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Title: Movement, survival, and delays of Atlantic Salmon *Salmo salar* smolts in the Piscataquis River, Maine, USA

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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 four dams (Guilford, Dover, Brown's Mill, and Howland) from 2005 to 2019. During this period, the downstream-most dam (Howland Dam) transitioned from full hydropower generation to seasonal turbine shutdowns, and later to be 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 rkm apparent survival averages of 0.972, 0.951, and 0.990 for Guilford, Dover, and Brown's Mill, 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 is further increased by the nature-like fish bypass (0.99). We used radio telemetry in 2019 (n = 75) and demonstrated that approximately 1/3 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 released upstream of Howland Dam. While smolts passing through Brown's Mill Dam had high survival, the dam caused extended delays, with median delay times surpassing 48 hours in most years. Most of the delays caused by Brown's Mill Dam occurred after fish had passed the dam, and may indicate a sub-lethal effect of passage. Overall, while survival through Howland Dam has improved, in aggregate, passage and delays caused by the three upstream dams represent a critical impediment to the effective use of the high quality spawning habitat found upstream.

INTRODUCTION

The Penobscot River 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 (U.S.) 2004; Saunders et al. 2006; United States Atlantic Salmon Assessment Committee 2019). Historically low numbers led to listing of the distinct population segment (DPS) in 2000, and the Penobscot River population was included in the DPS 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; United States Atlantic Salmon Assessment Committee

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 (United States Atlantic Salmon Assessment Committee 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 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 this species 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 systems' watershed (Fay et al. 2006; Saunders et al. 2006; Figure 1). However, this tributary has dams that impede both upstream adult and downstream smolts Migration. Migrating smolts in this tributary encounter up to four dams (Guilford, Dover, Brownsmill, and Howland; Table 1) before reaching the main-stem Penobscot River, where they encounter at least one dam (Milford Dam) before 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 spring of 2010. These shutdowns increased smolt survival at this dam, but survival remained low relative to other dams or to free flowing rivers (Stich et al. 2014, 2015a). In 2016, as part of the PRRP, a nature-like fish bypass was built at Howland Dam (Day 2009; Opperman et al. 2011; FERC 2018). This 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). Non-lethal 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 ~100 rkms to the Bay while passing either one additional dam (Milford Dam) if they stay in the main-stem Penobscot or three dams if they three dams if they migrate through an additional branch (Stich et al. 2015b). While 85% of individuals stay in the main-stem and only face one more dam, this dam is associated with low survival, and additive effects of crossing multiple dams may further lower survival. Therefore, considering the entire route and experience is important for assessing smolts migrating through the Piscataquis River.

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

METHODS

Study Site

Guilford Dam is the upstream-most dam in the Piscataquis river. It is ~181 river km (rkm) upstream from the Penobscot River Bay, and 82 rkm upstream of the confluence of the Piscataquis River with the Penobscot River. This confluence is in the town of Howland, coordinates 45°4’22’’N, 68°39’16’W, ~99 river kilometers (rkm) upstream from the Penobscot River Bay (rkm 0). Although this dam (Guilford) 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 Brownsmill Dam, located only 700 m downstream of Brownsmill Dam at rkm 164, therefore, this section of river is both the headpond of Brownsmill Dam, and the tailrace of Dover Dam. Brownsmill 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 2005-2009, the dam operated at full capacity for hydropower and starting in 2010, after being purchased by the Penobscot River Restoration Trust (PRRT), it had seasonal shutdowns from 2010 to 2015 to accommodate smolt migration. Finally, a nature-like fish bypass was completed in 2016 (FERC 2009, 2018; Day 2009).

Acoustic Receiver Array

Every year, from 2005 to 2019, an acoustic array consisting of up to 25 acoustic Vemco receivers (VR2 or VR2W; Amirix Vemco Ltd; vemco.com) 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 2005-2013 were deployed and described in previous works (Holbrook et al. 2011; Stich et al. 2015b), while the array from 2015-2019 is depicted in Figure 1. Each receiver contained an omnidirectional hydrophone scanning continuously at 69 kHz. Receivers were deployed upstream and downstream of each of the four dams in the river, therefore conferring information regarding dam approach and passage. In 2019, an additional acoustic receiver was deployed in the downstream powerhouse canal in Brownsmill 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 1,611 Atlantic Salmon smolts were acoustically tagged and released in the Piscataquis River (Figure 1) under the University of Maine IACUC protocols numbers A2014-10-04, and A2017-10-02. 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 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 Green Lake National Fish Hatchery (USFWS-GLNFH). The tagging and release procedures for years prior to 2014, are described in Holbrook et al. 2011 and Stich et al. 2014 and are similar to the procedures used from 2014 to 2019. Smolts tagged from 2014-2019 were anaesthetized using a 100 mg • L^{-1} solution of MS-222 (buffered with 20-mM $NaHCO_3$; pH=7.0), fork length (mm) and mass (g) were measured. A small (1 cm) incision was made offset from the ventral line. An acoustic tag (Vemco V9-6L; 2.0g 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; www.ethicon.com). After surgery, fish were transferred to a recovery tank. Following full recovery, fish were transported to the release site (permit DSRFH-2019-05-03-13:58) from Maine Department of Marine Resources). Fish were released in one of three release site: 1) Abbot, (rkm 187), upstream of all four dams in the river, 2) Brownsmill Tailrace (rkm 163.8) and upstream of Howland Dam, and 3) Milo, at rkm 133, also upstream of Howland Dam (Figure 1). The number of releases and sites of release varied from year to year (Table 2). However, during each year each individual had the same tagging procedures. Each year, fish were released at the same time, except for 2017-2019, in which there were two releases (early and late).

Radio receivers array

In 2019, a total of six radio receivers (Lotek Wireless models SRX400 or SRXDL; www.lotek.com) scanning through two different frequencies were installed at Brownsmill and

Howland Dams. At Brownsmill Dam, one receiver with two directional Yagi antennas was installed on the dam. One antenna was directed upstream (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 towards the powerhouse canal, while the other antenna was directed towards 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 the dam with a Yagi-Uda antenna pointing across the river to detect any fish that passed the dam and resumed migration.

Two radio receivers were installed in Howland Dam with two directional antennas each. One receiver was installed upstream of the dam, with one antenna directed towards the head-pond and the other antenna pointing towards the entrance of the nature-like fish bypass. The second receiver was installed on the dam, and had one antenna directed across the dam, and the other antenna directed towards 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 nano-tags (Lotek Wireless; www.lotek.com). A similar methodology as the one used for acoustic tagging was followed for radio tags. The antenna was inserted into a 20 gage, deflected-tip noncoring septum needle (Fisher Scientific; fishersci.com). 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; www.ethicon.com). After recovery, fish were transported and released on May 5, 2019, in the Dover Dam tailrace, 700 m upstream of Brownsmill 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 in Abbot (Table 2), this allowed us to compare annual effects on delays. As there were slight differences in reach (reach is a section of river between two receiver stations) lengths (Table 1), we also estimated movement rates (in rkm h^{-1}), and as reference, we also estimated movement rate for a free flowing reach (from rkm 132.6 to rkm 99.8).

