

Effects of dam-induced delays on system-wide survival of Atlantic salmon smolts during high-flow, high-survival years in the Penobscot River, Maine, USA

Alejandro Molina-Moctezuma ^a, Daniel S. Stich^b, and Joseph D. Zydlewski^{a,c}

^aDepartment of Wildlife, Fisheries, and Conservation Biology, University of Maine, Nutting Hall, University of Maine, Orono, ME 04469, USA; ^bDepartment of Biology, SUNY Oneonta, 108 Ravine Parkway, NY 13820, USA; ^cMaine Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, Nutting Hall, University of Maine, Orono, ME 04469, USA

Corresponding author: Alejandro Molina-Moctezuma (email: molina28@msu.edu)

Abstract

System-wide survival of hatchery-reared Atlantic salmon (*Salmo salar*) smolts was evaluated (2017–2019) in the Penobscot River and compared to survival estimates from previous years that spanned major changes (2005–2016). This system was transformed through two dam removals in 2012 and construction of a nature-like passage structure at a third. The main stem had three dams (five prior to 2012), while the main tributary had four dams (one with the new nature-like passage). We estimated survival using acoustic telemetry mark–recapture ($n = 1482$) from 2017 to 2019. Six release sites and two release dates were included to assess system-wide survival. Survival from 2017 to 2019 was higher than previous years, with total cumulative survival > 0.75 , independently of year and release sites, compared to survival < 0.5 in previous years. These years coincided with exceptional high flows not seen previously. We found an effect of delays on survival, longer delays associated with lower survival. Overall, survival in these years increased in all reaches relative to previous years except for one dam, Weldon Dam, which was a site of sustained high mortality.

Key words: survival, dams, migration, salmon, fish movement

Résumé

La survie à l'échelle du réseau de smolts de saumon atlantique (*Salmo salar*) élevés en éclosérie a été évaluée (2017–2019) dans le fleuve Penobscot et comparée à des estimations de la survie pour des années antérieures marquées par des changements majeurs (2005–2016). Ce système a été transformé par le retrait de deux barrages en 2012 et la construction d'une passe d'aspect naturel à un troisième barrage. Le cours principal comptait trois barrages (cinq avant 2012), alors que l'affluent principal en comptait quatre (dont un doté de la nouvelle passe d'aspect naturel). Nous avons estimé la survie sur la base d'étiquettes de télémétrie acoustique récupérées ($n = 1482$) de 2017 à 2019. Six lieux de lâcher et deux dates de lâcher ont été inclus pour évaluer la survie à l'échelle du réseau. La survie de 2017 à 2019 était plus élevée que durant les années précédentes, soit une survie cumulative totale de $> 0,75$, indépendamment de l'année et du lieu du lâcher, comparativement à une survie de $< 0,5$ les années précédentes. Ces années coïncidaient avec des débits exceptionnellement forts non observés antérieurement. Nous avons relevé un effet des retards sur la survie, les retards plus longs étant associés à une survie moindre. Dans l'ensemble, la survie durant ces années a augmenté dans tous les tronçons par rapport aux années précédentes, sauf pour un barrage, le barrage Weldon, qui était le site d'une mortalité élevée soutenue. [Traduit par la Rédaction]

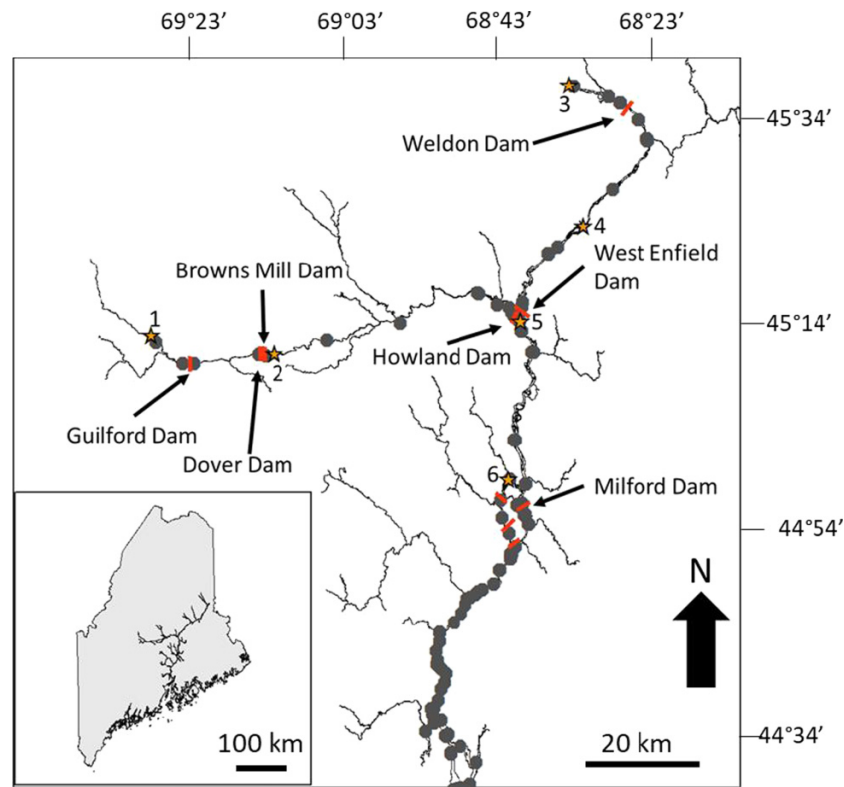
Mots-clés : survie, barrages, migration, saumon, déplacement du poisson

Introduction

The downstream migration of Atlantic salmon (*Salmo salar*) juveniles is a critical stage in their life cycle. During this stage, individuals undergo a series of morphological, physiological, and behavioral changes that prepare them for migration and life at sea (McCormick et al. 1998; Klemetsen et al. 2003). These changes include a transition toward a slimmer morphometry, which allows fish to be more hydrody-

namic (Taylor and McPhail 1985), as well as a silvery color providing camouflage that aids in avoiding predators (Evans et al. 2014). Physiological changes include upregulation of hypo-osmoregulatory mechanisms, including an increase in activity of the gill sodium–potassium ATPase (NKA) enzyme (McCormick et al. 2013), which facilitates transition from fresh to salt water. Despite the developmental changes that prepare individuals for their migration and life at sea, this

Fig. 1. Current map projection of the Penobscot River, Maine, USA, depicting locations of dams, acoustic receiver stations, and release sites for acoustically tagged Atlantic salmon smolts. Red lines represent dams. Gray circles represent the acoustic receiver stations, and the stars and numbers represent the release sites. The three dams not labeled in the Stillwater Branch (upstream to downstream) are Gillman Falls, Stillwater Dam, and Orono Dam. Map projection: NAD83.



migration is a period of high mortality. Both wild and hatchery-reared smolts face a series of new challenging conditions such as 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 have been demonstrated to increase their mortality (National Research Council (U.S.) 2004; Keefer et al. 2012; Norrgård et al. 2013).

