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ARTICLE

Movement, Survival, and Delays of Atlantic Salmon Smolts in the Piscataquis River, Maine, USA

Alejandro Molina-Moctezuma* **and Erin Peterson**
Department of Wildlife, Fisheries, and Conservation Biology, University of Maine, Nutting Hall, Orono, Maine 04469, USA

Joseph D. Zydlewski
U.S. Geological Survey, Maine Cooperative Fish and Wildlife Research Unit, and Department of Wildlife, Fisheries, and Conservation Biology, University of Maine, Nutting Hall, Orono, Maine 04469, USA

Abstract
Movement, delays, and survival of hatchery Atlantic Salmon *Salmo salar* smolts were evaluated through the Piscataquis River, a tributary of the Penobscot River in Maine, USA. We explored the effects of the river's four dams (Guilford, Dover, Browns Mill, and Howland dams) from 2005 to 2019. During this period, the downstream-most dam (Howland Dam) transitioned from full hydropower generation to seasonal turbine shutdowns and later was decommissioned with the construction of a nature-like fish bypass in 2016. We estimated survival through open-river reaches and at each dam using acoustic telemetry ($n = 1{,}611$). Dams decreased survival, with per-river-kilometer (rkm) apparent survival averages of 0.972, 0.951, and 0.990 for Guilford, Dover, and Browns Mill dams compared to a per-rkm survival of 0.999 for open-river reaches. Turbine shutdowns increased survival at Howland Dam (to around 0.95), which was further increased by the nature-like fish bypass (0.99). We used radiotelemetry in 2019 ($n = 75$) and demonstrated that approximately one-third of the fish used the bypass, while the remaining fish used alternative routes. Smolts successfully passing the three upstream dams had lower apparent survival through Howland Dam than smolts that were released upstream of Howland Dam. Although smolts passing Browns Mill Dam had high survival, the dam caused extended delays, with median delay times surpassing 48 h in most years. Most of the delays caused by Browns Mill Dam occurred after fish had passed the dam and may indicate a sublethal effect of passage. Overall, while survival through Howland Dam has improved, passage and delays at the three upstream dams in aggregate represent a critical impediment to the effective use of the high-quality spawning habitat found upstream.

The Penobscot River, Maine, hosts the largest population of endangered Atlantic Salmon *Salmo salar* in the United States. However, total adult returns in this river remain low (National Research Council 2004; Saunders et al. 2006; USASAC 2019). Historically low numbers led to listing of the distinct population segment in 2000, and the Penobscot River population was included in the distinct population segment in 2009 (USFWS and NOAA 2000, 2009). Because natural production is limited, spawning has been supplemented by stocking of hatchery-reared juveniles, with more than 90% of the migrating smolts resulting from stocking (Sheehan et al. 2011; USASAC 2014). Conservation efforts rely on these management efforts until conditions are more favorable. Reducing mortality of downstream-migrating smolts through dams that separate high-quality freshwater habitat from marine habitat is a critical component for recovery (USASAC 2014).

The smolt-to-adult return rate is low (Moring et al. 1995; USASAC 2012), indicating high mortality in the river or at sea. During migration, smolts face a series of

*Corresponding author: alejandro.molina@maine.edu
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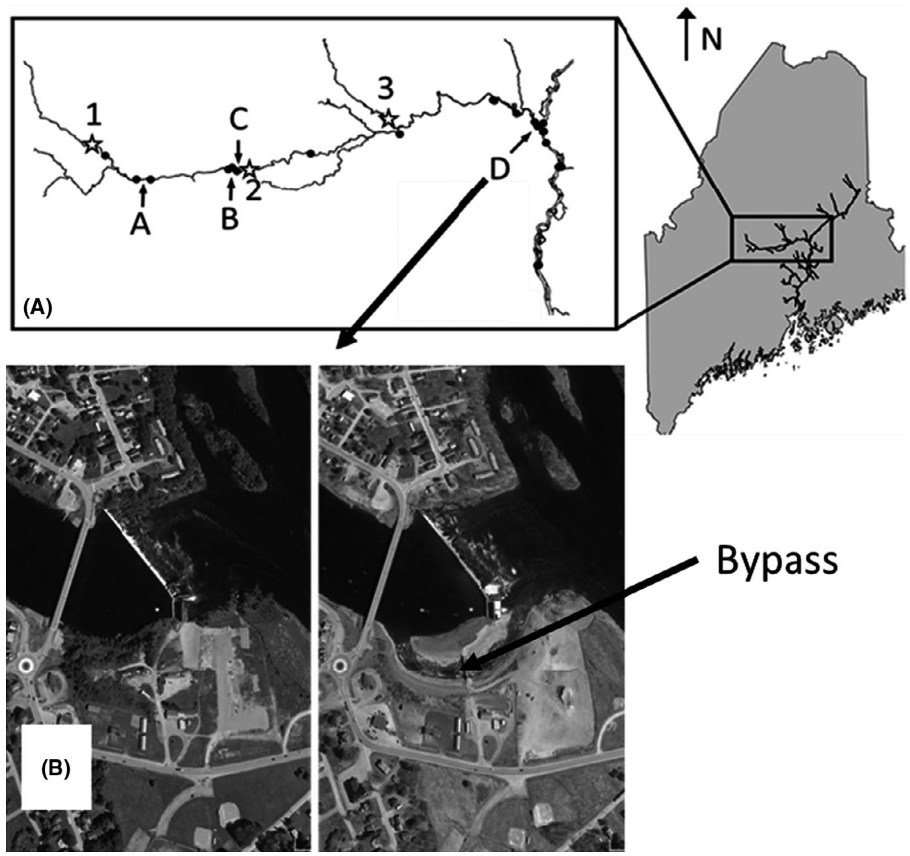

FIGURE 1. **(A)** Map of the Piscataquis River, showing its location in the state of Maine and the locations of acoustic receivers (black circles), release sites (stars labeled 1–3, where 1 = Abbot, 2 = Browns Mill Dam tailrace, and 3 = Milo), and dams (arrows labeled A–D, where A = Guilford Dam, B = Dover Dam, C = Browns Mill Dam, and D = Howland Dam). Howland Dam is located at the Piscataquis River's confluence with the Penobscot River. **(B)** Photographs show Howland Dam before (August 23, 2013) and after (April 28, 2016) the nature-like fish bypass was built (source of images: Google 2019).

new conditions and suffer high natural mortality. They encounter novel predators and the physiological challenge of increased salinity (Poe et al. 1991; Parrish et al. 1998; Aas et al. 2011). Smolts also face anthropogenic challenges, such as dams, that increase their mortality (Keefer et al. 2012; Norrgård et al. 2013). Dams are a primary cause for low abundance of Atlantic Salmon in the Penobscot River and remain a considerable source of mortality for smolts (Holbrook et al. 2011; Stich et al. 2014, 2015a).

The Penobscot River has been the focus of a sea-run fish restoration project (Penobscot River Restoration Project [PRRP]) that has dramatically changed river conditions. Changes include the removal of two lower main-stem dams, significantly improving connectivity. For Atlantic Salmon, the majority of high-quality habitat remains upstream of at least two dams (Day 2009; Opperman et al. 2011; Trinko Lake et al. 2012). The Piscataquis River is a major tributary of the Penobscot River, containing over 25% of the spawning habitat in the system's watershed (Fay et al. 2006; Saunders et al. 2006; Figure 1). However, this tributary has dams that impede both the upstream migration of adults and the downstream migration of smolts. Migrating smolts in this tributary encounter up to four dams (Guilford, Dover, Browns Mill, and Howland dams; Table 1) before reaching the main-stem Penobscot River, where they encounter at least one dam (Milford Dam) prior to reaching the ocean (Figure 1). An alternate path (through the Stillwater Branch) in the Penobscot River would result in passage through three more dams (Stich et al. 2014, 2015a). Therefore, smolts in the Piscataquis River may encounter as many as seven dams during seaward migration.

The downstream-most dam on the Piscataquis River (Howland Dam; Figure 1) has long been recognized as a point of high mortality (Holbrook et al. 2011) and was therefore purchased as part of the PRRP. As an interim step to decommissioning, the generating turbines at this dam were shut down during smolt migration starting in the spring of 2010. These shutdowns increased smolt survival at the dam, but survival remained low relative to

TABLE 1. Summary of the four dams on the Piscataquis River, Maine (NID-ID = dam identification number in the National Inventory of Dams by the U.S. Army Corps of Engineers; rkm = river kilometer).