We constructed six different generalized linear mixed-effect (GLMM) using package lme4 in program R (Bates et al. 2015). An information-theoretic approach to model selection, based on the corrected Akaike information criterion (AICc; Burnham and Anderson 2010), was used to identify the best fitting model. The log 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: dams (i.e. difference in delays among dams), and gage height at the closest USGS station as a surrogate for flow (USGS 2019a, 2019b) as both, a linear and a quadratic term. Finally, a null model (with a single parameter representing the random effect) was tested.

In order to analyze the migration rate, from the release point in Abbot (rkm 187) to the river kilometer 62.4 in the Penobscot River, we estimated Accumulated Time in the River (ATIN) for each year:

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

in which ATIN represents accumulated time in river, 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 (and the population median was obtained). This parameter was used, as it allows us to incorporate fish released in different rkm's 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. A total of 14 stations were used, Cormack-Jolly-Seber (CJS) mark recapture survival models were developed in program MARK (White and Burnham 1999), through the package RMark in program 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).

As the reaches had different lengths, reach length was explicitly entered in 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 system-wide for ϕ_{rkm} included year, release site, reach. For this covariate (reach) two alternative structures were considered: 1) each reach is different ("reach"), 2) all the free flowing reaches are binned, with dams identified as separate reaches ("reach type"; Free Flowing, Guilford, Dover, Brownsmill Dam, Howland). An additional treatment-term representing the nature-like fish bypass in Howland Dam was included exclusively for the reach containing this dam. As flow may influence survival, we used gage height at time of passage as a continuous individual covariate. Each individual was assigned four flow values as covariates, based on nearby USGS gages: gage height at USGS station 01031500 (USGS 2019a) at 1) timestamp of the last detection upstream of Guilford Dam, 2) timestamp of the last detection upstream of Dover Dam, 3) timestamp of last detection upstream of Brownsmill Dam, and 4) gage height at USGS station 01031400 (USGS 2019b) at the timestamp of the last detection upstream of Howland Dam. These stations were chosen because they were the closest to each respective dam. These covariates were modeled as predictors of survival through Guilford, Dover, Brownsmill, 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. These covariates were explored in their linear and a quadratic form. In order 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 the additive and interactive combinations of the covariates. Covariates for p included year, reach, flow, and release. A total of 1,042 models were run. All models were chosen *a priori*, as is recommended in CJS studies (White and Burnham 1999).

To assess goodness of fit of the survival models, we estimated the over-dispersion 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 AICc likelihood information approach was used (AICc; Burnham and Anderson 2010). This was used to determine the best fitting model (Table 3). We obtained a ΔAICc value for each model, which represents the difference between the AICc of each model with the best fitting model. Models for which ΔAICc < 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 apparent survival and the individual covariate.

Survival, path choice and delays in Brownsmill Dam and Howland Dam in 2019

In 2019 we estimated movement rates, and additional delay times of both Brownsmill Dam, and Howland Dam using the radio telemetry array. We also explored the potential effects of path choice on delays. 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 dam), 2) dam passage and path choice (path choice being spill or power-house canal for Brownsmill Dam, and spill or nature-like bypass for Howland Dam), 3) tailrace, 4) and successful passage (detected at a downstream receiver). Brownsmill. Using the data obtained from the radio receiver array, we also estimated survival, and path choice, using a hierarchical, multistate, mark-recapture model (Fig 2).

Spatially-explicit capture histories were developed for all 75 radio-tagged individual using detections at radio receiver antennas during the fish down-stream migration. The estimated parameters from this model were Φ_{rkm} (customarily termed S_{rkm} for multi-state 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 Brown's Mill Dam (proportion use of the powerhouse canal) and Howland(proportional use of the nature-like fish bypass). The model is similar to the multi-state model used by Stich et al. (2015). Finally, we estimated time elapsed between the first detections of each of the four locations previously described. Using the elapsed time data, we estimated the Accumulated Time in River from time of release. For Brownsmill Dam, we explored if there were differences in observed delays between individuals that migrated through the spillway, and individuals that migrated through the power-house canal using an independent 2-group Mann-Whitney U test.

RESULTS

Delays at dams and migration rate

We observed large individual variation in the delays caused by dams in the Piscataquis River. Consistently, for each of the four dams, some individuals passed the dam in less than 2 hours, while some were delayed for over 24 hours in each year (number changing per dam and per year). The best fit 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 dams, by the effects of flow (with lower flows causing higher delays), and by year (Figure 2).

In general, the three upstream dams caused the most delays and Brownsmill Dam caused the highest delays most years. For 7 of the 9 years explored, Brownsmill Dam had the highest median passage time of all dams (with a median higher than 24 h in four of the nine years), and it had the highest 75th percentile value in 8 out of 9 years, with this percentile being above 48 h for all those 8 years (i.e., more than 25% of the fish approaching this dam were delayed for at least 2 days on each of these years; Figure 2).

When exploring the effects of flow on delay time (irrespective of year), we can use the best ranking model that incorporated these two variables: Log Passage time $\approx \beta_0 + \beta_1(\text{Dams}) + \beta_2(\text{Flow}) + (1|\text{Age})$. All the coefficients of this model were significant. The effects of flow were the most evident at Brownsmill Dam. At this dam, the increase of flow greatly decreases the delays (delay decreased by 50% when gage height increased from 0.75 to 2.5 m). The effect of flow at Guilford Dam had a similar effect than at Brownsmill (with a 40% decrease when flow increased from 0.75 to 2.25). Even though the proportional effects of flow on delays were similar between these two dams, the delays at Brownsmill Dam were considerably higher. There were important differences in the flows (i.e., gage heights) that fish experienced when going through each dam, in different years. The highest flows were observed in 2012, 2017, 2018, and 2019, and therefore, the differences observed in passage time among years are likely to be affected by flow (Figure 3). While in 2017-2019 there were two delays, in general the differences in experience passing through dams were related to travel time.

The ATIN between Abbot, and rkm 64 in the Penobscot River changed considerably among years. ATIN varied from 180 hours in 2012 (lowest seen value), to 340 hours in 2017 (highest value). These differences were mainly driven by the delays at dams (Figure 3), and influenced by the diffrences in flow. The transit time through free flowing reaches differed among certain years too. movement ratemovement rate

Movement rate (km h^{-1}) was lower at all dams when compared to movement rate in free, unimpounded river reaches. When exploring the movement rate through the three upstream dams, irrespective of year, it becomes clear that, Brownsmill Dam, had the lowest movement rate in the Piscataquis River, followed by Guilford Dam. Dover Dam had relatively high movement rate, while Howland Dam had a movement rate that approached the free flowing river movement rate (Figure 4). However, there is still an effect of the dam, which is evident as the movement rate in an open river reach is considerably higher than all dams.

Path choice, and delays through Brownsmill Dam and Howland Dam in 2019

In 2019, we detected 17 individuals (out of 59 potential individuals) in the acoustic receiver deployed in the Brownsmill power house canal. This means that a minimum 28.8% of migrating individuals chose this route (because p is not estimated, the number using this route was not estimable). Fish moved rapidly through this path as all but one individual spent less than five hours between first detection upstream, and first detection downstream of the dam (this only includes individuals that were detected immediately downstream of Brownsmill 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 hours (a movement rate of 0.19 km/h). This is a slow migrating speed, when compared to the median movement rate in the next reach of the Piscataquis River (0.92 km h^{-1}).