The Penobscot River is the largest river in Maine, USA, and hosts the largest population of the endangered Atlantic salmon (*Salmo salar*) in the USA. 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). Limited wild spawning of Atlantic salmon occurs, but there is extensive stocking of eggs, fry, and smolts in the system. Therefore, most of the juveniles in the system are hatchery sourced, even when wild-reared (i.e., egg or fry stocked). Peak seaward migration of wild and wild-reared smolts generally occurs during late April and early May each year, as does the release of hatchery-reared smolts. Survival of these juveniles in the Penobscot River has been studied since 2005 using acoustic telemetry, and several dams have been identified as areas of high risk (Holbrook et al. 2011; Stich et al. 2014, 2015a).

The Penobscot River has changed significantly over the last decade. In 2004, the Penobscot River Restoration Project (PRRP) was initiated, with the goal of balancing restored ac-

cess to spawning habitat for diadromous fishes with continued hydropower production. Efforts from this project included decommissioning three dams in 2012 and upgrading fish passage at four dams, while increasing power generation at three remaining dams (in 2013). As part of this system-wide effort, a nature-like fish bypass for upstream and downstream movement of fish was also built during 2015 at the confluence of the Piscataquis River with the Penobscot River (Fig. 1; Opperman et al. 2011). As a result, survival of migrating smolts in this tributary has increased (Molina-Moctezuma et al. 2021). The project involved removing two dams in the mainstem of the river (in 2012 and 2013; previously the two downstream-most dams). Downstream passage was upgraded with a nature-like fish bypass at Howland Dam, right at the confluence of the Piscataquis River (the main tributary of the Penobscot) and the Penobscot River. Power production was increased at the dams in the Stillwater Branch, a branch that constitutes an alternative route around the downstream-most dam and that has relative low use (~10% of individuals use this route; Stich et al. 2015a). Despite the changes in the Penobscot River, smolt mortality has remained high at dams, in particular, Weldon Dam, Howland Dam, and Milford Dam (Holbrook et al. 2011; Stich et al. 2014, 2015a; Molina-Moctezuma et al. 2021; Fig. 1).

Several individual and environmental factors have been identified to affect survival of migrating smolts multiple river systems, including origin (Hvidsten and Lund 1988; Stich

et al. 2015a), length and condition (Armstrong et al. 2018) and physiological development (using gill NKA activity; Stich et al. 2015a), flow or discharge (Jensen and Johnsen 1999), and dam-caused delays, defined as a significant slower rate in movement in sections of river with a dam, compared to free-flowing sections of the river; (Lawrence et al. 2016; Molina-Moctezuma et al. 2021). Increased fish mortality at dams may be caused by higher exposure to predators (Poe et al. 1991; Caudill et al. 2007; Keefer et al. 2012) fish that are delayed at dams, but ultimately “successfully” pass the dams also exhibit higher mortality rates during the rest of their migrations (Molina-Moctezuma et al. 2021). Multiple reasons may cause decreased probability of survival for fish that got delayed at dams, smolts may be injured or otherwise compromised at dams, slowing their migration or causing delayed (latent) mortality in reaches downstream of a dam (Music et al. 2010; Nieland et al. 2015) and even later, when moving through the estuary (Stich et al. 2015c). Passage delays can cause important energetic impacts (Rubenstein 2021), which may in turn result in lower survival later on. In general, the mechanism of dam-related mortalities after passage remains an often unaccounted for and poorly understood phenomenon. There is a lack of studies across systems, with multiple release sites that can account for both (1) dam-induced mortality and (2) delay-induced mortality. Furthermore, there is a lack of understanding on whether any dam-caused delay may increase latent mortality, or if specifics dam in a system can cause higher mortality than others.

Dam-caused delays are affected by factors that can vary by individual (e.g., fish length), by dam, and by environmental factors, in particular discharge, with low discharge exacerbating delay-induced mortality. Low discharge is generally associated with low survival at dams (Stich et al. 2014, 2015a); thus, in years with reduced discharge, out-migrating smolts tend to have lower overall (or system-wide) survival probability. Moreover, low discharge has a clear and direct effect in slowing downstream migration. Fish that approach a dam under low discharge conditions experience considerably longer delays (i.e., time spent upstream of a dam before successfully passing it; Molina-Moctezuma et al. 2021). So, low discharge causes an increase in both mortality at dams and higher delay-induced mortality.

As reported in Molina-Moctezuma et al. (2021), from 2005 through 2015, flow conditions in the Penobscot River only had modest variation among years. During this time, cumulative survival of smolts in the Penobscot River was consistently low, remaining a critical impediment to restoration. Mean cumulative survival is only 0.25 for individuals released into the upper Penobscot River. Factors other than discharge also shape the probability of successful ocean entry. The goal of this study was to conduct a system-wide assessment of Atlantic salmon smolt survival in the Penobscot River after multiple changes associated with the PRRP were implemented in the system and compare them to the survival in previous years. To do this, we used acoustic telemetry data from 1482 fish tagged 2016–2019 to estimate apparent survival while accounting for imperfect detection using mark-recapture methods. In particular, we were able to have multiple release sites, and release times in 2017, 2018, and 2019,

thus allowing us to obtain system-wide survival for these years, and to explore the effects that delays and dams have on survival throughout the system. By chance, in 2017, 2018, and 2019, the spring discharge in the Penobscot River was highly favorable for migrating smolts, which causes high survival. Given the observed flow conditions, we were able to estimate system-wide survival, and the effects of dam-induced delays on survival of Atlantic salmon smolts during high-flow, high-survival years (i.e., during years with ideal environmental conditions). We compared our results with results produced in previous studies in this system.

Methods

Study site

The Penobscot River (Fig. 1) changed dramatically from the inception of the PRRP in 2004, through 2016, when it was completed. Specifically, Great Works, river kilometre (rkm) 59, and Veazie (rkm 48) dams were removed in 2012 and 2013, respectively (they were the two downstream-most dams, results are not presented for these dams, and these dams are not shown in any figures). Downstream passage was upgraded at Howland, Stillwater, and Orono Dams during those years (Fig. 1). A nature-like fish bypass channel was completed in fall 2015 at Howland Dam. Howland Dam has ceased power production but will remain in place to allow for continued access to the Howland boat launch.

Despite the changes in the system, multiple dams that influence the downstream migration of smolts are still present. Depending on where fish are stocked, they may encounter up to seven dams in the system. The dams in the system include four dams in the Piscataquis River: Guilford Dam, Dover Dam, Browns Mill Dam, and Howland Dam (rkms 179.5, 165.3, 164.5, and 99.5), and three dams in the Penobscot River: Weldon Dam, West Enfield Dam, and Milford Dam (rkms 147, 99.9, and 61). All the dams, except for Howland Dam, were operational. The confluence of the Piscataquis River and the Penobscot River occurs at rkm 99 (Fig. 1). The Stillwater Branch diverges from the mainstem Penobscot River at rkm 63, and the two converge again at rkm 51. Smolts using this path must pass the three dams: Gillman Falls, Stillwater, and Orono present in the 12 km Stillwater Branch.