Dam	NID-ID	Location (rkm)	Hydropower capacity (MW)	Dam height (m)	Dam length (m)	Reach length (rkm)	Downstream fish passage
Howland	ME00155	99.1	0.0	5.19	220	1.4	Bypass
Browns Mill	ME00156	164	0.6	7.31	70	0.9	Bypass
Dover	ME00157	165	0.3	3.65	61	0.8	None
Guilford	ME00158	181	0.0	3.66	51.51	1.7	None

that at other dams or in free-flowing rivers (Stich et al. 2014, 2015a). During 2016, as part of the PRRP, a nature-like fish bypass was built at Howland Dam (Day 2009; Opperman et al. 2011; FERC 2018). The bypass was anticipated to increase smolt survival, but not all nature-like fishways provide efficient passage (Bunt et al. 2012). This bypass channel was unproven for smolts migrating through Howland Dam.

In addition to increasing mortality risks, dams in the Piscataquis River also delay migration, which is known to reduce survival downstream (Ferguson et al. 2006; Stich et al. 2015a, 2015b). Nonlethal injuries may affect performance and decrease the probability of survival later in the migration. Lastly, an additive effect of crossing multiple dams is likely (Ferguson et al. 2006; Zydlewski et al. 2010), and successful migrants through the Piscataquis River still need to navigate approximately 100 river kilometers (rkm) to Penobscot Bay while passing either one additional dam (Milford Dam) if they stay in the mainstem Penobscot River or three dams if they migrate through an additional path, Stillwater Branch (Stich et al. 2015b). Although 85% of individuals stay in the mainstem Penobscot River and only face one more dam, this dam is associated with low survival, and the additive effects of crossing multiple dams may further lower survival. Therefore, considering the entire route and experience is important for assessing the smolt migration through the Piscataquis River.

Our goal was to analyze movement and survival of migrating smolts in the Piscataquis River from 2005 to 2019. We used radiotelemetry and acoustic telemetry to study survival through the three upstream dams and through Howland Dam before and after the nature-like fish bypass was built. We also explored the effects of passing multiple dams on smolt survival at Howland Dam. An important objective of this study was to identify areas of high migratory delay. In 2019, we complemented the study by analyzing path choice at two dams (Browns Mill and Howland dams). We related all of the measured parameters to changes at Howland Dam over the 15-year study period, dividing it into three discrete periods: (1) during dam operation (2005–2009), (2) after turbine shutdowns (2010–2015), and (3) after construction of the bypass (2016–2019).

METHODS

Study site.— Guilford Dam is the upstream-most dam in the Piscataquis River. It is approximately 181 rkm upstream from Penobscot Bay and 82 rkm upstream of the Piscataquis River's confluence with the Penobscot River. This confluence is in the town of Howland (45°4′22"N, 68°39′16"W), about 99 rkm upstream from Penobscot Bay (rkm 0). Although Guilford Dam does not produce hydropower, high mortality of smolts was observed through this reach (Stich et al. 2014). A considerable amount of high-quality habitat is found upstream of Guilford Dam (Fay et al. 2006; Saunders et al. 2006). Downstream of Guilford Dam is Dover Dam, located at rkm 165. The next downstream dam in the system is Browns Mill Dam, located at rkm 164, only 700 m downstream of Dover Dam; therefore, this section of river is both the headpond of Browns Mill Dam and the tailrace of Dover Dam. Browns Mill Dam has a downstream passage structure composed of a powerhouse canal (with 15.24-cm grates) that connects to a bypass system. Finally, Howland Dam is located directly upstream of the confluence (rkm 99.1). From 2005 to 2009, Howland Dam operated at full capacity for hydropower. After Howland Dam was purchased by the Penobscot River Restoration Trust in 2010, seasonal shutdowns were implemented at the dam from 2010 to 2015 to accommodate smolt migration. Finally, a nature-like fish bypass was completed at Howland Dam in 2016 (Day 2009; FERC 2009, 2018).

Acoustic receiver array.— Every year from 2005 to 2019, an acoustic array consisting of up to 25 receivers (Vemco VR2 or VR2W; Amirix Vemco Ltd.) was deployed in the Piscataquis River. The number and exact position of the receivers varied slightly by year but the general locations did not. The receivers used from 2005 to 2013 were deployed and described in previous works (Holbrook et al. 2011; Stich et al. 2015b), while the array used from 2015 to 2019 is depicted in Figure 1. Each receiver contained an omnidirectional hydrophone scanning continuously at 69 kHz. Receivers were deployed upstream and downstream of each dam on the Piscataquis River, thus conferring information regarding dam approach and passage. In 2019, an additional acoustic receiver was deployed in the downstream powerhouse canal at Browns Mill Dam. Coverage extended from rkm 187 (town of Abbot) to rkm 62.4 (see Figure 1); this represents the Piscataquis River and a section of the Penobscot River. The deployment was complemented with over 100 receivers deployed downstream of rkm 62.4, which were pooled and treated as the final detection event.

Acoustic tagging and releases.— From 2005 to 2019, a total of 1,611 Atlantic Salmon smolts were acoustically tagged and released in the Piscataquis River (Figure 1) in accordance with Protocols A2014-10-04 and A2017-10-02 approved by the Institutional Animal Care and Use Committee at the University of Maine. The number of fish tagged and released changed from year to year (Table 2); however, due to the low number of detections in 2014, the fish that were released in 2014 were removed from most analyses. Fish were either wild (2010–2011) or hatchery reared at the U.S. Fish and Wildlife Service (USFWS) Green Lake National Fish Hatchery (GLNFH). The tagging and release procedures for years prior to 2014 were described by Holbrook et al. (2011) and Stich et al. (2014) and are similar to the procedures used from 2014 to 2019. Smolts tagged from 2014 to 2019 were anaesthetized using a 100-mg/L solution of tricaine methanesulfonate (MS-222; buffered with 20-mM $NaHCO_3$; pH 7.0), and FL (mm) and mass (g) were measured. A small (1 cm) incision was made offset from the ventral line. An acoustic tag (Vemco V9-6L; 2.0 g in water; Stich et al. 2015b) was inserted intraperitoneally, and the incision was closed with two simple knots using absorbable Vicryl sutures (Ethicon 4-0 RB-1). After surgery, fish were transferred to a recovery tank. Following full recovery, fish were transported to the release site (Maine Department of Marine Resources Permit DSRFH-2019-05-03-13:58). Fish were released in one of three release sites: (1) Abbot (rkm 187), upstream of all four dams on the river; (2) the Browns Mill Dam tailrace (rkm 163.8), upstream of Howland Dam; and (3) Milo (rkm 133), also upstream of Howland Dam (Figure 1). The number of releases and the sites of release varied from year to year (Table 2). However, during each year the same tagging procedures were used for each individual. Each year, fish were released at the same time, except for 2017–2019, in which there were two releases (early and late).

Radio receiver array.— In 2019, a total of six radio receivers (Lotek Wireless Model SRX400 or SRXDL) scanning through two different frequencies were installed at Browns Mill and Howland dams. At Browns Mill Dam, one receiver with two directional Yagi antennas was installed on the dam. One antenna was directed upstream

TABLE 2. Data summary for acoustic- and radio-tagged Atlantic Salmon in the Piscataquis River, Maine, from 2005 to 2019, showing year, release site, type of tag, and number of fish tagged and released (*n*). An asterisk (*) represents naturally reared fish. Mean FL and mass are presented with SD.

