represent percentage of fish in each year that met the passage standard of utilizing the fish lift in less than 48 h (shown in dark gray).

Before and After Transit Times

In 2014, transit times from the former Veazie Dam head pond to successful passage at Milford Dam ranged from 1 to 80 d (median = 4 d). Similarly, transit times from the Great Works Dam head pond to successful passage at Milford Dam ranged from <1 to 79 d (median = 4 d). In 2015, Veazie Dam head pond to successful passage at Milford Dam transit times ranged from 3 to 33 d (median = 8 d), and Great Works Dam head pond to successful passage at Milford Dam transit times were between 1 and 27 d (median = 4.5 d). Across all years prior to changes to the lower river, transit times for adult salmon from the Veazie Dam head pond to successful passage at Milford Dam ranged from <1 d to 172 d (median values ranging from 5 to 23 d). Transit times from the Great Works Dam head pond to successful passage at Milford Dam prior to modifications ranged from <1 d to 103 d (median values of 1 to 2 d).

There was no difference between transit times in 2014 and 2015 for movement both from the former Veazie Dam head pond to Milford Dam passage and from the former Great Works Dam head pond to Milford Dam passage. Transit times from the Veazie Dam head pond to Milford Dam passage before and after the changes in the Penobscot River were comparable in most years; however 2014 and 2015 did have lower median transit times than 2010 and 2011. Differences in Great Works Dam head pond to Milford Dam passage transit times were detected in multiple years. Median transit time in days from the Great Works Dam head pond to successful passage at Milford Dam was higher in 2014 and 2015, after the installation of the new fish lift, than in 2002–2004, when the Denil fishway was still in use. Differences are summarized by lettered group membership in Figure 6.

DISCUSSION

Our results show that upstream migrating adult Atlantic Salmon are not being delayed at the dam remnants after the removal of the Veazie and Great Works dams. Tagged salmon were also not delayed at the modified Orono Dam just upstream of the confluence of the Stillwater Branch and the

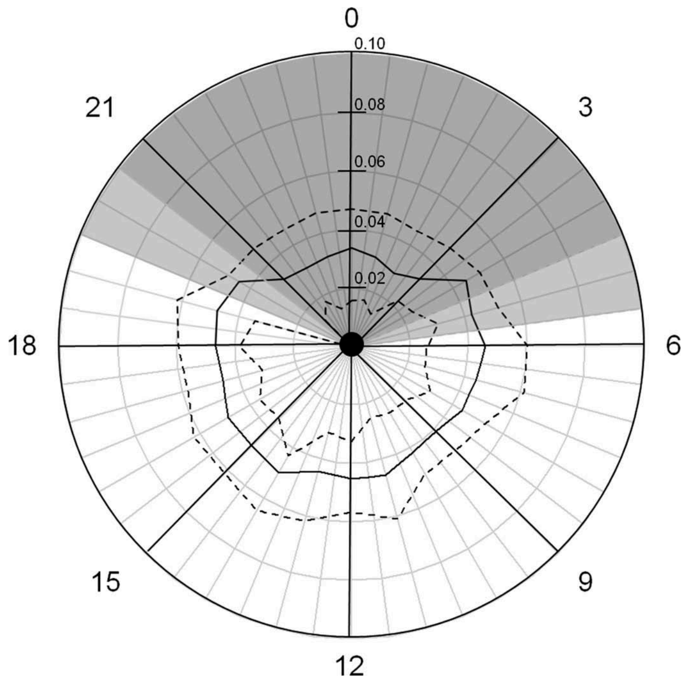

FIGURE 5. Radial plot showing the median (solid line) proportion of hourly observations that occurred during hours thoughout the day for individual Atlantic Salmon, with 25% and 75% percentiles indicated by dashed lines. Dark gray shading indicates hours of darkness, while light gray shading indicates the approximate time of shifting sunrise and sunset times throughout the study period in May and June of 2015.

main stem of the Penobscot River. Movement rates through these sections were similar to other nearby open-river sections and were within the range reported for upstream movements of Atlantic Salmon in other studies in the Penobscot River and elsewhere (Økland et al. 2001; Gorsky 2005; Thorstad et al. 2005, 2008). Prior to the dam removals, migrating adults spent significant time in the lower river due to delays experienced at Veazie and Great Works dams, and passage at these dams was often highly variable (Shepard 1989; Holbrook et al. 2009). The removal of the lower main-stem dams has greatly increased the rate of salmon movement from tidal reaches to the base of Milford Dam, despite the increased flow on the Stillwater Branch.