The delays of radio-tagged smolts moving through Howland, and Brownsmill Dam in 2019 were similar to the ones observed in acoustically-tagged fish. The median time between approaching the dam (first detection in the headpond), and passage (first detection in the tailrace) was 9 hours, and the 75th percentile was above 48 hours. Furthermore, the slowest 25% of the successful fish took longer than 48 hours to travel from the tailrace of the dam, to receiver antenna placed 1.8 rkms 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, before resuming migration (Figure 5; Brownsmill). There were no differences in delays depending on path choice (independent 2-group Mann-Whitney U Test: W= 359, p-value = 0.486). We observed almost no delays for Howland, 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 hours, while the 75th percentile was just below 5 hours. The estimated Ψ_{AB} for Brownsmill Dam was 0.32 (CI: 0.21-0.45), which is consistent with what we observed using acoustic telemetry (where 28.8% of the fish used the powerhouse canal). The estimated Ψ_{AB} for Howland Dam was 0.30 (CI: 0.18-0.47). The best model only included reach as a survival covariate, meaning that there are likely no differences in survival depending on the path choice (Table 5).

Survival in the Piscataquis River

The best fitting model incorporated differences in survival between reach types (each of the four dams, and one free flowing river; Table 4), while probability of recapture varied by reach and by year. Probability of recapture varied from 0.8 to 0.99, with an average of 0.92. It included an effect of release, with higher survival on fish released downstream of Brownsmill Dam, it had an effect of Year, and gage height as an individual covariate for Guilford, Dover, and Howland Dam, but not for Brownsmill Dam (which had perfect or near perfect survival in most years; Figure 9). The effects of flow were linear on the three dams, and some of the effects of flow were likely confounded in the annual effect (as there were differences in the experienced flows per year). Finally, even though this model included a system-wide annual effect, it also incorporated a term specifically for Howland Dam that incorporated the effects of the nature like fish bypass (i.e. there were annual differences system-wide, while the construction of the nature-like fish bypass had an additional effect on survival exclusively for the Howland reach). Survival varied considerably between years, as can be seen in the accumulated survival during their migration, obtained from these survival estimates (Figure 6).

As apparent survival (ϕ_{rkm}) is at its lowest in reaches with dams, we explored the differences between years for all four dams and for free-flowing reaches (i.e., composite of all free flowing reaches). There were clear differences (based on the best-fitting model), among years and dams (Figure 7). Survival at Guilford Dam was generally low with great 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 stark contrast, survival at Brownsmill Dam was high during all year, often not distinguishable from free flowing reaches. Survival at Howland Dam was low in 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 show that survival in Howland Dam, increased after the turbine shutdowns started in 2010, and then it increased furthermore after the construction of the nature-like fish bypass in 2016. While survival increased comparatively, it is still lower than those observed for the free flowing reach (Figure 7), and despite the increase in survival, there wasn't an effect of path choice on survival

The effect of flow was linear, and in all cases, increased flows led to increased Φ_{rkm}. This relationship was clear at Guilford, in which the Φ_{rkm} changed from under 0.8 to 1 with an increased gage height of just 0.5 m (Figure 8 A). Dover Dam also had an important effect of flow, with survival increasing from 0.8 to 1. However, for Dover Dam, this change requires an increase in gage height of almost 2 m (Figure 8 B). For Howland Dam, the influence of gage height was complex over time. Survival was higher during low flows after the construction of the bypass, compared to the years before the construction of the bypass. Individuals passing through Howland Dam experienced higher flows in general during the years in which the nature-like fish bypass was in place (Figure 8 C). This combination of higher flows, and the nature-like fish bypass may explain the high survival from 2016-2019 in this dam. Because flow has

DISCUSSION

Conditions in the Penobscot River system have drastically changed since the start of the Penobscot River Restoration Project. This project had a main goal of restoring 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 the confluence of this river with the Piscataquis River. More than 25% of the high-quality habitat available for spawning 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 upstream migration of adults (Izzo et al. 2016). Only one of the dams in the system-, the Howland Dam has been modified with the construction of a nature-like fish bypass. The three upper (excluding Howland Dam) dams have not been extensively modified despite the negative effects that they have on survival (Guilford Dam and Dover Dam) or movement rate (Guilford Dam and Brownsmill Dam). Effective use of the habitat available in the Piscataquis River, would require that smolts spawned (or stocked) in this river can successfully migrate to the Penobscot River, and then to the ocean. Therefore, exploring the effects that are caused by the remaining dams in this 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 towards the ocean.

Dam-caused delays can increase mortality rates during their migration (Castro-Santos and Haro 2003; Marschall et al. 2011; Nyqvist et al. 2017). Therefore, understanding 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. Brownsmill 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 towards solving delays.

The results from the radio-tagged study in Howland Dam, confirmed that this dam caused minimum delays (from 2016-2019, 95% passed it within 24 hours). Delays were reduced following the construction of the bypass, however only ~30% of individuals used the bypass. Therefore, while 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.

Brownsmill Dam had the lowest mortality, but had the highest delays (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 powerhouse canal. However, we found that the time spent in this canal is minimum (median under 3 h), and does not explain the delays observed at this dam. Our 2019 study shows that most of the delays observed at Brownsmill Dam happened 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, before being observed ~1.5 rkms 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 finding a passage route. While the causes of these delays are unknown, understanding them are an important step towards characterizing the migration of smolts in this river, and potential causes of delays in other systems.

High flows reduced migrating delays, and in certain cases these delays were half of what's seen during low flows (e.g. Brown's Mill; Figure 3). While we tested the path choice in Brownsmill in 2018, this was a year of high flows. Therefore, the patterns observed might be markedly different during a low flow year. At each dam there were individuals that passed the dam almost immediately, as well as individuals 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 the passage of smolts through dams, as has been observed in other systems (Kemp et al. 2006). Not only did high flows affected delays, but flows can affect survival through dams. There were important differences among years in delays, and they might be related to other environmental traits such as temperature, that were not measured.

Dams remain one of the biggest impediments for successful migration in this 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. While there was an effect of flow on survival, the effects of flow were lessened after the construction of the nature-like fish bypass. Three of the four years in which the nature-like fish bypass has been in place, have experienced some of the highest flows of the past 12 years, which might have coincidentally reduced mortality at this dam. At the upper dams, Guilford Dam, and Dover Dam caused relatively high mortality. Flow also had an effect on survival at these two dams (with higher probability of mortality at lower flows). Brownsmill Dam has consistently had high probability of survival, comparable with survival in free flowing reaches. This dam has the highest survival of all dams in the system. Our inability to detect an effect of flow on survival in this dam, is likely because most years' survival was perfect or near perfect. While most of the focus of this work was looking at specific areas of the river, it's important to look at the whole experience migrating smolts face in this river.