Year	Release site	Tag type	*n*	FL (mm)	Mass (g)
2005	Milo	Acoustic	85	191 ± 11.1	76.9 ± 14.1
2006	Milo	Acoustic	72	196 ± 11.3	86.2 ± 18
2009	Milo	Acoustic	120	181 ± 9.18	72.2 ± 9.7
2010	Abbot*	Acoustic	75	169 ± 8.07	44.8 ± 7.18
2010	Milo	Acoustic	100	189 ± 10.7	71.7 ± 13
2011	Abbot*	Acoustic	75	146 ± 8.15	58.4 ± 27.2
2011	Milo	Acoustic	100	188 ± 21.8	73.6 ± 16.5
2012	Abbot	Acoustic	72	199 ± 10.5	84 ± 14.4
2013	Abbot	Acoustic	75	185 ± 11.3	70.1 ± 13.2
2014	Abbot	Acoustic	75	191 ± 10.3	70 ± 12.4
2015	Abbot	Acoustic	75	186 ± 10.4	65.7 ± 11.9
2016	Abbot	Acoustic	75	191 ± 11.1	75.4 ± 13.5
2016	Browns Mill Dam tailrace	Acoustic	75	194 ± 11.1	77.8 ± 12.1
2017	Abbot	Acoustic	80	190 ± 10.8	70.8 ± 12.7
2017	Browns Mill Dam tailrace	Acoustic	80	187 ± 9.3	67.9 ± 10
2018	Abbot	Acoustic	74	191 ± 10.4	77.5 ± 13.8
2018	Browns Mill Dam tailrace	Acoustic	78	190 ± 9.9	75.6 ± 13.2
2019	Abbot	Acoustic	75	180.5 ± 10.1	62.7 ± 10.3
2019	Browns Mill Dam tailrace	Acoustic	75	180.7 ± 10.1	61.9 ± 10.7
2019	Dover Dam tailrace	Radio	75	179.7 ± 10.6	60.1 ± 11.4
Total			1,611		

(to detect initial dam approach), while the other antenna was directed across the dam. A second receiver with two directional Yagi–Uda antennas was installed at the downstream powerhouse canal. In this receiver, one antenna was directed toward the powerhouse canal, while the other antenna was directed toward the tailrace of the dam (downstream of the dam). Additionally, an omnidirectional "dropper" antenna was connected to this receiver and was deployed in the powerhouse canal at the bypass entrance. This setup allowed us to discern different fish movement patterns, including (1) initial approach, (2) passage through the spillway, (3) entrance into the powerhouse canal, and (4) passage through the bypass. An additional radio receiver was placed 2.1 rkm downstream of Browns Mill Dam, with a Yagi–Uda antenna pointing across the river to detect any fish that had passed the dam and resumed migration.

Two radio receivers, each with two directional antennas, were installed at Howland Dam. One receiver was installed upstream of the dam, with one antenna directed toward the headpond and the other antenna pointing toward the entrance of the nature-like fish bypass. The second receiver was installed on the dam; one antenna was directed across the dam, and the other antenna was directed toward the exit of the bypass. Additional radio receivers were installed downstream (~30 rkm).

Radio-tagging and release.— Seventy-five hatchery-reared smolts were radio-tagged at the USFWS-GLNFH with NTF-6-1 (2.5-g) coded NanoTags (Lotek Wireless). A similar methodology as the one used for acoustic tagging was followed for radio tags. The antenna was inserted into a 20-gauge, deflected-tip, noncoring septum needle (Fisher Scientific). The needle was inserted through a ventral incision and passed from inside the peritoneal cavity through the body wall posterior and dorsal to the pelvic fin. The needle was removed, leaving only the antenna in the opening through the body wall. The radio tag was pushed into the peritoneal cavity, and the ventral incision was closed with a single interrupted knot using 4-0 absorbable Vicryl sutures (Ethicon). After recovery, fish were transported and released on May 5, 2019, into the Dover Dam tailrace, 700 m upstream of Browns Mill Dam (Figure 1).

Analysis of delays at dams and migration rate.— We used the acoustic receivers that were deployed directly upstream and downstream of each dam to measure individual delays at dams. A delay was only measured if an individual was detected at both upstream and downstream receivers. Delay was estimated as the difference between the time of first detection at the upstream and downstream receivers. We only estimated delay times for years with releases at Abbot (Table 2), which allowed us to compare annual effects on delays. As there were slight differences in reach length (here, "reach" is defined as a section of river between two receiver stations; Table 1), we also estimated movement rates (rkm/h). As a reference, we estimated the movement rate of smolts in a free-flowing reach (from rkm 132.6 to rkm 99.8).

We constructed six different generalized linear mixed-effect models using the package lme4 in R (Bates et al. 2015; R Core Team 2019). An information-theoretic approach to model selection based on the corrected Akaike's information criterion (AIC_c; Burnham and Anderson 2010) was used to identify the best-fitting model. The logarithm of delays was used as a response variable. Year was used as a random effect and was included in every model. The explanatory variables used in the models were dam (i.e., difference in delays among dams) and gauge height at the closest U.S. Geological Survey (USGS) station as a surrogate for flow (USGS 2019a, 2019b) as both a linear term and a quadratic term. Finally, a null model (with a single parameter representing the random effect) was tested.

To analyze the migration rate from the release point at Abbot (rkm 187) to rkm 62.4 in the Penobscot River, we estimated the accumulated time in the river (ATIN) for each year:

$$\mathrm{ATIN_{NR}} = \sum_{i=1}^{\mathrm{NR}} \left(\mathrm{Median}\, D_{ij}\right)_i,$$

where NR represents the reach number (each reach represents a section of river between two stations for which a transit time was estimated for each fish) starting from upstream and D_{ij} represents time spent in each reach (transit time) for each individual (the population median was obtained). This parameter was used because it allowed us to incorporate fish released at different sites (rkm) and at different times in a single parameter.

Survival in the Piscataquis River.— Survival in the Piscataquis River was estimated using mark–recapture models (Lebreton et al. 1992). Spatially explicit encounter histories were developed for each individual using receiver stations as a "recapture occasion" during the smolt one-way migration. We used a total of 14 stations. Cormack–Jolly–Seber mark–recapture survival models were developed in program MARK (White and Burnham 1999) via the package RMark in R (Laake 2013; R Core Team 2019). In these models, we estimated apparent survival (ϕ) and detection probability (p; analogous to recapture probability) using maximum likelihood estimations and the logit-link function (Lebreton et al. 1992).

Because the reaches had different lengths, reach length was explicitly entered into the models so that an estimate of ϕ represents apparent per-rkm survival (ϕ_{rkm}) rather than apparent survival per reach (ϕ_{reach}). The covariates incorporated systemwide for ϕ_{rkm} included year, release site, and reach. For this covariate (reach), two alternative structures were considered: (1) each reach was different ("reach") or (2) all free-flowing reaches were binned, with dams identified as separate reaches (reach type; free flowing and Guilford, Dover, Browns Mill, and Howland dams). An additional treatment term representing the nature-like fish bypass at Howland Dam was included exclusively for the reach containing this dam. As flow may influence survival, we used gauge height at the time of passage as a continuous individual covariate. Each individual was assigned four flow values as covariates based on two nearby USGS gauges: (1) gauge height at USGS station 01031500 (USGS 2019a) at the time stamp of the last detection upstream of Guilford Dam, (2) gauge height at USGS station 01031500 at the time stamp of the last detection upstream of Dover Dam, (3) gauge height at USGS station 01031500 at the time stamp of the last detection upstream of Browns Mill Dam, and (4) gauge height at USGS station 01031400 (USGS 2019b) at the time stamp of the last detection upstream of Howland Dam. These USGS stations were chosen because they were the closest to each respective dam. The covariates were modeled as predictors of survival through Guilford, Dover, Browns Mill, and Howland dams; thus, when any of these covariates was included in a model, it was constrained exclusively to the reach that included the dam. Covariates were explored in their linear and quadratic forms. To explore whether flow affected survival through all dams, we ran models that included a single dam, two dams, three dams, or all four dams in all possible combinations. We also included models exploring all of the additive and interactive combinations of the covariates. Covariates for p included year, reach, flow, and release. In total, 1,042 models were run. All models were chosen a priori, as is recommended for Cormack–Jolly–Seber studies (White and Burnham 1999).

To assess goodness of fit of the survival models, we estimated the overdispersion parameter $\hat{c}$, which is a variance inflation factor (Burnham 1987). We used the median-$\hat{c}$ method (Fletcher 2012). The goodness-of-fit $\hat{c}$-estimate for the fully parameterized model was below 2 ($\hat{c} = 1.488$); therefore, the AIC_c likelihood information approach was used (AIC_c; Burnham and Anderson 2010) to determine the best-fitting model (Table 3). We obtained an AIC_c difference (ΔAIC_c) value for each model, which represents the difference between the AIC_c of each model and that of the best-fitting model. Models for which ΔAIC_c was less than 2.0 were considered to be competing models. Estimates of ϕ_{rkm} and p were obtained for the best-fitting model. In case the best-fitting model included an individual covariate, the coefficient was obtained to describe the relationship between ϕ_{rkm} and the individual covariate.