The removal of Veazie and Great Works dams on the Penobscot River probably allows migrants better access to cool water during high summer temperatures. Three tagged salmon made downstream movements after reaching Milford Dam during the months of July and August when water temperature was high (up to 26°C). Two of these fish reascended the river and successfully passed Milford Dam after spending time in the lower river. During summer months, fish were located in the mouth of the Stillwater Branch and the mouths of Great Works and Sedgeunkedunk streams. At least one fish exited our study area and moved into the estuary. This behavior is consistent with increased use of tributaries observed in the Columbia and Snake rivers during high temperatures (Keefer et al. 2004a; Goniea et al. 2006), as well as past work in the Penobscot River, which documented that adult salmon use Great Works Stream as thermal refuge (Holbrook et al. 2009). Prior to the removal of Great Works and Veazie dams, little thermal refugia existed between the two lowermost dams, and fish that successfully passed Veazie Dam were then often trapped below Great Works Dam during the summer (Holbrook et al. 2009). While few fish were tracked during high temperatures in this study, this behavior suggests that the removal of the two lower main-stem dams may allow adult salmon access to more coolwater refugia or access to the estuary during thermally stressful temperatures.

After upstream migration through the lower portion of the Penobscot River, almost all tagged salmon were able to eventually pass Milford Dam. Since Milford Dam is now the first dam on the main stem of the Penobscot River that migrating Atlantic Salmon face on their journey upstream, successful passage at the new fishway is critical to recovery. In previous studies, fishway function has often been looked at in terms of attraction and passage efficiency. Attraction efficiency can be defined as the proportion of tagged fish released that are located within 3 m of a fishway entrance (Bunt et al. 1999) or near enough to a fishway entrance for a fish to detect the attraction flow (Aarestrup et al. 2003). Passage efficiency can be defined as the proportion of fish detected at the fishway entrance that are then detected at the fishway exit (Bunt et al. 1999; Aarestrup et al. 2003). In terms of passage efficiency, between 95% and 100% of tagged fish that were detected near or inside the lower fishway entrance successfully used the lift during the two study years. Attraction efficiency at the fish lift is also high because all fish that reached Milford Dam were detected inside the fishway entrance at some point during the study. Notably, in 2015 all fish were detected near the fishway entrance within 24 h of reaching the dam. While our tailrace detections from 2014 have a lower percentage of fish in the tailrace in less than 24 h (67%), we believe this was an artifact of poor detection efficiency on the tailrace antenna because fish that were detected repeatedly on the lower PIT antenna inside the fishway were often not detected on the tailrace antenna.

While the detection data from the Milford Dam radiotelemetry array indicate that the Milford fish lift has a high attraction efficiency and passage efficiency, tagged fish experienced substantial delays prior to successful passage. The current regulatory passage standard of 95% passage within 48 h was not met in either year of this study, and our estimates fall well below the target value (50% in 2014 and 34.7% in 2015; Figure 4). Few studies have examined Atlantic Salmon behavior at fish lifts. Reported passage efficiencies range from 47% (Croze et al. 2008) to 87% (Larinier et al. 2005) at lifts located on European rivers. In the study conducted by Croze et al. (2008) on the River Garonne, France, mean delay time at the fish lift was 12.5