Acoustic telemetry array

Each year from 2016 to 2019, an acoustic telemetry array consisting of up to 150 Vemco acoustic receivers (VR2W; Innovasea; innovasea.com) was deployed in the Penobscot River after ice-out, generally early April. Each receiver contained an omnidirectional hydrophone scanning continuously at 69 kHz. In some cases, multiple receivers were deployed across the river to increase detection probability. Detections from these receivers were pooled and treated as a single station. Receiver stations were deployed throughout the river, and the maximum distance between receiver stations was 15 rkms. Receivers were deployed upstream and downstream of each of the dams studied (within rkm 1), thereby conferring information regarding dam approach and passage

Table 1. Number of acoustically tagged Atlantic salmon smolts released at each of six sites 2016–2019 in the Piscataquis and Penobscot rivers, Maine, USA.

Year	Piscataquis		Penobscot				Total
	1. Abbot	2. Browns Mill	3. Weldon	4. Mattawamkeag	5. Confluence	6. Stillwater	
2016	75	75	—	—	—	—	150
2017	80	80	80	80	80	50	450
2018	80	80	80	80	80	50	450
2019	77	77	78	75	75	50	432

Table 2. Mean data for all release groups from 2016 to 2019.

Year	Release	Gill NKA	FL (mm)	FL range (mm)	Mass (g)	Mass range (g)
2016	Early	4.04 (1.73)	192.2 (10.6)	162–216	76.6 (12.7)	45.8–114.2
2017	Early	3.03 (1.67)	185.3 (9.2)	165–217	67.2 (10.7)	46.3–104
	Late	3.61 (2.02)	189.7 (10.4)	160–214	69.1 (11.8)	46.5–109
2018	Early	3.83 (2.13)	190.2 (9.8)	169–220	76.8 (12.8)	52.3–119.2
	Late	4.67 (2.67)	190.1 (9.2)	169–225	74.3 (12.7)	52.9–129.9
2019	Early	3.95 (1.49)	180.1 (10.2)	160–209	61.4 (12.7)	42.0–98.8

Note: Data include mean gill sodium-potassium ATPase (NKA) enzyme, mean fork length (FL, mm), FL range (mm), mean mass (g), and mass range (g). Numbers in parentheses represent standard deviations.

(Fig. 1). In 2016, the array did not include any receivers upstream of West Enfield Dam.

Tagging and releases

Atlantic salmon smolts (natural and wild reared) have been tagged and released in the Penobscot River for survival analysis since 2005. From 2005 to 2015, releases were described in Holbrook et al. (2011) and Stich et al. (2015c). To compare survival estimates from these studies with survival under the new conditions (2016–2019), hatchery-reared Atlantic salmon smolts ($n = 1482$) were acoustically tagged and released into the Penobscot River (Fig. 1). The number of fish tagged and released varied among years and sites (Table 1). There were only two release sites in 2016, both in the Piscataquis River: (1) Abbot (upstream of all four dams in the Piscataquis River) and (2) Browns Mill (downstream of Brown's Mill Dam, and upstream of Howland Dam). From 2017 to 2019, there were six release sites: two in the Piscataquis River, three in the main stem Penobscot River, and one in the Stillwater Branch, which allowed us to estimate system-wide survival these years. The Piscataquis River release sites were the same as previously described: (1) Abbot and (2) Browns Mill; and the Penobscot releases were (3) Weldon (upstream of Weldon Dam), (4) Mattawamkeag (downstream of Weldon Dam and upstream of West Enfield Dam), (5) Confluence (at the confluence of the Penobscot and Stillwater Rivers), and the (6) Stillwater Branch (immediately downstream of Gillman Falls; Fig. 1).

All fish were hatched and reared at the U.S. Fish and Wildlife Service, Green Lake National Fish Hatchery. Smolts were anesthetized using a 100 mg·L⁻¹ solution of MS-222 (buffered with 20 mmol·L⁻¹ NaHCO₃; pH = 7.0), and fork length (mm) and mass (g) were measured (Table 2). All fish had a fork length higher than 160 mm and a mass higher than 42.0 g. A nonlethal gill biopsy (4–6 filaments) was

taken from the front, left gill arch of each fish prior to tagging for gill NKA activity measurement. Gill biopsies were quick frozen using dry ice, and the individual biopsies were stored at –80 °C in 100 µL SEI buffer (250 mmol·L⁻¹ sucrose, 10 mmol·L⁻¹ Na₂-EDTA, and 50 m·mol·L⁻¹ imidazole). A small (1 cm) incision was made offset from the ventral line approximately 1 cm posterior to the pectoral-fin girdle. An acoustic tag (Vemco V9-6 L) was inserted intraperitoneally, and the incision was closed with two simple, interrupted knots using absorbable vicryl sutures (Ethicon 4-0 RB-1; www.ethicon.com). The tags were 21 mm long, 1.6 g in water, 2.9 g in air, and were programmed with a nominal delay of 30 s for 33 days, and then a nominal delay of 80 seconds for the rest of the battery life. After surgery, fish were transferred to a recovery tank. Fish recovered for at least 3 h and were then checked for full recovery. Following full recovery, fish were transported to their release site using isolated transport tank, with density lower than one fish per two gallons. Fish were released immediately after arrival, river and hatchery temperature were similar, and only the tagged fish cohort was released (no untagged fish). Transport time to the release site varied between 1 and 2 h. These methods have yielded high postsurgery and postrelease survival (over 99%) in previous years (Holbrook et al. 2011; Stich et al. 2015a).

Discharge data

Discharge was obtained for years 2010–2019 using from the West Enfield Gage 01034500 (USGS 2019). A subset of the discharge data was obtained to include dates from 24 April to 15 May each year (the smolt migration “window”; McCormick 1994). This time interval spanned all releases and the estuary entry (passing the last dam, Milford Dam) by at least 90% of the individuals in all years.

Gill NKA assay

Gill NKA (enzyme code 3.6.3.9; IUBM 1992) activity (expressed as $\mu\text{mol ADP} \cdot (\text{mg protein})^{-1} \cdot \text{h}^{-1}$) was analyzed using the method of McCormick (1993). Concentration of NADH at 25 °C and 340 nm was used to measure kinetic rate of ouabain-inhibitable ATP hydrolysis. Protein concentration in gill samples was determined using the bicinchoninic acid method (Smith et al. 1985) with a protein quantitative assay (Pierce 23 225; thermofisher.com). Gill samples from each fish were analyzed in triplicate for gill NKA activity and protein concentration.