The experience from migrating smolts in this river changed dramatically from year to year. ATIN from the release site Penobscot River varied from a median of 170 hours in 2012 to over 300 hours in 2017. Considering that delays at Guilford and Brownsmill dams were consistently over 48 hours for the slowest 25% of smolts, these 48 hours might represent over 20% of the total time spent in this river. If we consider that fish had to go through four dams, it is then 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 varied from 0.5 to about 0.85 with great year to year variability. This year to year variability was best explained by flows and changes to the Howland Dam downstream passage. Despite the high year-to-year variation, a considerable proportion of the migrating fish did successfully reach Milford Dam. **It is reasonable to assert that individuals that successfully reach the lower river may be affected by their experiences in the Piscataquis River later in the migration. In particular, as temperatures may increase, delays and upstream experience might have a profound effect on survival.**

Most of the focus of the effects of dams on smolts has been on immediate mortality, however, the latent effects of dams, and the dam-caused-delays can be substantial. Our best-fitting model suggests a difference in survival in Howland Dam, depending on release sites, with lower survival for fish that had to pass multiple dams before arriving to Howland Dam. These differences might be due to an additive effect of passing multiple or delays (Castro-Santos and Haro 2003; Ferguson et al. 2006; Nyqvist et al. 2017). There is evidence in other populations that passing multiple dams may reduce survival downstream in salmonids (Ferguson et al. 2006; Stich et al. 2015a, 2015b; Faulkner et al. 2019), and 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 fresh- 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, as well as physiological preparedness, and the timing of estuary entrance which affect 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 get delayed for several days by the time they get to the Penobscot River. Individuals that successfully reach the Penobscot River, still have ~ 99 rkms to get to the Bay, and may experience 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) delays might cause a mismatch between the 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 an effect 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, as smolt survival is low in most systems, and most systems with Atlantic Salmon contain multiple dams, understanding the effects of dams on delays and the effects of these delays on survival can help understand the factors that affect smolt migration.

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TABLE 1

Summary of the four dams found in the Piscataquis River. NID-ID represents the number of the dam in the National Inventory of Dams by the Army Corps of Engineers

Dam	NID-ID	RKM	Hydropower capacity (Mw)	Dam Height (m)	Dam length (m)	Reach length (rkm)	Downstream fish passage
Howland	ME00155	99.1	0	5.19	220	1.4	Bypass
Brownsmill	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	3.66	51.51	1.7	None

TABLE 2

Data summary for acoustically and radio tagged fish in the Piscataquis River from 2005-2019, showing year, release site, type of tag, and number of fish tagged and released (n). An asterisk (*) represents nature-reared fish. Fork length and mass present the standard deviation.

Year	Release site	tag type	n	Fork Length	Mass
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 Tailrace	Acoustic	75	194 ± 11.1	77.8 ± 12.1
2017	Abbot	Acoustic	80	190 ± 10.8	70.8 ± 12.7
2017	Browns Mill Tailrace	Acoustic	80	187 ± 9.3	67.9 ± 10
2018	Abbot	Acoustic	74	191 ± 10.4	77.5 ± 13.8
2018	Browns Mill 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 Tailrace	Acoustic	75	180.7 ± 10.1	61.9 ± 10.7
2019	Dover Tailrace	Radio	75	179.7 ± 10.6	60.1 ± 11.4
TOTAL			1611		

TABLE 3. Model selection results for delays in the four dams of the Piscataquis River, Maine. All represent generalized linear mixed effects models explaining delays (log-normal distributed). All models included year as a random effect. The model represented by ~1 is a constant model in which a single parameter (intercept) is estimated.

Model	AICc	ΔAIC
Dam + Flow	6647.771	0
Dam + Flow^2	6650.737	2.966
Dams	6672.55	24.779
Flow	7258.562	>100
Flow^2	7258.62	>100
1	7315.313	>100

TABLE 4. Model selection results for the multi-year CJS survival models for acoustically-tagged Atlantic Salmon smolts. The four top models are shown, as well as the top two models

without flow as a variable. The parameters estimated in the CJS model were corrected for differing interval sizes, and were ϕ_{rkm} (apparent survival per rkm) and p (probability of detection). Y represents year, rt represents “reach type” (i.e. four dams, and “free flowing”), nlfb represents a term that was only applied to Howland Dam, and represents the presence of the nature-like fish bypass

ϕ	**p**	**npar**	**AIC**	**ΔAIC**	**wAIC**	**Deviance**
~Y + rt + release + flow* + nlfb	~Y × reach + release	161	7964.1	0	0.5	7628.0
~Y + rt + release + flow + nlfb	~Y × reach + release	160	7961.9	2.2	0.49	7628.0
~Y + rt + release + flow* + nlfb	~Y × reach × release	176	8034	72.1	<0.01	7720.0
~Y + rt + release + flow + nlfb	~Y × reach × release	177	8034.1	74.3	<0.01	7628.0
~Y + reach + release	~Y × reach × release	256	9224.7	>100	<0.01	7212.2
~Y × reach + release	~Y × reach + release	294	9054.2	>100	<0.01	7724.2