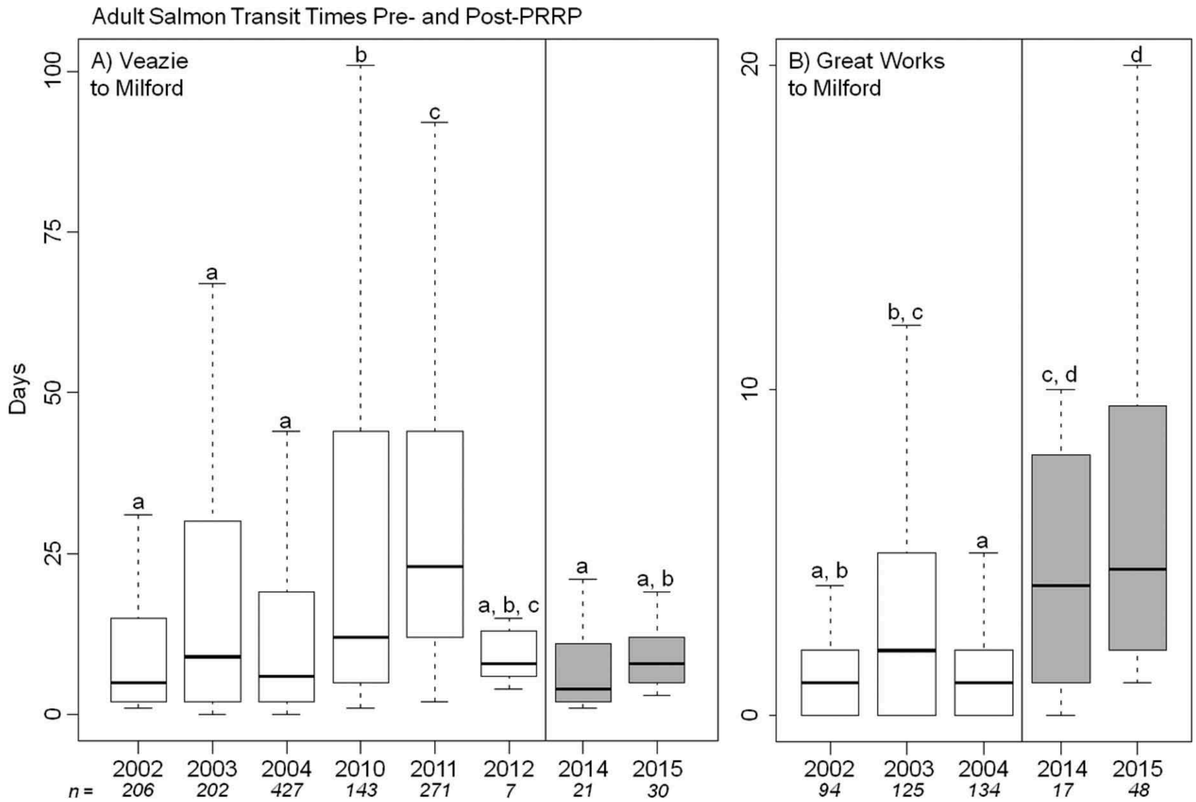

FIGURE 6. Transit times of adult Atlantic Salmon in the years before (open) and after (gray) the removal of the Great Works Dam and the installation of the new Milford fish lift. Transit times are calculated from passage at Veazie or Great Works to passage at Milford Dam. Data collected from 2002 to 2004 and 2010 to 2012 utilized PIT telemetry; data collected in this study (2014 – 2015) utilized radiotelemetry. Outliers are excluded from this plot for simplicity. Sample sizes are denoted below each year, and significant differences are indicated by different lowercase letters.

d. On the Gave de Pau River, France, a median delay time of 9 d was reported at the Baigts hydroelectric plant (Larinier et al. 2005). While delay times differed across systems, behavior of tagged salmon in our study was similar to the behavior of Atlantic Salmon at the fish lifts in Europe. Authors reported tagged fish rapidly approaching the entrance to the fish lift after arriving at the dam (74% in less than 24 h [Larinier et al. 2005]; 79% within 1 h [Croze et al. 2008]) and then making multiple visits to the entrance before successfully being trapped and lifted. In the second year of our study, tagged salmon located the fishway rapidly but made multiple visits, often over many days (or weeks), before successful passage. It should also be noted that the number of visits per fish in this study may represent a conservatively low estimate based on our chosen criteria (30 min between visits), and fish may be making more frequent passage attempts. Future focus on behavior near and inside the fishway entrance would be beneficial in regards to determining frequency of passage attempts.