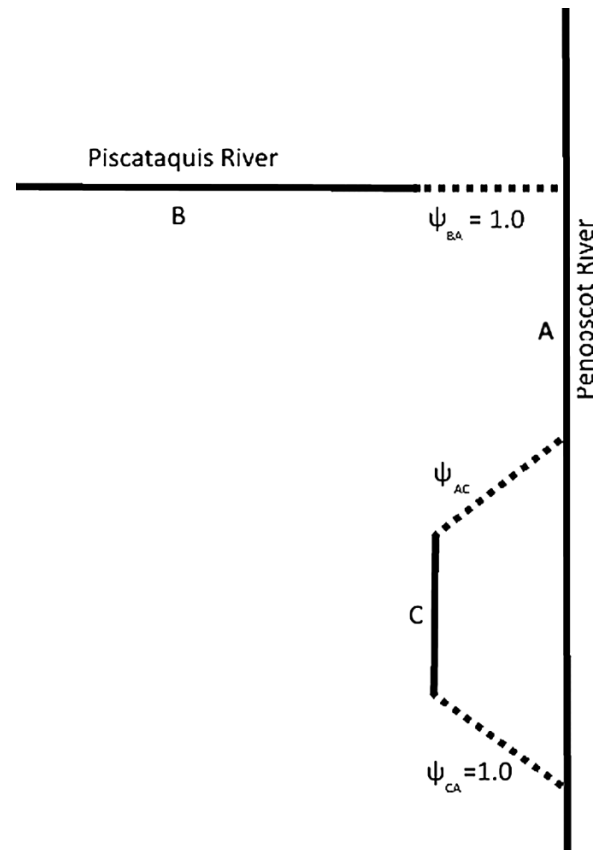
Survival and path choice

Spatially explicit capture histories were developed for each tagged individual using detections at the acoustic receivers during the fish downstream migration. Each acoustic receiver station (detections from a single receiver or pooled from multiple co-located receivers) were interpreted as a “recapture occasion” during the smolt migration. Receiver locations depended on river access and they were not evenly spaced; however, for each dam, receivers were placed within rkm 1 upstream of a dam and within rkm 1 downstream of a dam. Distance between receivers varied from rkms 2 to 15 (Fig. 1). To account for different potential path choices during downstream, different “states” were defined. Detections in the mainstem Penobscot River were defined as occurring in state “A”, detections in the Piscataquis River defined as state “B”, and detections in the Stillwater Branch were defined as state “C”. This allowed us to independently estimate survival at in each branch, as well as estimate the probability of individuals migrating through either the Stillwater Branch or through the Penobscot River (i.e., the probability that an individual will go from “A” to “C”, represented, by ψ_{AC}). All other transitions were either fixed to 0, as they were impossible under the assumption of unidirectional downstream migration (e.g., probability of transitioning from the Stillwater Branch to the Piscataquis River) or fixed to 1 if only one outcome is possible (e.g., probability of transition from the Piscataquis River to the Penobscot River; Fig. 2). Survival was estimated using multistate mark-recapture models (Lebreton et al. 1992). While states are generally presented as “stratums” or “states” in MS models, we present them as “river”, as they represent different “rivers” of the system.

Model selection and estimation of survival

As Atlantic salmon smolts must migrate to the ocean to complete their life cycle, the migration was assumed to be one-dimensional (river) and unidirectional (i.e., fish only move downstream). Therefore, we used models and methods that were normally used for survival through time and were used to estimate survival through space. Therefore, instead of using “time” as a parameter, we used “reach”, as we estimated survival through reaches. Models were developed in program MARK (White and Burnham 1999), through the package RMark (Laake 2013) in program R (R Core Team 2019). Models were then compared using corrected Akaike information criterion (AIC_c ; White and Burnham 1999), and using the best performing model, we estimated survival (S),

Fig. 2. Diagram of model states within the Penobscot River, Maine, USA, with the three transitional areas (ψ) in the spatially explicit multistate mark-recapture model used to estimate apparent survival of acoustically tagged Atlantic salmon smolts 2016–2019. Probability of transitioning to the Penobscot River (A) from the Piscataquis River (B) and Stillwater Branch were fixed during estimation (ψ_{BA} and $\psi_{CA} = 1.00$). Probability of using the Stillwater Branch was estimated as the state transition probability ψ_{AC} .



detection probability (p), and probability of using the Stillwater Branch (ψ_{AC}) using maximum likelihood estimation, and the logit-link function (Lebreton et al. 1992).

As the reaches had different lengths, reach length was explicitly entered in all models, so that an estimate of S represents apparent survival per rkm (S_{rkm}), rather than apparent survival per reach (S_{reach}). An information-theoretic approach to model selection, based on AIC_c (Burnham and Anderson 2002) was used to compare different models with different covariates to assess relative support for each competing model. Each model can be interpreted as a biological hypotheses. To develop the models, we used a combination of group and individual covariates, different spatial effects on survival, and different effects of previous experience on survival.

Individual and group covariates

The group covariates incorporated in the models included (1) year (i.e., differences in survival per year), (2) release date (early or late release), (3) river (generally called stratum or state in multistate models; differences in survival among the

Piscataquis, the Stillwater Branch, and the mainstem Penobscot River, this covariate needed to be included in every model), and (4) “cohort”: in mark-recapture models, cohort represents the capture occasion in which an individual was captured, tagged, and released (e.g., if an individual was captured during the third capture/recapture occasion, then it would be part of the third cohort, and the fourth occasion would represent the first time said individual could be recaptured). In this case, as receiver stations represented recapture occasions, an individual released upstream of the seventh receiver set was modeled as having been released on the sixth occasion (and thus, first recapture occasion would have been seventh). As both, fish released in the Piscataquis and fish released in the Penobscot shared cohorts, these did not fully represent release locations, but an interactive model, including both river and cohort, represents all different releases (as river was present in every model, all models, including reach, represented all different releases). Individual covariates included in the model were (1) fish length, (2) mass, and (3) gill NKA activity.

Spatial and prior-experience effects

Four different spatial effects on survival were included in the models. These spatial effects on survival included (1) $S(.)$: constant survival, in which survival is constant among all reaches, and single parameter estimated, in which there is no difference in S_{rkm} among reaches, (2) S_{dam} : survival (S_{rkm}) is different between free flowing reaches, and reaches containing dams (two parameters), (3) S_{dams} : survival (S_{rkm}) is different between free flowing reaches, and among reaches containing dams (this model estimates one S_{rkm} for free flowing reaches, and an S_{rkm} for each of the 10 reaches containing a dam; 11 parameters), and finally (4) $S_{\text{diffreach}}$ (this model estimates S_{rkm} for each reach, estimates survival is different for each dam). When present, this effect ($S_{\text{diffreach}}$) has many parameters to obtain survival of each of the 40 independent reaches.

Finally, we included the effects of previous dam passage on the probability of surviving when passing another dam further downstream. These effects were incorporated as space-varying covariates, and they were only included to models in which survival was hypothesized to be different among all reaches ($S_{\text{diffreach}}$) or among dams (S_{dams}) so that a covariate could be included for each specific dam reach. Stillwater dams were excluded from these effects (low number of individuals using the Stillwater Branch). These effects were applied only to the three most downstream dams, Howland Dam, West Enfield Dam, and Milford Dam. We explored this model in these three dams, as there were multiple releases upstream of them, and fish with multiple experiences approached them. In these models, we tested potential effects of prior experience on the probability of survival passing a reach containing one of these three dams. We tested multiple effects that represent different hypotheses; all effects were individual. (1) Number of dams: probability of surviving through specific dam is driven by the number of dams that an individual has already passed during the study (po-

tentially one, three, or four dams depending on route and dam). (2) Specific dams: this effect represents the hypothesis that survival was linked to the specific dam(s) passed, rather than the number of dams, and it allows for latent effects of dams to be different among them. (3) Delays: this effect represented the hypothesis that mortality was not caused by the number of dams passed, but by the delay incurred during passage of each dam. Delay was calculated for each smolt at each dam as the time difference between first detection upstream, and first detection downstream of a dam (i.e., passage time). This was a spatially dynamic covariate, were all incurred prior to arrival to a dam would be added. This covariate was z -value standardized to deal with potential overparameterization.