Survival, path choice, and delays at Browns Mill and Howland dams in 2019.— In 2019, we estimated movement rates and additional delay times at both Browns Mill and Howland dams using the radiotelemetry array. We also explored the potential effects of path choice on delays.

TABLE 3. Model selection results for Atlantic Salmon smolt delays at the four dams on the Piscataquis River, Maine (AIC_c = corrected Akaike's information criterion; $\Delta AIC_c = AIC_c$ difference). All represent generalized linear mixed-effects models explaining delays (lognormally distributed); all models included year as a random effect. The model denoted "~1" is a constant model in which a single parameter (intercept) is estimated.

Model	AIC_c	ΔAIC_c
Dam + Flow	6,647.771	0.000
Dam + Flow^2	6,650.737	2.966
Dam	6,672.55	24.779
Flow	7,258.562	>100
Flow^2	7,258.62	>100
~1	7,315.313	>100

The positioning and direction of the radio receiver antennas allowed us to recognize four different kinds of fish locations for both dams: (1) detection in the headpond (i.e., first approach to the dam), (2) dam passage and path choice (path choice being spillway or powerhouse canal for Browns Mill Dam and spillway or nature-like bypass for Howland Dam), (3) tailrace, and (4) successful passage (detected at a downstream receiver). Using the data obtained from the radio receiver array, we also estimated survival and path choice by using a hierarchical, multistate mark–recapture model (Figure 2).

Spatially explicit capture histories were developed for all 75 radio-tagged individuals using detections at radio receiver antennas during the downstream migration. The estimated parameters from this model were ϕ_{rkm} (customarily termed S_{rkm} for multistate approaches and not presented in the Results), p (detection probability), and Ψ (transition probability between states). We used Ψ to estimate path choice regarding passage through Browns Mill Dam (proportional use of the powerhouse canal) and Howland Dam (proportional use of the nature-like fish bypass). The model is similar to the multistate model used by Stich et al. (2015). Finally, we estimated time elapsed between the first detections at each of the four locations previously described. Using the elapsed time data, we estimated the ATIN from time of release. For Browns Mill Dam, we used an independent two-group Mann–Whitney–Wilcoxon test to explore whether there were differences in observed delays between individuals that migrated through the spillway and those that migrated through the powerhouse canal.

RESULTS

Delays at Dams and Migration Rate

We observed large individual variation in the delays caused by four dams in the Piscataquis River.

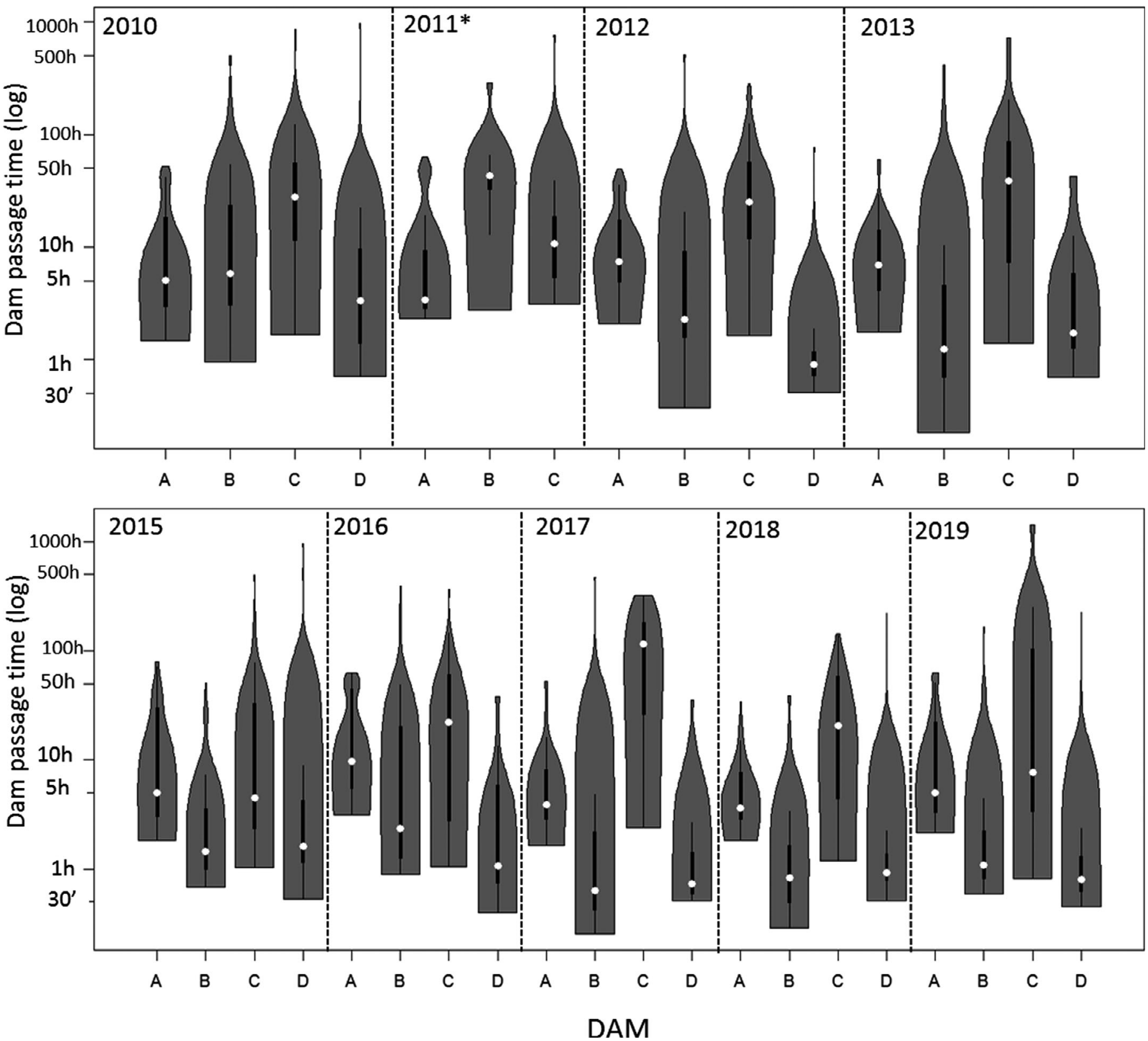

FIGURE 2. Dam passage time for Atlantic Salmon smolts at the four dams on the Piscataquis River from 2010 to 2019. The *y*-axis is time ($\log_e$ scale), and the *x*-axis represents the dams (A = Guilford Dam; B = Dover Dam; C = Browns Mill Dam; D = Howland Dam). For 2011, we only estimated delay times for the three upstream-most dams. During 2014, there were not enough detections in the Piscataquis River to estimate delay times.

Consistently, for each dam, some Atlantic Salmon smolts passed the dam in less than 2 h, whereas others were delayed for over 24 h in each year (with the number changing per dam and per year). The best-fitting model to predict delays was the interactive model that incorporated year, dam, and flow as explanatory variables (Table 3). Therefore, the individual variation observed can be partially attributed to dam, the effects of flow (with lower flows causing higher delays), and year (Figure 2).

In general, the three upstream dams caused the greatest number of delays and Browns Mill Dam caused the longest delays in most years. For 7 of the 9 years explored, Browns Mill Dam had the highest median passage time of all dams (median > 24 h in 4 of the 9 years). Browns Mill Dam had the highest 75th-percentile value in 8 of the 9 years, with this percentile being above 48 h for each of those 8 years (i.e., more than 25% of the fish approaching this dam were delayed for at least 2 d during each of the 8 years; Figure 2).

When exploring the effects of flow on delay time (irrespective of year), we can use the best-ranking model: $\log_e$(Passage time) ≈ $\beta_0 + \beta_1$(Dam) + β_2(Flow) + (1|Age). All of the coefficients of this model were significant. The effects of flow were the most evident at Browns Mill Dam, where an increase in flow greatly decreased the delays (delay decreased by 50% when gauge height increased from 0.75 to 2.50 m). Flow had a similar effect at Guilford Dam (with a 40% decrease in delay when gauge height increased from 0.75 to 2.25 m). Even though the proportional effects of flow on delays were similar between Browns Mill and Guilford dams, the delays at Browns Mill Dam were considerably greater. There were important differences in the flow (i.e., gauge height) that fish experienced when going through each dam during different years. The highest flows were observed in 2012, 2017, 2018, and 2019; therefore, the differences observed in passage time among years were likely to be affected by flow (Figure 3). Although there were two delays (due to the use of two releases) during 2017–2019, in general the differences in experience passing through dams were related to travel time.