Despite an increase in movement rates through the regions of Veazie and Great Works dams after their removals, overall transit times through the lower river were similar after changes to the lower Penobscot River due to the extensive delays incurred at Milford Dam. As demonstrated by the PIT data from 2002 to 2004, transit time from the Great Works Dam head pond to the area below Milford Dam was often short, and delay times at Milford Dam were low compared with the other dams in the lower section of the system. Other telemetry studies in the Penobscot River showed similar results, with most Atlantic Salmon using the Denil fishway at Milford Dam within a day after being detected below the dam (Shepard 1989). Additionally, all tagged fish that successfully passed Great Works Dam in 2005 and 2006 were able to pass Milford Dam in 3.7 d or less (Holbrook et al. 2009). While the transit times from the former Great Works Dam head pond to the base of the Milford Dam in this study were short, delay times at the Milford Dam fish lift were markedly higher than those at the Denil fishway in previous years. Median delay times in this study were lower than those previously seen at the now-removed Great Works and Veazie dams; however, between 30% and 40% of adult Atlantic Salmon over the two study years were delayed longer than a week before successfully passing.

In terms of migratory transit times through the lower Penobscot River, our results suggest that the benefits of dam removal have the potential to be offset by the lack of timely passage at the Milford Dam fish lift. While overall passage success at Milford Dam remains high, improving passage time would be beneficial to the recovery of Atlantic Salmon in the system. Considerable delays in upstream progress could have multiple impacts on the overall migration success of adult Atlantic Salmon in the Penobscot River. Extensive delays at dams have been shown to decrease energetic reserves needed for spawning success and lower the probability of survival (Dauble and Mueller 1993; Geist et al. 2000). Additionally, long delays before passage at Milford Dam could result in adults being exposed to poor passage conditions at dams further upstream that would have been avoided otherwise. Passage success at both Howland and West Enfield dams on the Penobscot River (rkm 100) are reduced by high temperatures and low flows (Gorsky 2005; G. A. Maynard, M. T. Kinnison, University of Maine, and J. Zydlewski, unpublished data). Because the peak of the Penobscot River run typically enters in June, long delays at Milford Dam would cause fish to be exposed to high river temperatures during migration. This was observed in both 2014 and 2015 in this study.

It is unlikely that the regulatory standard will be met and delays decreased at the Milford fish lift without modifications that increase the probability of capturing adult salmon in the lift hopper. The fishway is currently operated primarily during daytime hours; however, our data showed that salmon did move upstream during the hours that the lift was not operational and approached the fishway entrance at all hours. The river reach with the highest percentage of movement at night was the Great Works Dam remnants, which also represents one of the shortest reaches in our study, so it is possible that more fish were moving at night in other reaches but were not detectable due to the distance between receivers. This is consistent with other studies that have documented upstream migration of salmonids at night (Gowans et al. 1999; Rivinoja et al. 2001). We note that while there were nocturnal movements of salmon around the fishway entrance, analysis of the PIT detections indicated a peak in detections in the late morning (G. A. Maynard, unpublished data). Similar trends have been noted at other fishways (Gowans et al. 1999; Keefer et al. 2013; Thiem et al. 2013), suggesting that entrance and use of multiple styles of fishways may be dependent on visual cues. However, since Atlantic Salmon are approaching the fishway entrance at all hours of the day, continuous operation of the lift is an untested method that may increase trapping efficiency.

Since the tagged salmon are in the area of the fishway, there is the potential that the delays observed are due to an unknown factor inside the lower fishway entrance. One potential factor that could influence these delays is the highly aerated attraction flow in the lower entrance, which can discourage fish from entering or moving through the fishway (Clay 1995). It is unclear how many of the visits to the fishway included salmon entering the lower fishway entrance or if fish were remaining a short distance away from the fishway. When fish do enter the fishway, another potential influential factor is suboptimal operation of the V-shaped gate at the hopper entrance. Previous studies have documented low probabilities of passing through V-shaped entrances to lift holding pools for Atlantic Salmon (0.15 in Larinier et al. 2005; 0.17 in Croze et al. 2008) and have additionally documented that up to 40% of entries through a V-shaped gate can result in salmon returning to the area outside of the fish lift (Croze et al. 2008). Both hesitation to both enter and frequently return back through the V-shaped gate could be contributing to the delays observed at the Milford Dam fish lift. Further investigation into behavior near the V-shaped gate would be valuable for optimizing the design and operation of the lift.