We tested all possible combinations of group and individual covariates, different spatial effects on survival, and different effects of previous experience on survival; we also estimated detection probability and probability of transition (use of Stillwater Branch) from the best model. For detection probability, our models looked at (1) differences among all reaches (reach \times river) and (2) differences among reaches and years (reach \times river \times year; 120 parameters, as one value is estimated for each reach each year). Finally, for the probability of transition (ψ_{AC}), we tested for differences in year, and release date. Finally, we also had a constant model. We used AIC_c in program MARK and in RMark for all model selection and survival estimates (Lebreton et al. 1992; White and Burnham 1999; Laake 2013).

Goodness of fit

To confirm that our models comply with model fit assumptions, we assessed goodness of fit of the model with the most parameters, we estimated the over-dispersion parameter \hat{c} , which is a variance inflation factor (Burnham 1987). We used the median \hat{c} method to estimate \hat{c} of the saturated model (Fletcher 2012). The \hat{c} estimate for the fully parameterized model was minimal ($\hat{c} = 1.25$), and thus, adjusting to QAIC would have minimal consequences; therefore, the AIC_c information approach was used for model comparison (AIC_c ; Burnham and Anderson 2002). This was used to determine the best fitting model (Table 3). We obtained a ΔAIC_c value for each model, which represents the difference between the AIC_c of each model with the best fitting model. Models for which $\Delta AIC_c < 2.0$ were considered competitive. Estimates of S_{rkm} and p were obtained for the best fitting model. In cases when the best-fitting model included a continuous covariate, coefficients were used to describe the relationship between apparent survival and the covariate.

Cumulative survival

From rkm survival estimates, we were able to estimate survival for a whole reach using the formula: $S_{\text{reach}} = S_{\text{rkm}}^{\text{reachlength}}$. Confidence intervals were obtained using the delta method. Cumulative survival was estimated for each reach with the following equation:

$$S_{\text{cumulative}} = \prod_i^n S_{\text{reach}}$$

Table 3. Model results for the Capture–Mark–Recapture Multi-State models ran.

S	P	ψ	npar	AIC _c	Δ AIC _c	W	Deviance
$S_{\text{diffreach}} + \text{river} + \text{year} + \text{delays} + \text{NKA}$	Reach \times year	year	93	380 957	0	0.865	380 770
$S_{\text{diffreach}} + \text{river} + \text{year} + \text{delays}$	Reach \times year	year	92	380 961	3.89	0.122	380 776
$S_{\text{diffreach}} + \text{river} + \text{cohort} + \text{delays} + \text{NKA}$	Reach \times year	year	95	380 965	7.88	0.006	380 778
$S_{\text{diffreach}} + \text{river} + \text{cohort} + \text{delays}$	Reach \times year	year	94	380 967	10.17	0.004	379 054
$S_{\text{diffreach}} + \text{river} + \text{release} + \text{delays} + \text{NKA}$	Reach \times year	year	91	380 970	27.74	0.001	380 790

Note: Only the top five models are shown. “npar” represents number of parameters. $S_{\text{diffreach}}$ represents a model in which S_{rkm} is different among all reaches, river represents the three branches or rivers (Piscataquis, Penobscot and Stillwater), delays represent the accumulated effect of transient time through dams, and NKA represents the activity of the gill NKA sodium-potassium ATPase enzyme. Cohort represents the rkm where fish were released (i.e., “cohort” in a mark-recapture setting, not in a biological sense). Release represents whether it was an early or late release. Reach represents each particular reach in the system (analogous to “time” in traditional mark-recapture models). Bolded rows represent models with an Δ AIC_c lower than 2. AIC_c, corrected Akaike information criterion.

Previous studies

We compared the movement, delays, and survival results obtained from this study (2016–2019) to results from previous studies with a similar methodology. We obtained mean reach survival and mean movement rate from 2005 to 2016 (Holbrook et al. 2011; Stich et al. 2014). We estimated cumulative survival and cumulative delays for the historic data and compared our results to previous results.

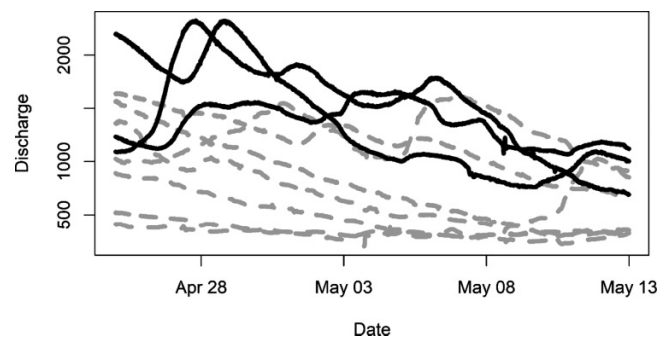
Results

Discharge data and delays

The spring discharge observed in the Penobscot River was high during 2017, 2018, and 2019, coincident with the upper river smolt migration window. Each of these three years, ranked in the top five observed discharges during the 1991–2019 period. There was also no other sequence of years during which discharge was consistently high for three consecutive years. When comparing the time series of discharge observed during the smolt migration window for the previous 10 years, it is evident that the magnitude of discharge observed for 2017, 2018, and 2019 were considerably higher than historical averages. This is especially true for the early part of the migration from 25 April through 1 May. For the 5–12 May time period, the values were still high but were comparable to what has been observed in previous years (Fig. 3).

Delays in Atlantic salmon smolt migration were higher at dams in the Piscataquis River than in the Penobscot River. Delays at dams had great annual and individual variation, with passage times varying from 2 hours to up 10 days at certain dams (e.g., Brownsmill Dam and Guilford Dam). Cumulative delays (sum of mean time spent in upstream sections of the river) were higher at the Piscataquis River than the Penobscot River. The two dams that caused the highest delays were in the Piscataquis; thus, fish released upstream of Guilford Dam had the longest accumulated delays, up to 18 total days spent upstream of dams before getting to the lower Penobscot (Fig. 4). Fish released in the Penobscot had less than 72 hours of accumulated delays total. Milford Dam caused minimum delays (median delays less than 8 hours) and thus did not have an important effect on cumulative delays.

Fig. 3. Comparison of mean daily discharge ($\text{m}^3 \cdot \text{s}^{-1}$) during the smolt migration window 2010–2019 (10 years) at USGS gage 01034500 in the Penobscot River, Maine, USA. Discharge for 2017, 2018, and 2019 are represented by the solid lines, while discharges for the other 7 years are represented by the gray dashed lines.



Survival

Apparent survival per kilometre (S_{rkm}) of Atlantic salmon smolts varied between 0.85 and 1.00 depending on year, river reach, and cumulative delays experienced by individual fish. The best supported model included $S_{\text{riverreach}}$ (differences in survival among all reaches), river (differences in survival among the three rivers: Piscataquis (A), Penobscot (B), Stillwater (C)), and year (differences among years), as categorical explanatory variables (groups), and an effect of delays at dams (time-varying individual covariate) as well as NKA as an individual covariate (Table 3). With the lowest survival (0.85) seen at Weldon Dam during 2018, and the highest survival seen at most free flowing reaches as well as some reaches containing dams.