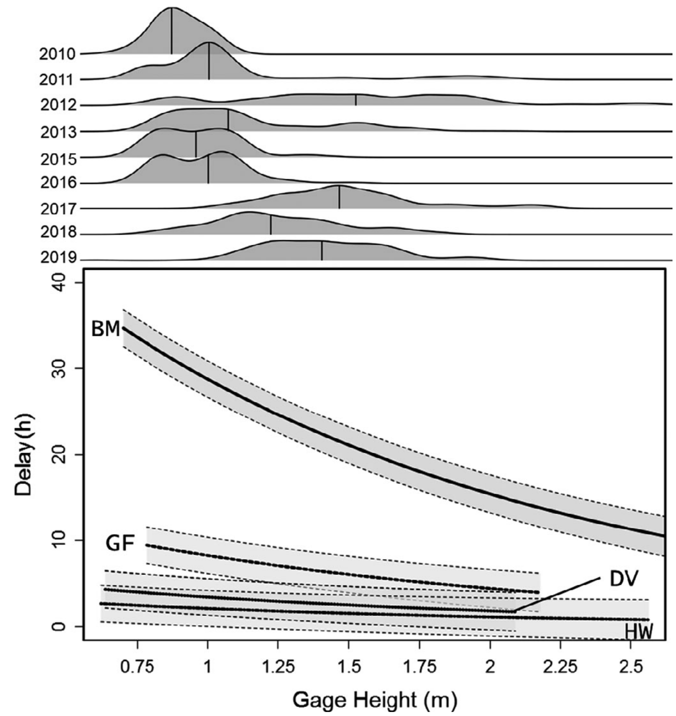

FIGURE 3. Effects of flow (with gauge height used as a proxy) experienced by downstream-migrating Atlantic Salmon smolts on passage delays at Guilford (GF), Dover (DV), Browns Mill (BM), and Howland (HW) dams based on the best-fitting model: Delay ~ Dam + Flow + (1|Year). The upper panel represents the distribution of the data for each year (2010–2019). Because gauge height data were obtained for each individual at the moment of passing each dam, smolts could have up to four values (depending on release site and survival). All data points are presented in the upper (distribution) plot, while the lower panel represents the effects of flow on delays at each of the four dams. Confidence envelope represents the SE.

The ATIN between Abbot and rkm 64 on the Penobscot River changed considerably among years, varying from 180 h in 2012 (lowest observed value) to 340 h in 2017 (highest observed value). These differences were mainly driven by the delays at dams (Figure 3) and were influenced by the differences in flow. The transit time through free-flowing reaches differed among certain years as well.

Movement rate (rkm/h) of smolts was lower at all dams when compared to movement rate in the free, unimpounded river reach. When exploring the movement rate through the three upstream dams irrespective of year, it became clear that Browns Mill Dam had the lowest smolt movement rate in the Piscataquis River, followed by Guilford Dam. Dover Dam had a relatively high movement rate, while Howland Dam had a movement rate that approached the free-flowing reach movement rate (Figure 4). However, there was still an effect of dam, as evidenced by the movement rate in the open-river reach being considerably higher than the movement rates at all dams.

Path Choice and Delays through Browns Mill and Howland Dams in 2019

In 2019, we detected 17 individuals (out of 59 potential individuals) at the acoustic receiver deployed in the Browns Mill Dam powerhouse canal. This means that a minimum 28.8% of migrating individuals chose this route (because p was not estimated, the number using this route was not estimable). Fish moved rapidly through this path, as all but one individual spent less than 5 h between the first detection upstream and the first detection downstream of the dam (this only includes individuals that were detected immediately downstream of Browns Mill Dam, $n = 21$). However, if we include the individuals that were detected at the next receiver station (13 rkm downstream), the median increases to 66 h (a movement rate of 0.19 rkm/h). This is a slow migration rate in comparison with the median movement rate in the next reach of the Piscataquis River (0.92 rkm/h).

The delays of radio-tagged smolts moving through Howland and Browns Mill dams in 2019 were similar to the delays observed for acoustically tagged fish. For Browns Mill Dam, the median time between approaching the dam (first detection in the headpond) and passage (first detection in the tailrace) was 9 h, and the 75th percentile was greater than 48 h. Furthermore, the slowest 25% of the successful fish took longer than 48 h to travel from the tailrace of the dam to the receiver antenna placed 1.8 rkm

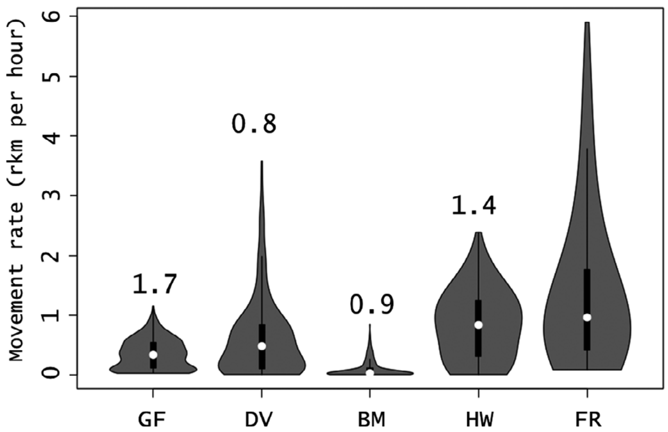

FIGURE 4. Movement rate (river kilometers [rkm]/h) of Atlantic Salmon smolts through each of the four dams (GF = Guilford Dam; DV = Dover Dam; BM = Browns Mill Dam; HW = Howland Dam) on the Piscataquis River and in a free-flowing reach (FR; a single ~20-rkm, unimpounded section of the river). The numbers above the violin plots represent the reach length (rkm) for each dam.

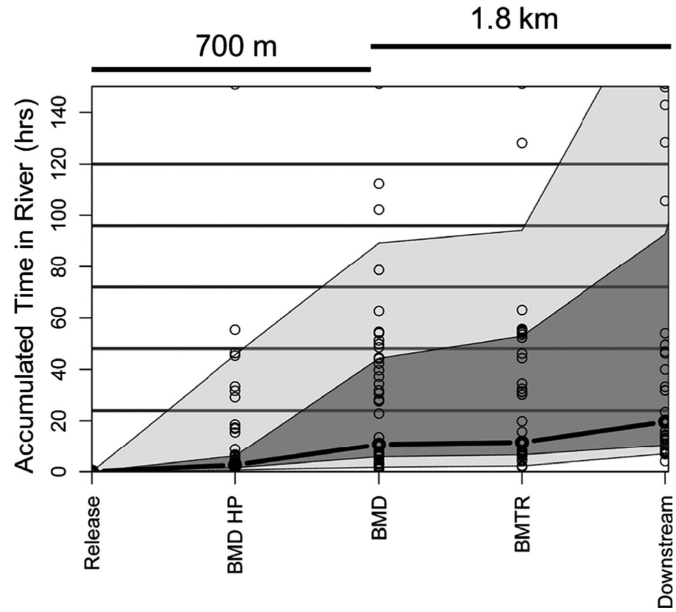

FIGURE 5. Delays for radio-tagged Atlantic Salmon smolts released in the Piscataquis River, depicting the accumulated time in the river from release approximately 700 m upstream of Browns Mill Dam to radio antennas placed 1.8 river kilometers (rkm) downstream of the dam (2.5 rkm total). The black line represents the median accumulated time in the river, while the shaded regions represent the 25th–75th percentiles and 5th–95th percentiles. Data are presented for the Browns Mill Dam headpond (BMD HP), detections at the Browns Mill Dam spillway or powerhouse canal (BMD), and the Browns Mill Dam tailrace (BMTR). The horizontal lines represent each iteration of 24 h.

below the dam. The delays were minimal between the first detection at either the spillway or powerhouse canal and the first detection in the tailrace, meaning that most delays occurred either during the initial approach or after individuals had passed the dam but before resuming migration (Figure 5; Browns Mill Dam). There were no differences in delay depending on path choice (independent two-group Mann–Whitney–Wilcoxon test: $W = 359$, $P = 0.486$). We observed almost no delays for Howland Dam; the median time difference between first detection at the headpond (approach to the dam) and first detection at the tailrace (after passing the dam) was just 1.75 h, while the 75th percentile was just below 5 h. The estimated Ψ_{AB}, probability of transition from A (main stem) to B (passage facility, in this case powerhouse canal) for Browns Mill Dam was 0.32 (95% CI = 0.21–0.45), which is consistent with what we observed using acoustic telemetry (i.e., 28.8% of the acoustic-tagged fish used the powerhouse canal). The estimated Ψ_{AB} (A stands for the main stem and B for the nature-like fish bypass) for Howland Dam was 0.30 (95% CI = 0.18–0.47). The best model only included reach as a survival covariate, meaning that there were likely no differences in survival depending on the path choice (Table 4).