*flow effect only on Guilford, Dover, and Howland Dams

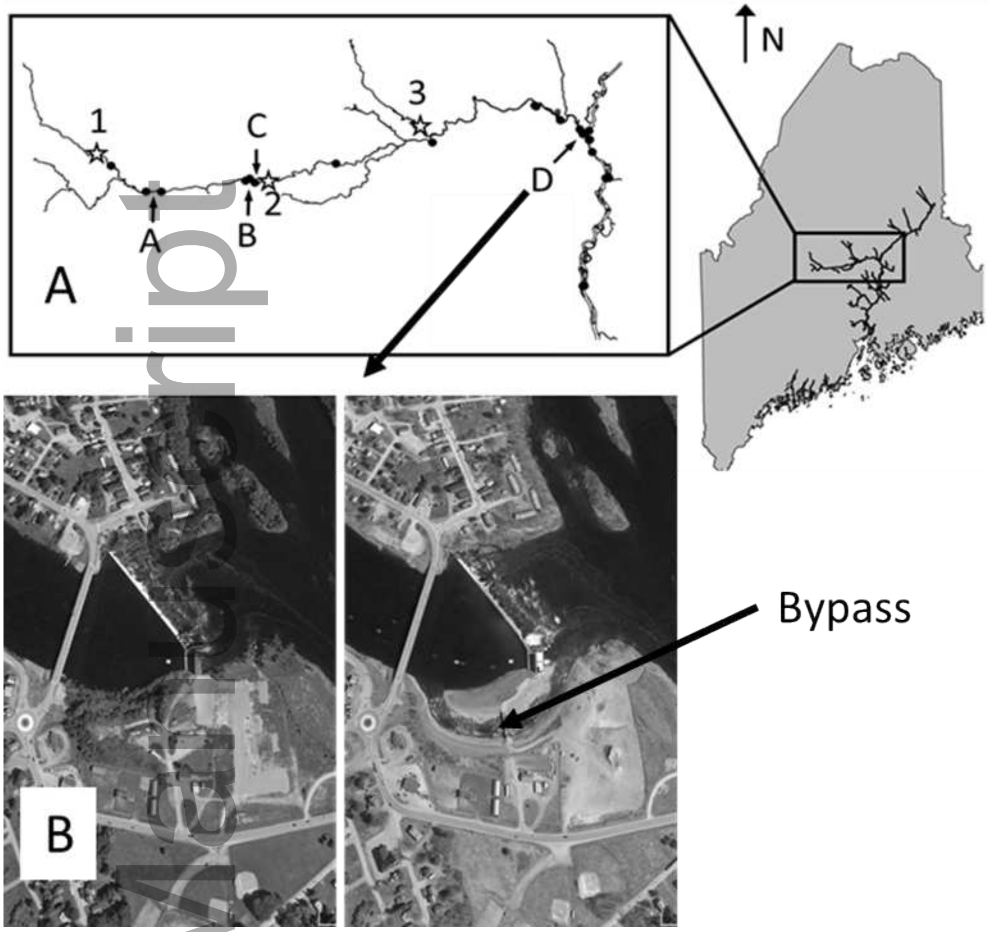

FIGURE 1

A) Map of the Piscataquis River, showing location in the state of Maine (right of map), locations of acoustic receivers (black circles), locations of dams (arrows), and release sites (stars). A represents Guilford Dam, B represents Dover Dam, C represents Brownsmill Dam and D represents Howland Dam. Howland Dam is located right at the confluence of the Piscataquis River with the Penobscot River. For the release sites 1 represents Abbot, 2 represents Brownsmill Dam Tailrace, and 3 represents Milo. B) Howland Dam, before and after the nature-like fish bypass was built. Before picture image was taken on 8/23/2013, the after picture was taken on 4/28/2016. Images Google © 2019.

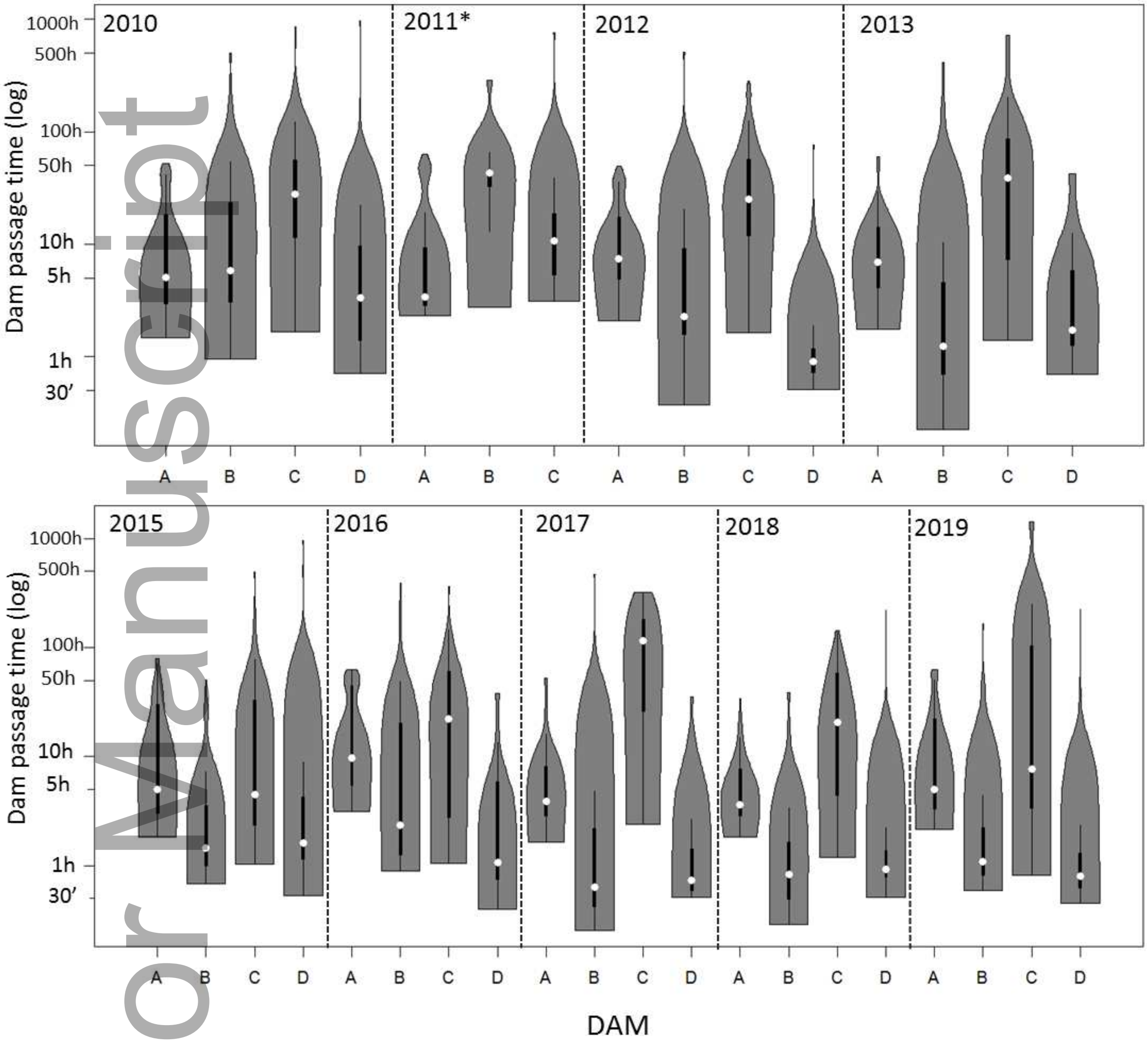

FIGURE 2

Dam passage time for the four dams in the Piscataquis River for 9 years. Y axis is time in log-scale, and the X axis represents the dams: A) Guilford Dam, B) Dover Dam, C) Brownsmill Dam, and D) Howland Dam. For 2011 we only estimated delay times for the three most upstream dams. During 2014, there were not enough detections in the Piscataquis to estimate delay times.