Individual and group covariates

Survival was generally lower at dams than in undammed river reaches in all years, and reductions in survival varied among dams and river strata (Fig. 5). In the Piscataquis River, S_{rkm} at the first dam (Guilford Dam) was between 0.98 and 0.99 depending on the year, while survival through each of the next two dams (Dover Dam and Browns Mill Dam) was between 0.99 and 1. The lowest survival in the Piscataquis

Fig. 4. Accumulated delays (minutes) approaching dams for acoustically tagged Atlantic salmon released upstream of Guilford (Piscataquis River) or upstream of Weldon (Penobscot River). Bold line represents median, and polygons represent the 0.05, 0.25, 0.75, and 0.95 percentiles. The left panel represents Piscataquis River releases ($n = 617$ fish), and the right panel represents upper Penobscot River releases ($n = 475$ fish). Values before dams represent the accumulated delays of individuals approaching the dam, and the values following dams are the accumulated delays after passing the dam.

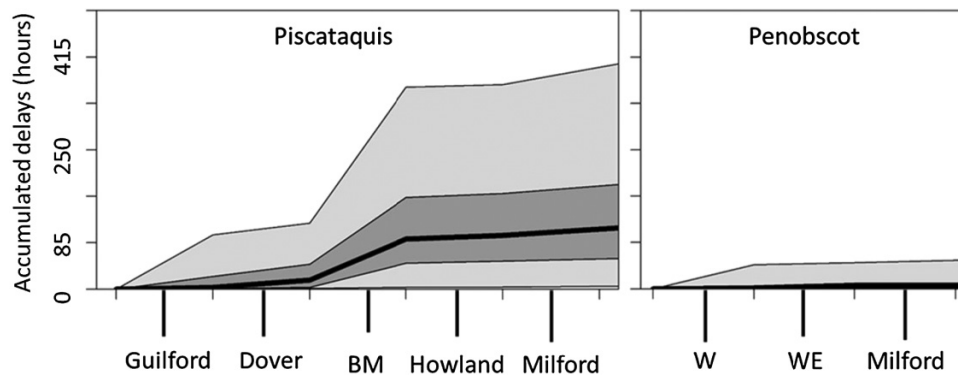
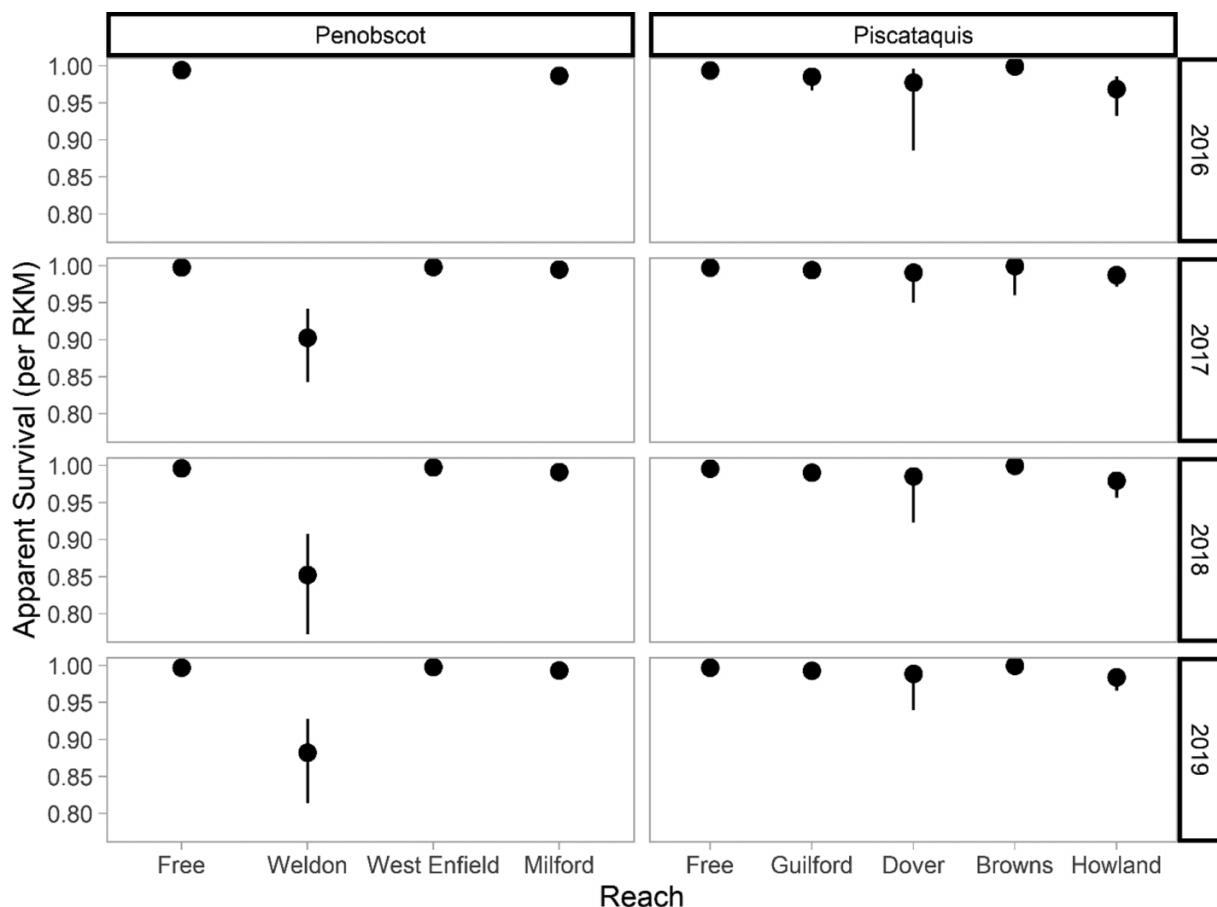


Fig. 5. Survival observed for (A) the Piscataquis River reaches and (B) the Penobscot River reaches. The reach is represented by the x-axis (starting with the first encountered reach), while apparent per river kilometre (rkm) survival is presented in the y-axis. Free represents a free-flowing section of river, and Browns represents Brownsmill Dam.

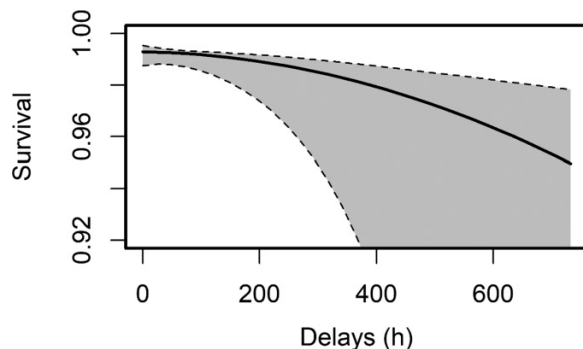


River was at Howland Dam, with S_{rkm} consistently below 0.98 (Table S1).

In the Penobscot River, the lowest S_{rkm} was observed for the reach containing the most-upstream dam (Weldon Dam) in all available years. Smolt survival through the reach in-

cluding the dam was under 0.95 per kilometre, the lowest survival through any reach in the system. Smolts also experienced reduced survival during passage through West-Enfield and Milford dams, with S_{rkm} varying between 0.96 and 0.97 for each of these. Survival in the lower river was greater than

Fig. 6. Effects of cumulative delays (hours) on per river kilometre (rkm) survival (S) of acoustically tagged Atlantic salmon smolts during downstream passage through Howland Dam at the confluence of the Piscataquis and Penobscot rivers, Maine, USA. Delays longer than 400 h were extremely rare.