Survival in the Piscataquis River

The best-fitting model incorporated differences in survival between reach types (each of the four dams and the combined free-flowing reaches; Table 4), while the probability of recapture varied by reach and by year. Probability of recapture varied from 0.80 to 0.99, with an average of 0.92. It included an effect of release, with higher survival of fish released downstream of Browns Mill Dam; it had an effect of year and included gauge height (proxy for flow) as an individual covariate for Guilford, Dover, and Howland dams but not for Browns Mill Dam (which had perfect or near-perfect survival in most years; Figure 6). The effects of flow were linear on the three dams (Guilford, Dover, and Howland dams), and some of the effects of flow were likely confounded with the annual effect (as there were differences in the experienced flows per year). Finally, even though this model included a systemwide annual effect, it also incorporated a term specifically for Howland Dam, which represented the effects of the nature-like fish bypass (i.e., there were annual differences systemwide, while the construction of the nature-like fish bypass had an additional effect on survival exclusively for the Howland Dam reach). Survival varied considerably between years, as can be seen in the accumulated survival during the migration (Figure 7).

Because ϕ_{rkm} was at its lowest in reaches with dams, we explored the differences between years for all four dams and for the composite of free-flowing reaches. There were clear differences (based on the best-fitting model) among years and dams (Figure 6). Survival at Guilford Dam was generally low, with high annual variation (between 0.93 and 1.0 for the whole 1.7-rkm reach). Survival at Dover Dam was also low (between 0.92 and 1.0). In

TABLE 4. Model selection results for the multi-year Cormack–Jolly–Seber survival models for acoustic-tagged Atlantic Salmon smolts in the Piscataquis River, Maine. The top four models are shown, as are the top two models without flow as a variable. The parameters estimated in each model (ϕ_{rkm} = apparent survival per river kilometer [rkm]; p = probability of detection) were corrected for differing interval sizes (Y = year; rt = reach type [i.e., the four dams and free-flowing reaches]; nlfb = term that was only applied to Howland Dam and represents the presence of the nature-like fish bypass; k = number of parameters; AIC_c = corrected Akaike's information criterion; ΔAIC_c = AIC_c difference; w = Akaike weight). Asterisks (*) indicate a flow effect only on Guilford, Dover, and Howland dams.

ϕ_{rkm}	p	k	AIC	ΔAIC	w	Deviance
~Y + rt + Release + Flow* + nlfb	~Y × Reach + Release	161	7,964.1	0.0	0.50	7,628.0
~Y + rt + Release + Flow + nlfb	~Y × Reach + Release	160	7,961.9	2.2	0.49	7,628.0
~Y + rt + Release + Flow* + nlfb	~Y × Reach × Release	176	8,034.0	72.1	<0.01	7,720.0
~Y + rt + Release + Flow + nlfb	~Y × Reach × Release	177	8,034.1	74.3	<0.01	7,628.0
~Y + Reach + Release	~Y × Reach × Release	256	9,224.7	>100	<0.01	7,212.2
~Y × Reach + Release	~Y × Reach + Release	294	9,054.2	>100	<0.01	7,724.2

stark contrast, survival at Browns Mill Dam was high during all years and was often indistinguishable from survival in free-flowing reaches. Survival at Howland Dam was low during the years prior to the construction of the nature-like fish bypass (generally $\phi_{rkm} < 0.95$). There were also consistent differences between releases, with lower survival for the Abbot releases. Results showed that survival at Howland Dam increased after the turbine shutdowns started in 2010 and then increased further after construction of the nature-like fish bypass in 2016. Although survival increased comparatively, it was still lower than survival observed for the free-flowing reaches (Figure 6), and despite the increase in survival, there was no effect of path choice on survival.

The effect of flow was linear: in all cases, increased flows led to increased ϕ_{rkm}. This relationship was clear at Guilford Dam, where ϕ_{rkm} changed from under 0.8 to 1.0 with an increase in gauge height of just 0.5 m (Figure 8A). Dover Dam also had an important effect of flow, with survival increasing from 0.8 to 1.0. However, for Dover Dam this change required an increase in gauge height of almost 2 m (Figure 8B). For Howland Dam, the influence of gauge height was complex over time. Survival was higher during low flows after the construction of the bypass compared to the years before bypass construction. Individuals passing through Howland Dam experienced higher flows in general during the years in which the nature-like fish bypass was in place (Figure 8C). This combination of higher flows and the presence of the nature-like fish bypass may explain the high survival from 2016 to 2019 at this dam.

DISCUSSION

Conditions in the Penobscot River system have drastically changed since the start of the PRRP. The project's main goal was to restore populations of sea-run fish (including Atlantic Salmon) to the Penobscot River while maintaining energy production (Day 2009). As a result, two dams were removed, and now only one dam remains in the lower main-stem Penobscot River below its confluence with the Piscataquis River. More than 25% of the high-quality habitat available for spawning in the Penobscot River system is present in the Piscataquis River (Saunders et al. 2006), and this river still contains four dams that delay downstream-migrating smolts and reduce their survival (Stich et al. 2014) while also impeding the upstream migration of adults (Izzo et al. 2016). Only one of the dams in the Piscataquis River system, Howland Dam, has been modified with the construction of a nature-like fish bypass. The three dams upstream of Howland Dam have not been extensively modified despite their negative effects on survival (Guilford and Dover dams) or movement rate (Guilford and Browns Mill dams). Effective use of the habitat available in the Piscataquis River would require smolts that are spawned or stocked in this river to successfully migrate to the Penobscot River and then to the ocean. Therefore, exploring the effects of the remaining dams in the Piscataquis River is vital for the recovery of the population. In particular, dams are an important cause of delays for downstream-migrating fish, and they decrease the movement rate during migration toward the ocean.

Dam-caused delays can increase mortality rates during salmon migration (Castro-Santos and Haro 2003; Marschall et al. 2011; Nyqvist et al. 2017). Therefore, understanding the specific causes and conditions associated with site-specific delays is of great importance for a species in decline like the Atlantic Salmon (Parrish et al. 1998). Our results confirm that dams represent the areas of highest delays in the system. The general consistency in delays among dams indicates that there might be design or operational factors that increase delays and are dam specific (Bunt et al. 2012). Identifying these factors may be a first step toward solving the delays.

The results from the radio-tagging study at Howland Dam confirmed that this dam caused minimum delays