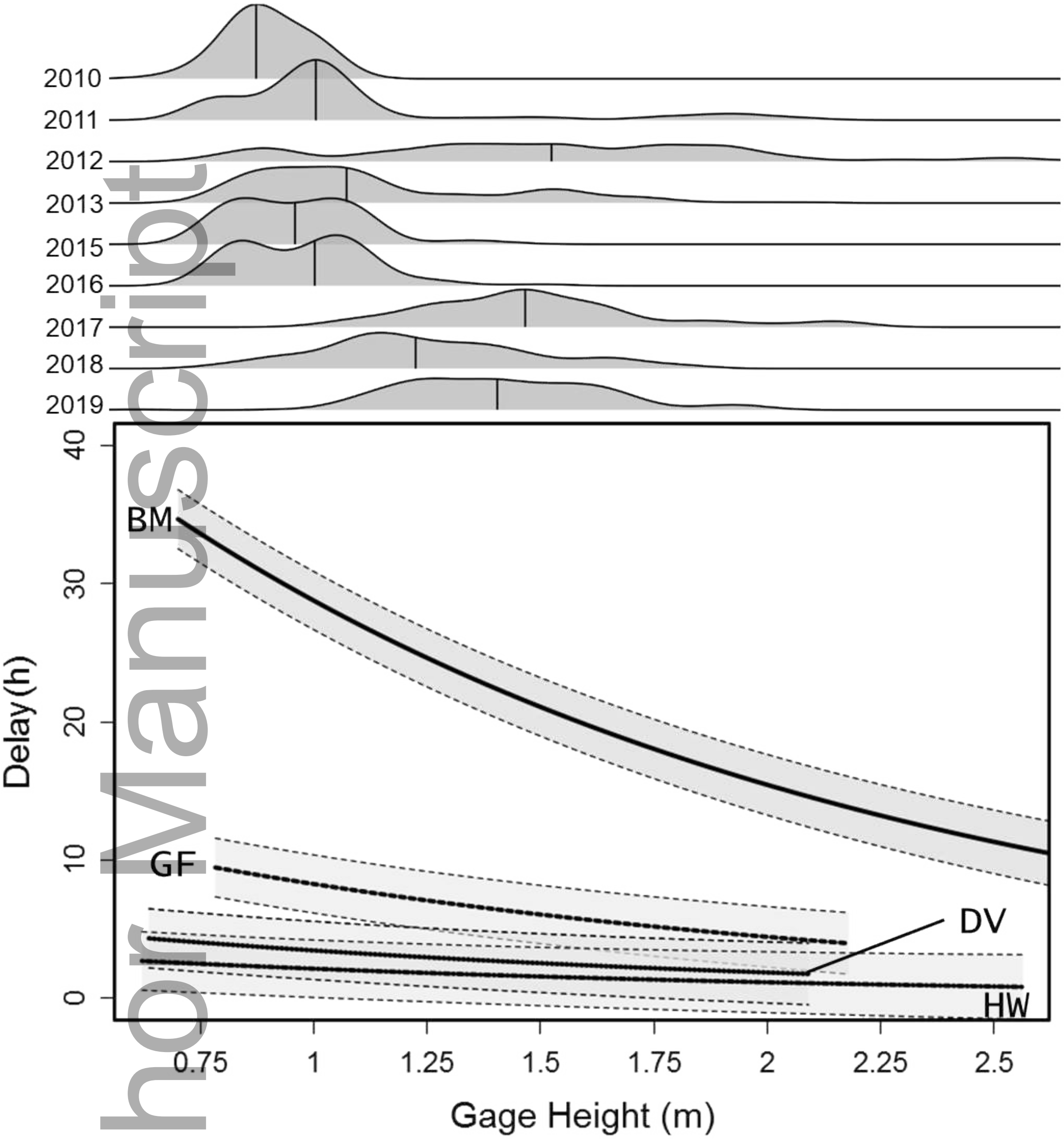

FIGURE 3

Effects of flow (Gage height used as proxy) experienced by downstream migrating smolts passing through Guilford (GF), Dover (DV), Brownsmill (BM), and Howland Dam (HW) on delays based on the best fitting model: delays ~ dams + flow + (1|year). The upper panel represents the distribution of the data for each year. As gage height data was obtained for each individual at the moment of passing each dam, individuals might 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 for each of the four dams. Confidence envelope represents standard errors.

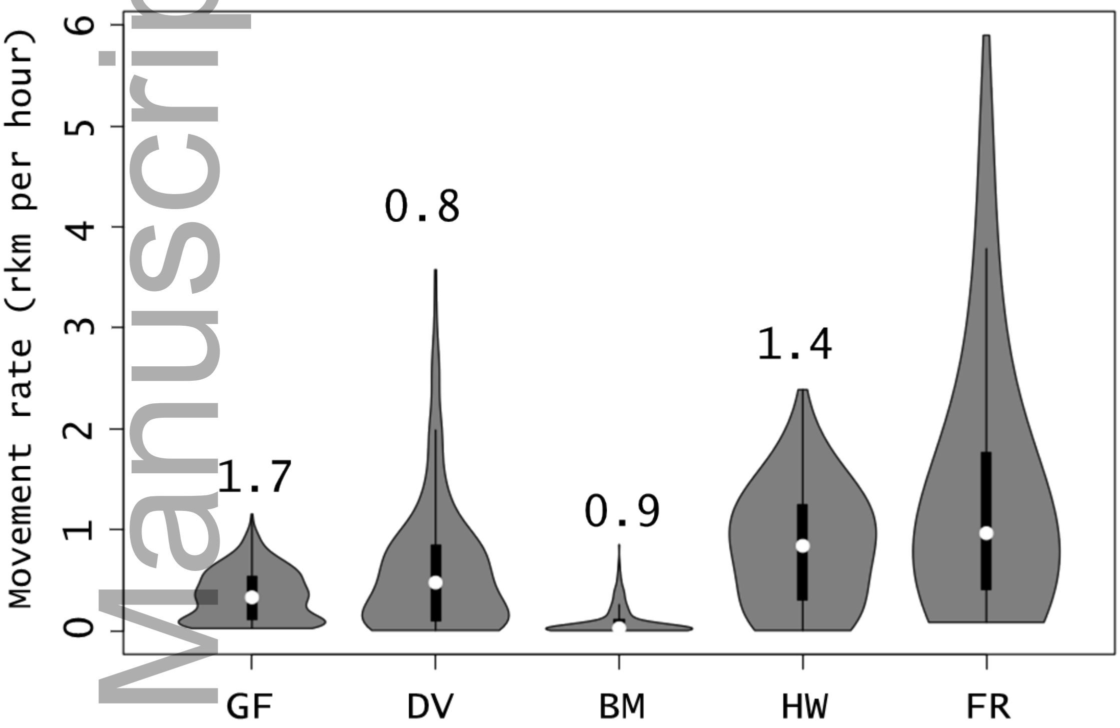

FIGURE 4

Movement rate through each one of the 4 dams in the Piscataquis River (rkm × h^{-1}), and a "free-flowing reach" (a single ~20 rkm unimpounded section of river). The numbers above of the violin plots represent the reach length for each of the dams.