0.99 in all reaches except during 2016, where survival was reduced to 0.985 between rkm 20 and 17 in the Penobscot River estuary. Detection probability changed among reaches and years, with a mean of 0.82 (Table S1).

Effects of prior experience on survival

The best supported model included an effect of delays. The models that included these effects consistently ranked better than the models that included an effect of (1) numbers of dams passed or (2) specific dams passed. This means that the probability of survival at each dam is potentially affected by the individual experience during migration. Specifically, individuals that experienced longer delays at dams had lower survival probabilities when passing future dams. Individuals that passed dams but did not experience delays had survival probabilities comparable to those of individuals that had not passed dams before. This was best illustrated at Howland Dam, where apparent survival estimates for the entire 2.7 rkm reach varied from 0.98 for individuals experiencing short or no delays (less than 15 hours total) to 0.95 for individuals experiencing long delays (individuals experiencing multiday delays of at least 48 hours; Fig. 6).

Models that included the effect of delays consistently ranked better than models that included release site, or models that included an interaction of both. Models that included gill NKA also ranked best, in which the β (slope parameter) was positive (higher gill NKA was related to higher survival).

Movement and survival through the Stillwater Branch

There were differences in path choices and survival of Atlantic salmon smolts through the Stillwater Branch and main-stem Penobscot River among years. The mean (and 95% CI) probability of using the Stillwater Branch for migration (ψ_{AC}) was 0.076 (0.014–0.098) in 2016 when discharge was within the typical range observed historically (1996–2015). In 2017, the mean probability of using the Stillwater Branch increased to 0.221 (0.175–0.27) and remained elevated in 2018 (0.141, 0.105–0.188), and 2019 (0.166, 0.13–

0.212) when discharge was in the 95th percentile of those reported for 1996–2019. These values are relatively high when compared with previous observations, in which probability of choosing the Stillwater averaged 0.12 (Holbrook et al. 2011; Stich et al. 2014, 2015a). However, our estimates follow anticipated trends relative to discharge that were documented previously in this system (Stich et al. 2014).

Cumulative survival through the Stillwater Branch from 2017 to 2019 varied between 0.987 and 0.99 and was similar among years. Although survival in 2016 was lower (0.980), this year had a lower number of individuals released in the system (150 individuals released, compared to ~450 released in the other years), had lower survival through the Piscataquis River (0.55 cumulative survival to the Stillwater Branch), and had the lowest percentage of fish choosing the Stillwater Branch (less than 10%). Cumulatively, these circumstances resulted in a low number of individuals in the Stillwater Branch available for estimating survival. This makes obtaining a reliable estimate impossible although these results likewise follow expected patterns (lower survival and lower probability of using Stillwater Branch) based on lower discharge observed in 2016 and the results of previous studies (Stich et al. 2015a).

Cumulative survival

Cumulative survival of Atlantic salmon smolts from release sites to the ocean (Fig. 7) was higher in all years 2016–2019 compared to the observed averages obtained from previous studies from 2005 to 2015 (Stich et al. 2015a). However, smolt survival was also considerably higher 2017–2019 than in 2016. These three years represent the highest cumulative survival observed during any time period in this system, with a mean cumulative survival greater than 0.5 for all years 2017–2019, independent of where fish were released, considerably higher than the averages observed in previous studies (Fig. 7). Fish released in the Stillwater Branch had the highest cumulative survival (between 0.84 and 0.92 depending on the year), while fish released upstream of Weldon Dam had the lowest cumulative survivals, varying between 0.50 and 0.62 (Fig. 8).

Discussion

System-wide survival estimates of Atlantic salmon smolts migrating downstream through the Penobscot River watershed in 2017, 2018, and 2019 were the highest that have been observed in the system regardless of release day and release site (Fig. 5). These results are likely due to a combination of river restoration (specifically dam removal) activities and favorable discharge. Depending on the release site, cumulative out-migrant survival ranged from 0.6 for individuals that were released in the upper Piscataquis (individuals that had to pass at least five dams) to 0.9 for individuals released in the Stillwater Branch. This is an extraordinarily high survival estimate in the Penobscot River, even compared with fish previously tagged and released into the Stillwater Branch (Stich et al. 2015a). In total, more than 80% of all released individuals in these years successfully completed their migration to the Penobscot Bay. These 3 years with record high survival

Fig. 7. Apparent survival per river kilometre (rkm; S_{rkm}) of acoustically tagged Atlantic salmon smolts in the Penobscot River, Maine, USA for years 2005–2015 (A) and years 2016–2019 (B). Each bubble represents 1 rkm. Data for left panel were obtained from previously published data (Stich et al. 2015c).