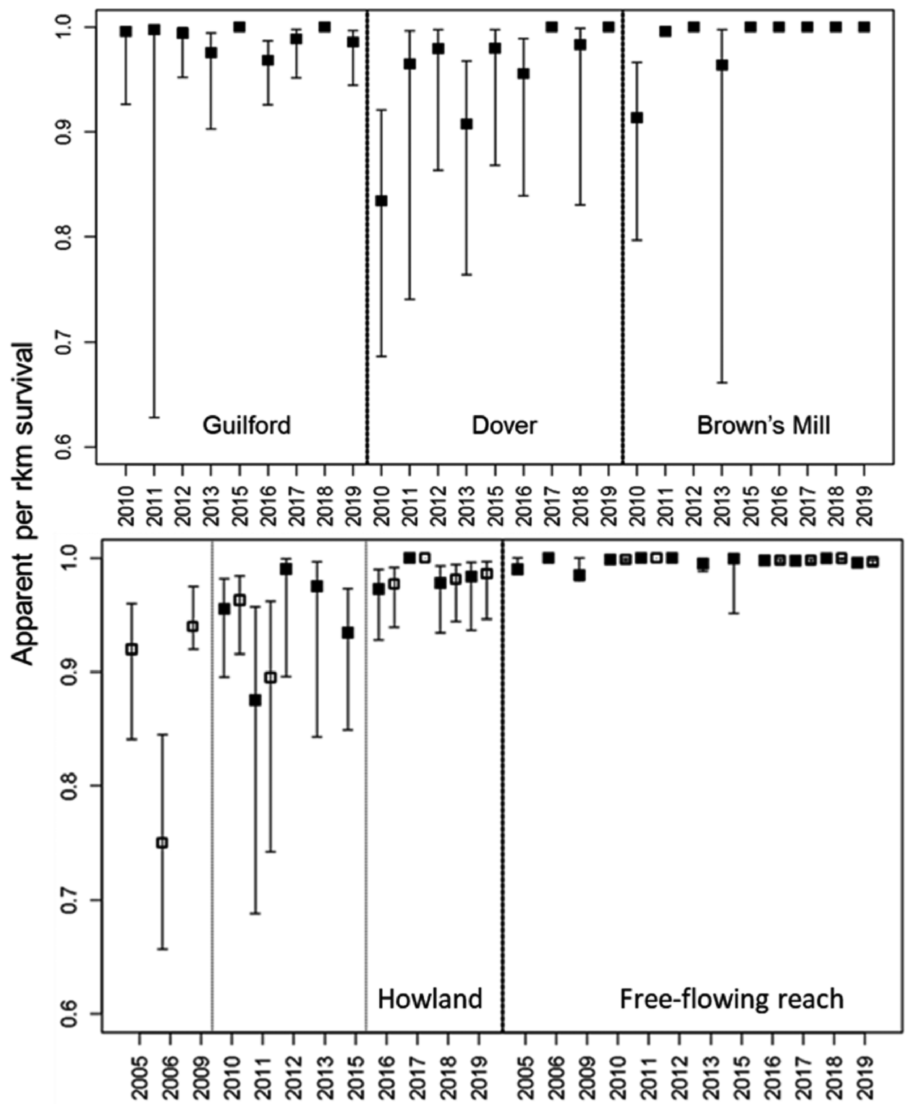

FIGURE 6. Annual per-river-kilometer survival (ϕ_{rkm}) of Atlantic Salmon smolts at each of the four dams in the Piscataquis River system and in free-flowing reaches for 12 years using the best-ranking model in which survival was explained by year, reach type, release, and flow. Error bars represent the SE. The black squares represent the Abbot releases, while open squares represent releases at either Milo or the Browns Mill Dam tailrace. The vertical lines for Howland Dam represent the changes in the system (first line = turbine shutdown; second line = construction of the nature-like fish bypass).

(from 2016 to 2019, 95% passed it within 24 h). Delays were reduced after construction of the bypass; however, only about 30% of individuals used the bypass. Therefore, although the bypass is used by the smolts, it is not the preferred route and the reduction in delays may be partially explained by other factors, such as flow.

Browns Mill Dam had the lowest mortality but the highest delays (in all years except 2011). This dam has a downstream passage structure composed of a powerhouse canal (with 15.3-cm grates) that connects to a bypass system. About 32% of the individuals used the powerhouse canal. However, we found that the time spent in this canal was minimum (median < 3 h) and therefore does not explain the delays observed at Browns Mill Dam. Our 2019 study indicated that most of the delays observed at the dam occurred at two different points: (1) in the headpond after dam approach but before passing the dam and (2) in the tailrace after passing the dam but before being observed approximately 1.5 rkm downstream. Interestingly, the majority of observed delays occurred after individuals had passed the dam. Thus, the delay is likely a result of passing the dam rather than difficulty in finding a passage route. Although the causes of these delays are unknown, understanding them will be an important step

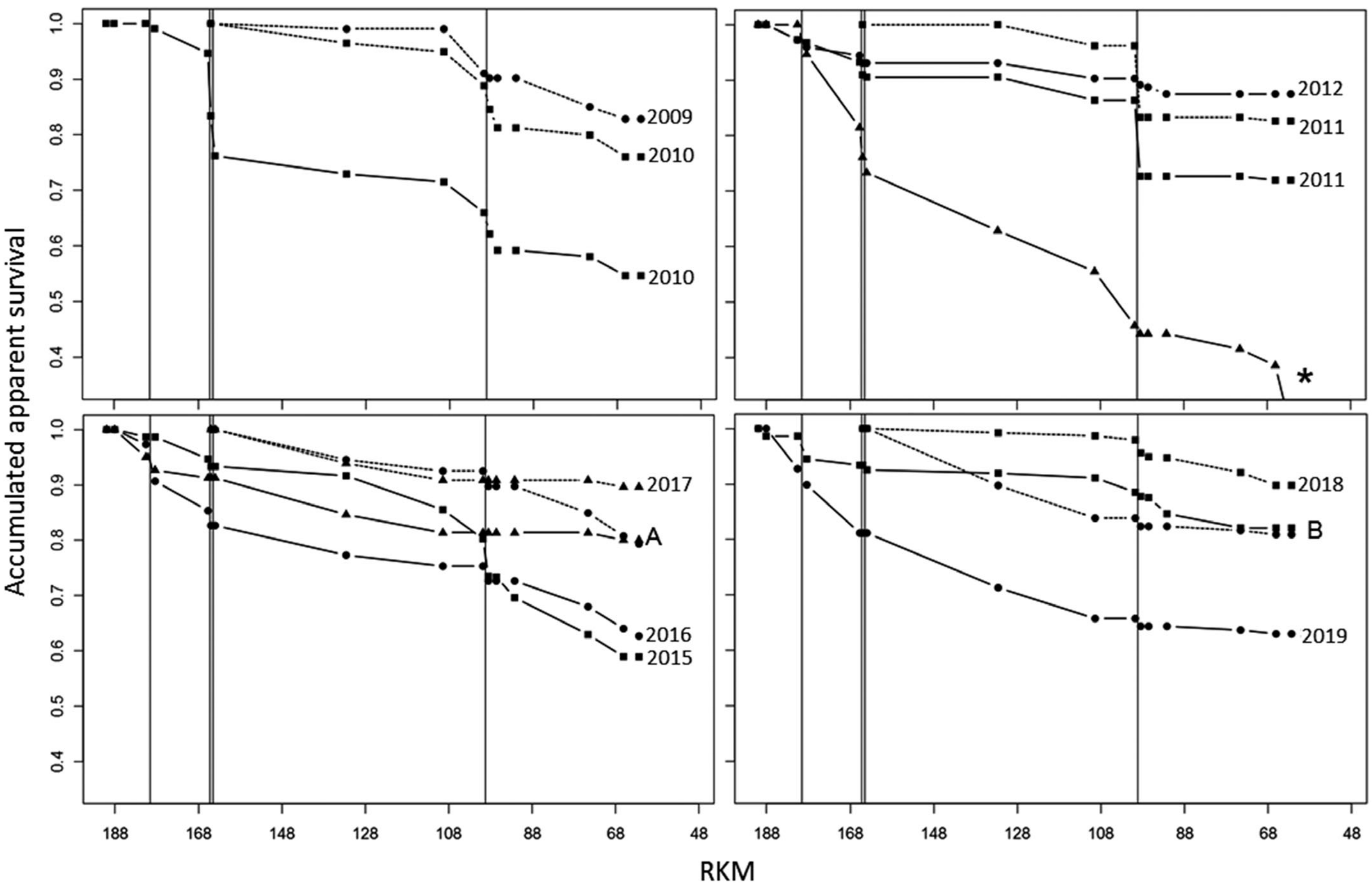

FIGURE 7. Accumulated apparent survival (ϕ) of Atlantic Salmon smolts from 2009 to 2019 (except 2014) using the best-ranking model, in which survival was explained by year, reach type, release, and flow. Accumulated survival was obtained using the ϕ point estimates. Solid lines represent releases at Abbot (river kilometer [rkm] 188); dotted lines represent releases at either Milo or the Browns Mill Dam tailrace (in both cases, the releases were downstream of Browns Mill Dam). Data labeled A represent 2017 (Abbot release) and 2016 (Browns Mill Dam tailrace release), while data labeled B represent 2018 (Abbot release) and 2019 (Browns Mill Dam tailrace release). Survival in 2013 (indicated by the asterisk [*]) for the last point estimate was 0.29 and is not shown on the graph.

toward characterizing the migration of smolts in the Piscataquis River and the potential causes of delays in other systems.