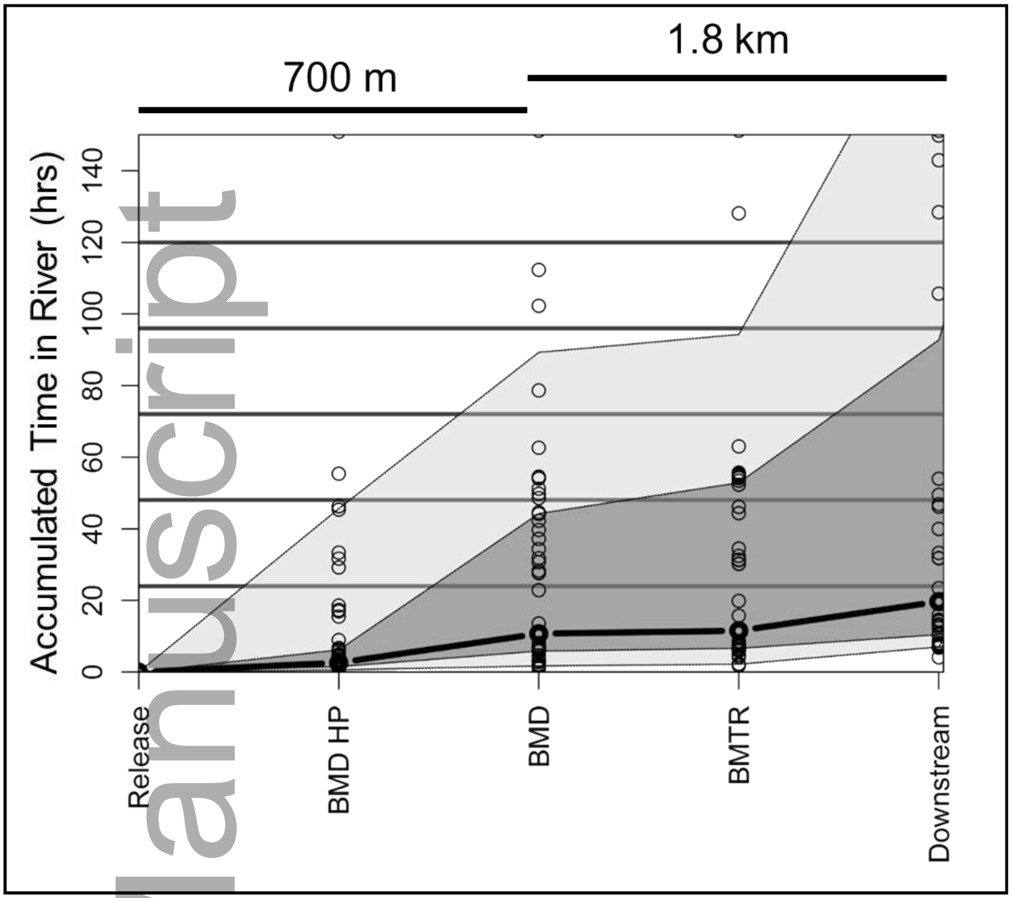

FIGURE 5

Delays for radio-tagged Atlantic Salmon smolts released in the Piscataquis River. Accumulated time in river from release ~700 meters upstream of Brownsmill Dam, to radio antennas placed 1.8 rkms downstream of the dam (2.5 rkms total). The black line represents the median accumulated time in river, while the shaded regions represent the 25-75th percentile, and the 5-95th percentiles. BMD HP represents the headpond, BMD represents either detections at the Brownsmill Dam spillway or powerhouse canal, and BMTR represents the tailrace. The horizontal lines represent each iteration of 24 hours.

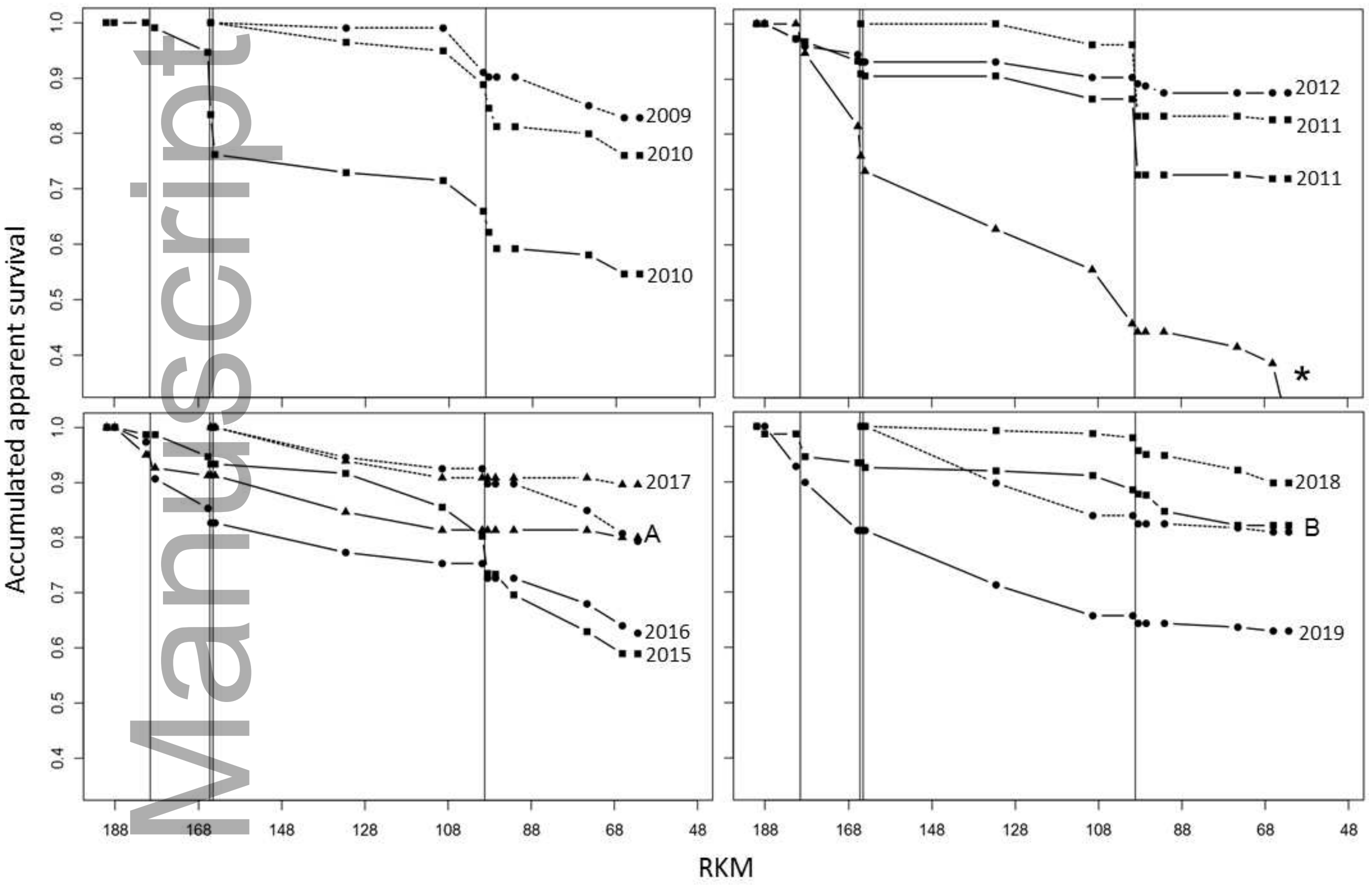

FIGURE 6.

Accumulated apparent survival (ϕ) from 2009 to 2019 (except 2014) using the best ranking model where survival is explained by year, reach type, release, and flow.. Accumulated survival was obtained using the ϕ point estimates. Continuous lines represent releases in Abbot, rkm 188. Broken lines represent releases in either Milo, or Browns Mill Tailrace (in both cases, the releases were downstream of Brownsmill Dam). A represents 2017 (Abbot release), and 2016 (Brownsmill Tailrace release), while B represents 2018 (Abbot release), and 2019 (Brownsmill Tailrace release. Survival in 2013 (*) for the last point estimate was 0.29, and is not shown in graph.