Previous studies in the Penobscot River have attributed migration delays and poor passage rates at dams to poor attraction at fishways (Shepard 1989), flow and temperature influences (Gorsky 2005; Holbrook et al. 2009), and lack of migration motivation due to homing to lower river stocking sites (Shepard 1989). The data from our study suggests that attraction at the fishway entrance is probably not the limiting factor at Milford Dam because all fish in 2015 were detected near the fishway entrance within 24 h of reaching the dam. Additionally, fish made multiple visits to the fishway entrance before successful passage, further supporting the contention that the attraction flow was effective. We were not able to detect any relationships between proportion of the day spent near the fishway entrance and environmental factors. However, this may have been due to the limited scale of this study.

While the origin of the study fish is unknown, it is unlikely that homing to lower-river stocking sites contributed to the delays at the Milford Dam fish lift. The majority (69/73) of fish used during the study were MSW fish, spending 2–3 years at sea. The Penobscot River has a large smolt stocking program, and in the smolt years of interest, all fish were stocked in multiple locations that were at least 10 rkm above Milford Dam (U.S. Fish and Wildlife Service, unpublished data). In addition, the movements that tagged fish displayed below Milford Dam were not consistent with the searching phase described by Økland et al. (2001), which included erratic upstream and downstream movements in river stretches that averaged 7.7 to 14.9 km over two study years as salmon homed to spawning areas in the River Tana in Norway. In previous studies in the Penobscot River, Atlantic Salmon stocked in the main stem of the river near the head of tide made more downstream movements than fish stocked in tributaries near spawning grounds (Power and McCleave 1980). In contrast, most tagged fish in our study moved directly upstream and then remained in the area below Milford Dam for multiple days or weeks before passing. The number and duration of visits to the fishway entrance suggest that tagged salmon were actively seeking a way upstream, since they were often moving towards and away from the dam. As such, it is unlikely that tagged salmon had entered a natural resting period during the migratory phase.

Prior to and during the years of this study, adult returns were at historical lows in the Penobscot River, and the best method to capture adults for tagging was via the Milford Dam trap and handling facility, requiring fish to be transported and released downstream. After release and recovery from tagging, all fish displayed directed upstream movement that is consistent with the first phase of Atlantic Salmon upstream migration, i.e., the “migratory phase” described by Økland et al. (2001). The effects of gastric tagging and displacement downstream on our study fish were probably minimal because the majority of salmon resumed upstream migration within 24 h of release. Additionally, while all but two (captured at the Orono Dam trap in 2014) tagged fish used in this study were not naive to the fish lift at Milford Dam, it is unlikely that long delay times were due to fish having experienced the fishway once before. Studies have not been designed to specifically test the effects of using nonnaive fish to study passage time; however, a previous study with Atlantic Salmon on the River Nidelva showed no differences in migratory speed or length of stay at a tunnel outlet between fish captured downstream of a power station and fish collected at the fish passage facility (Thorstad et al. 2003). Similarly, researchers conducting a study involving anadromous Brown Trout *S. trutta* found no differences in attraction or passage efficiency of a nature-like bypass between fish initially captured upstream and downstream of the bypass weir (Aarestrup et al. 2003). In our study, the two fish that were initially captured at the Orono Dam trap (and therefore had not experienced the Milford fish lift) were delayed 4 and 21 d below the dam, supporting the conclusion that delays longer than 48 h are not due to fish having experienced the fishway before.

Overall recovery of Atlantic Salmon in the Penobscot River is highly dependent on the effectiveness of the new fishway installed at Milford Dam. The most recent action plan for Atlantic Salmon in the Gulf of Maine has identified dams as a major threat to Atlantic Salmon passage, creating a need to restore full passage as a priority in the recovery of the species (NMFS 2016). All high-quality rearing habitat for Atlantic Salmon within the Penobscot River watershed is located upstream of the Howland and West Enfield dams (Fay et al. 2006), which are just upstream of the confluence of the Piscataquis and the main stem of the Penobscot River (rkm 100). After successful use of the Milford Dam fish lift, adults must travel almost 40 rkm upstream and pass at least one more dam to reach ideal spawning habitat. As shown in our study, passage efficiency at the new Milford Dam fish lift is high. However, our results show that while adult Atlantic Salmon are able to locate the new fish lift entrance quickly and make multiple visits to the lift, passage of these fish is significantly delayed under the operational conditions in 2014 and 2015. With Atlantic Salmon often present near the fishway, efforts to improve passage time at the fish lift would probably benefit from focusing on behavior inside the fishway entrance to increase the probability of capturing adult migrants in the lift hopper.

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