High flows reduced migration delays, and in certain cases these delays were half of what was seen during low flows (e.g., at Browns Mill Dam; Figure 3). Although we tested the path choice at Browns Mill Dam in 2018, this was a year of high flows. Therefore, the patterns observed might have been markedly different during a low-flow year. At each dam, there were smolts that passed the dam almost immediately as well as smolts that were delayed for over a day, showing high individual variability. There may be some environmental conditions that affect the movement and passage of individuals as well as some individual traits that affect smolt passage through dams, as has been observed in other systems (Kemp et al. 2006). Not only did high flows affect delays, but flows can affect survival through dams. There were important among-year differences in delays, which might be related to other environmental traits that were not measured, such as temperature.

Dams remain one of the greatest impediments to successful migration in the Piscataquis River system (Holbrook et al. 2011; Stich et al. 2014). Our results confirm that apparent mortality is still high at dams in this river when compared to free-flowing reaches. Although there was an effect of flow on survival, the effects of flow were lessened after the construction of the nature-like fish bypass at Howland Dam. Some of the highest flows of the past 12 years occurred during 3 of the 4 years in which the nature-like fish bypass was in place, which might have coincidentally reduced mortality at this dam. Among the upper three dams, Guilford and Dover dams caused relatively high mortality. Flow also had an effect on survival at these two dams (with higher probability of mortality at lower flows). Browns Mill Dam has consistently had a

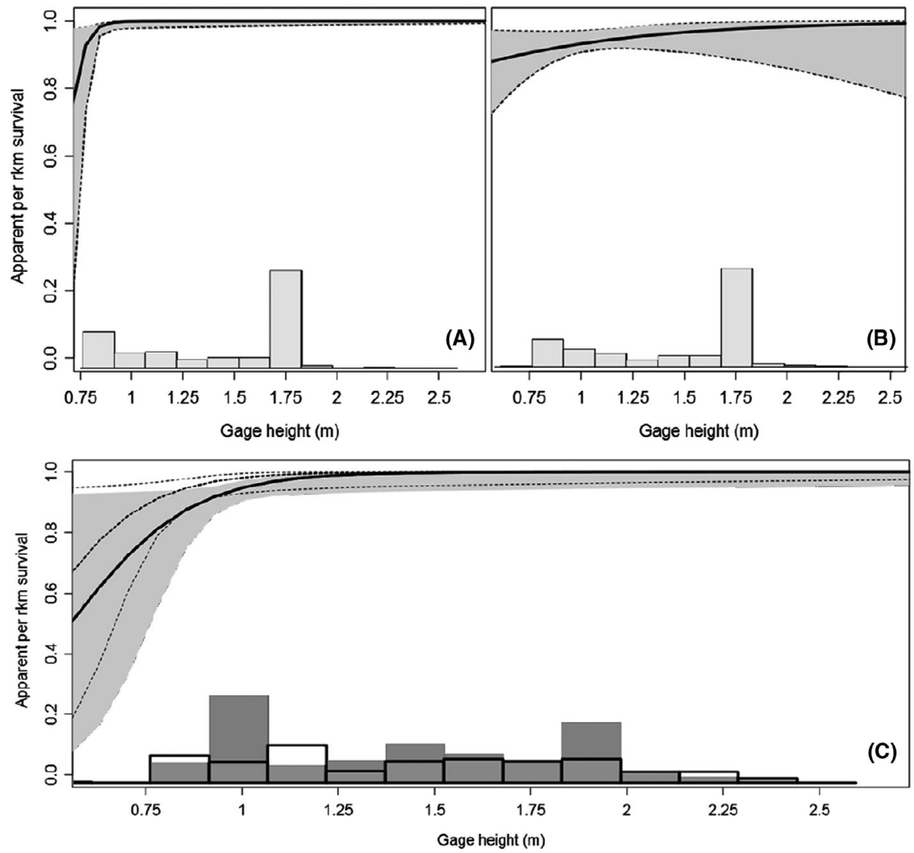

FIGURE 8. Relationship between gauge height (m) and apparent per-river-kilometer survival (ϕ_{rkm}) of Atlantic Salmon smolts at the three dams for which there was an effect (Guilford, Dover, and Howland dams) using the coefficients (β) obtained from best-ranking model. For **(A)** Guilford Dam and **(B)** Dover Dam, the line represents the predicted point estimates, and the confidence envelope represents the 95% CI; the histograms represent the gauge heights experienced by migrating individuals. For **(C)** Howland Dam, the solid line and polygon represent the apparent survival and 95% CI for the years before the nature-like fish bypass was built, and the dashed lines represent the apparent survival and 95% CI for the years after the nature-like fish bypass was built. The histograms in panel C represent the gauge heights experienced during years before (gray histogram) and after (open histogram with solid black border) the nature-like fish bypass was built.

high probability of smolt survival, comparable with survival in free-flowing reaches. This dam is associated with the highest smolt survival of all dams in the system. Our inability to detect an effect of flow on survival at Browns Mill Dam is likely because survival there was perfect or near perfect during most years. While our work was primarily focused on specific areas of the Piscataquis River, it is important to examine the whole experience faced by migrating smolts in this river.

The experience of migrating smolts in the Piscataquis River changed dramatically from year to year. The ATIN from the release site to the Penobscot River varied from a median of 170 h in 2012 to over 300 h in 2017. Considering that delays at Guilford and Browns Mill dams were consistently over 48 h for the slowest 25% of smolts, those 48 h might represent over 20% of the total time spent in the river. If we consider that fish had to pass four dams, it is clear that the overall experience of fish moving through this tributary is mostly dominated by the influence of the dams. Cumulative survival in the Piscataquis River varied from 0.50 to about 0.85, with great among-year variability. This variability was best explained by flows and changes to Howland Dam downstream passage. Despite the high year-to-year variation, a considerable proportion of the migrating fish did successfully reach Milford Dam on the Penobscot River. It is reasonable to assert that individuals that successfully reach the lower river may be affected later in the migration by their experiences in the Piscataquis River. In particular, as temperatures may increase, delays and upstream experience might have a profound effect on survival.

Regarding the effects of dams on smolts, most of the focus has been applied to immediate mortality; however, the latent effects of dams and the dam-caused delays can be substantial. Our best-fitting model suggested a difference in survival at Howland Dam depending on release site, with lower survival for fish that had to pass multiple dams before arriving at Howland Dam. These differences might be due to an additive effect of passing multiple dams or encountering multiple delays (Castro-Santos and Haro 2003; Ferguson et al. 2006; Nyqvist et al. 2017). There is evidence that passing multiple dams may reduce survival downstream in other populations of salmonids (Ferguson et al. 2006; Stich et al. 2015a, 2015b; Faulkner et al. 2019), including those in the Penobscot River system (Stich et al. 2015a).

Delays caused by dams might contribute to a mismatch between physiological preparedness and estuary arrival. During the smolt migration, high mortality occurs during the transition from freshwater to salt water in the estuary and in coastal waters (Kocik et al. 2009; Holbrook et al. 2011; Thorstad et al. 2012; Stich et al. 2015a). This mortality has been linked to novel predators, experiences during the freshwater portion of the migration, physiological preparedness, and the timing of estuary entrance, which affects temperature (as temperature increases) and physiological development (Hvidsten and Lund 1988; Handeland et al. 1996; Davidsen et al. 2009). Smolts that are delayed in this system might reach the estuary outside of the "smolt window," which may negatively affect their survival and performance (McCormick 1994; McCormick et al. 1998). Smolts upstream of Guilford Dam in the Piscataquis River need to pass four dams and may be delayed for several days by the time they arrive at the Penobscot River. Individuals that successfully reach the Penobscot River still must travel about 99 rkm before reaching Penobscot Bay, and they may suffer negative consequences of their experience in the Piscataquis River, such as (1) lower survival going through additional dams in the Penobscot River, (2) lower survival in the estuary (Stich et al. 2015a), and (3) a delay-related mismatch between estuary arrival and physiological preparedness (McCormick et al. 1998).

When exploring smolt migration in the Piscataquis River, it is important to not only focus on the mortality experienced in this river, but to remember that the individual experiences in this river might have effects later in the migration. As over 25% of the available habitat in the Penobscot River system is found in the Piscataquis River, this river represents an essential area and a potential point of focus for Atlantic Salmon recovery in the Penobscot River system. Furthermore, given that (1) smolt survival is low in most systems and (2) most systems with Atlantic Salmon contain multiple dams, an understanding of dams' effects on delays and, in turn, the effects of such delays on survival can help to address the factors that affect smolt migration.

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ORCID

Alejandro Molina-Moctezuma https://orcid.org/0000-0002-9782-6460

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