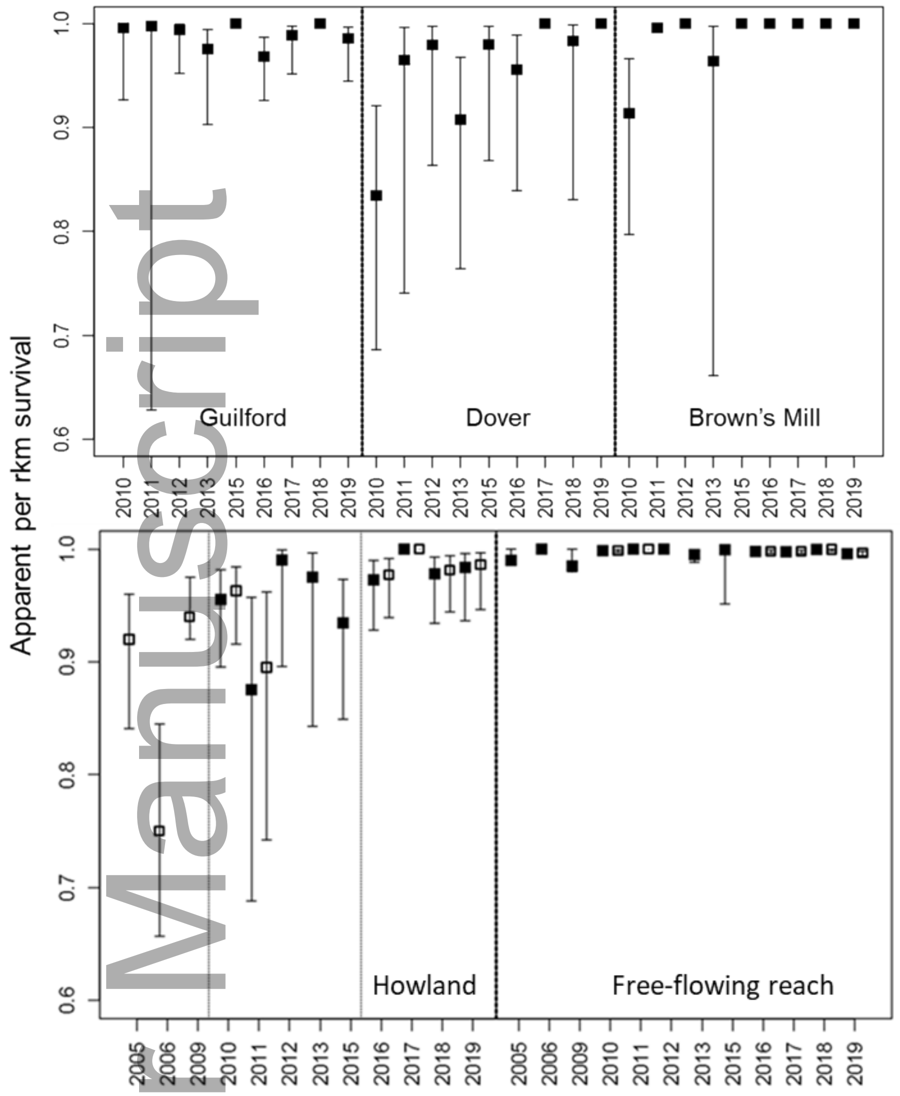

FIGURE 7.

Annual per rkm survival (ϕ_{rkm}) for each of the four dams in the system, and for a free flowing reach for 12 years using the best ranking model where survival is explained by year, reach type, release, and flow. Error bar represent standard errors. The black squares represent the Abbot releases, while white squares represent releases in either Milo, or Brownsmill Tailrace. The vertical lines for Howland represent the changes in the system (before changes, turbine shutdowns, and the nature-like fish bypass).

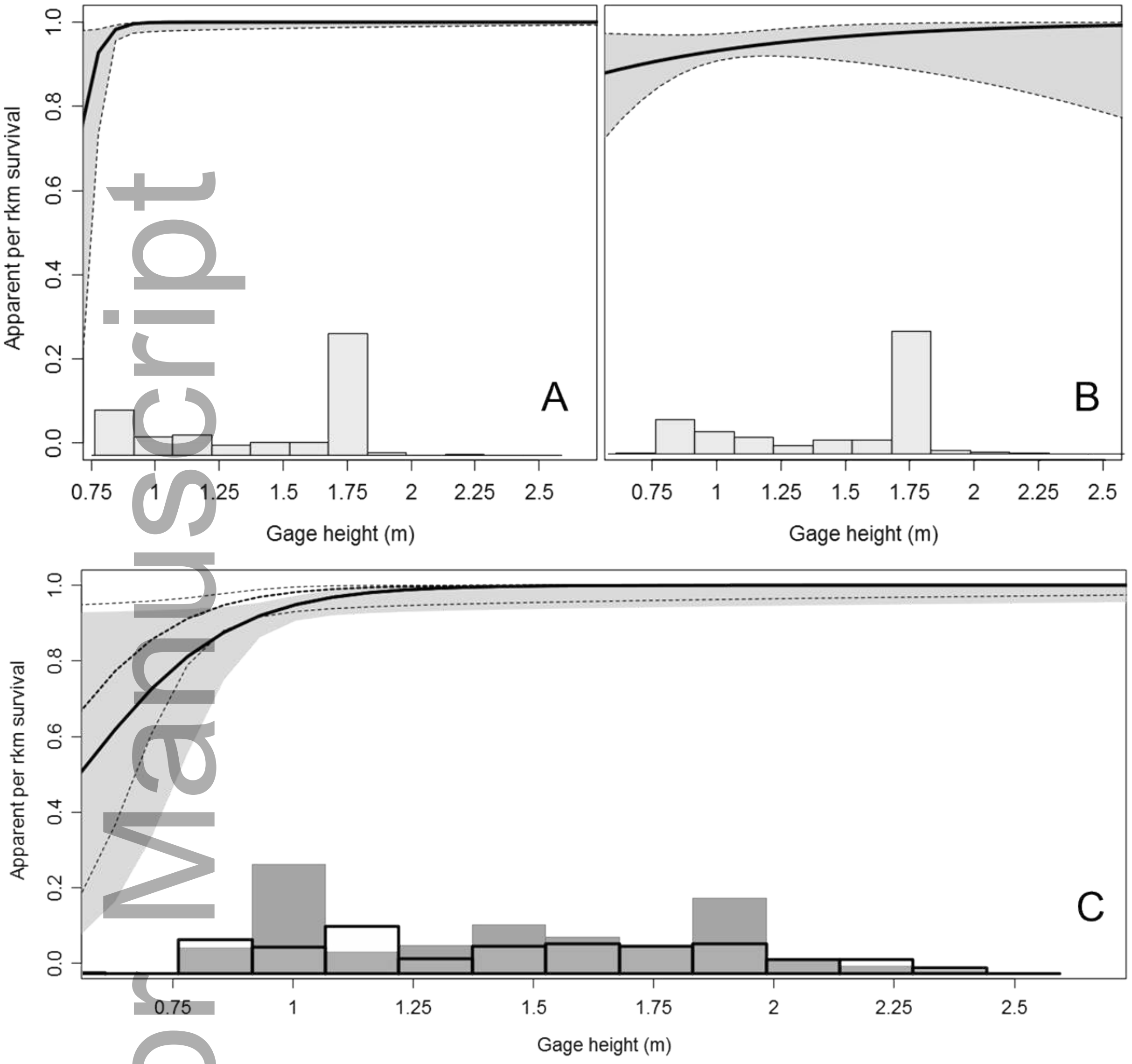

FIGURE 8

Relationship between gage height (meters), and apparent per rkm survival (ϕ_{rkm}) for the three dams in which there was an effect (Guilford, Dover, and Howland Dam) 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 95% confidence interval. The histogram represents the experienced gage heights by migrating individuals. For c) Howland Dam, the solid line and polygon represent the apparent survival and 95% confidence interval for the years before the nature-like fish bypass was built, and the dashed lines represent the apparent survival and 95% confidence interval for the years after the nature-like fish bypass was built. The gray histogram represents the gage heights experienced on years before the nature-like fish bypass was built, and the white histogram represents the same for years after the bypass was built.