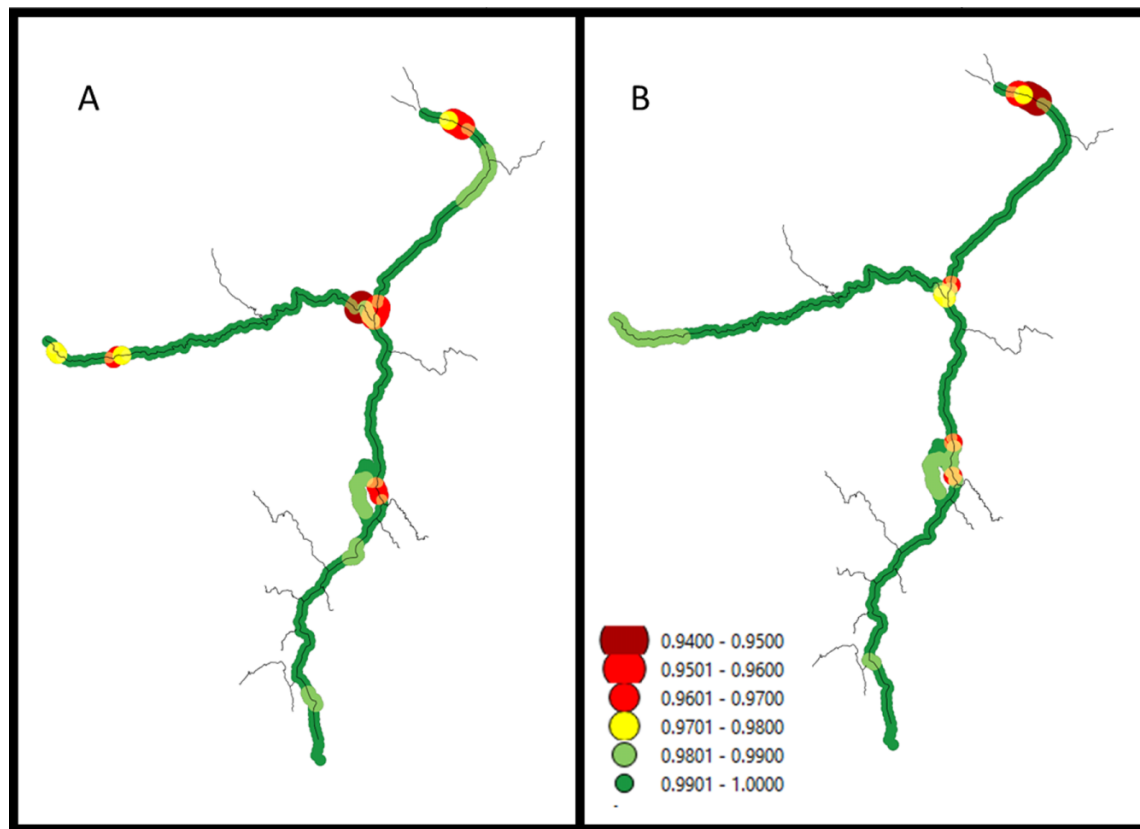
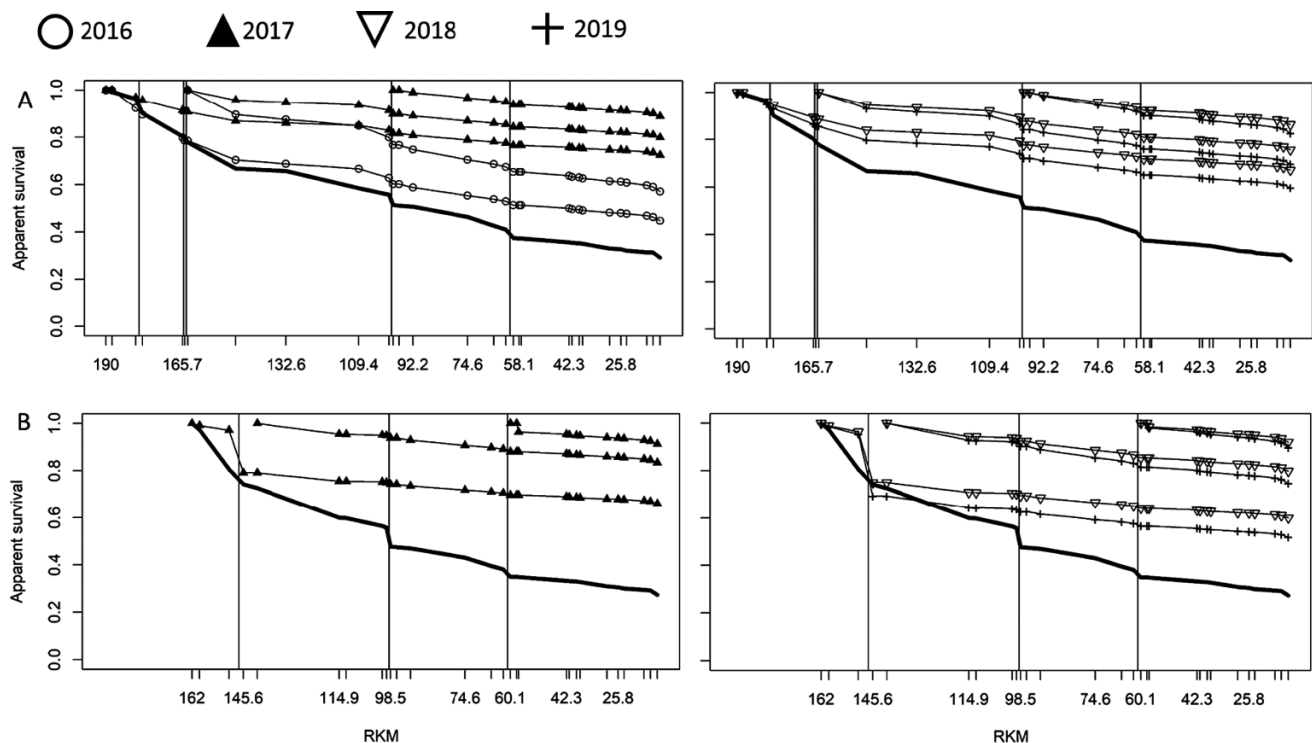


Fig. 8. Cumulative survival of acoustically tagged Atlantic salmon smolts released in the Piscataquis (A) and Penobscot (B) rivers during 2016–2017 (left) and 2018–2019 (right) by river kilometre (rkm). Vertical lines indicate locations of dams. The bold line represents mean cumulative survival for each migration route during 2005–2015.



correlated with the 3 years with the highest flows from 2015 to 2019. While, historically, mortality in the Penobscot River has occurred in dams, during these years survival increased in both dams, and free-flowing reaches. Unfortunately, as the flows were consistently high in the whole system during these years, we do not have specific data on the relationship between flow and survival.

The smolt-to-adult return ratio in North American Atlantic salmon is low, and much of this is due to high mortality incurred during the freshwater and early marine migrations (Moring et al. 1995; United States Atlantic Salmon Assessment Committee 2019). However, a two-fold increase in survival in the freshwater segment of the migration (total system-wide survival increasing from under 0.4 to over 0.8) could clearly contribute to higher returns. While marine mortality is high, it has been observed in North American Atlantic salmon that freshwater and estuarine mortality can be higher than coastal mortality (Kocik et al. 2009; Hawkes et al. 2019).

The Penobscot River has one of the lowest return rates for hatchery-reared Atlantic salmon compared to other North American Rivers (Chaput 2012) and also one of the highest cumulative mortality rates for smolts during a decade of previous study (Holbrook et al. 2011; Stich et al. 2014, Stich et al. 2015a). The most recent years of study (2016–2019) represent a consistent departure from the generally low survival of the previous decade and thus represent an excellent opportunity to explore the effects of smolt survival on adult returns. In the Maine Department of Marine Resources “Historical Trap Counts” documents (with data regarding salmon returns), 2019 and 2020 also represent the years with the highest adult returns since 2011. While simulations have been used to explore the effects of smolt survival on adult returns (Nieland et al. 2015; Pardo and Hutchings 2020), there has been no empirical comparison of system-wide survival of smolts and adult returns in the Penobscot River.

The Penobscot River has changed dramatically during the last decade, and the potential and realized effects of these changes on Atlantic salmon alone have been explored extensively (Holbrook et al. 2009; Nieland et al. 2015; Stich et al. 2015a, 2015b, 2015c; Izzo et al. 2016; Molina-Moctezuma et al. 2021). In 2016, a new nature-like fish bypass was built and completed at Howland Dam, at the confluence of the Piscataquis River in 2016 downstream of which fish must still pass 1–3 additional dams depending on migration route (Stillwater Branch or Penobscot River). While the data show increased survival at this dam during the last years, this increased survival was coincident with a system-wide increase linked to favorable flow conditions for passage. A 3-year window might be suboptimal, particularly if the conditions are similar among years. Therefore, any conclusions as to the effects of passage improvements are confounded by environmental conditions, warranting a cautious interpretation.

We confirmed an effect of delays at upstream dams on smolt survival through Howland Dam. It is reasonable to expect that in years when conditions cause increased delays upstream, decreased survival at Howland Dam may occur. Future survival assessments for this dam could explore survival across a range of conditions and incorporate potential effects of delays into study design. While the effects of these de-

lays on estuary survival have been convincingly documented (Stich et al. 2015c), the manifestation of this effect may be related to increased temperatures, and a mismatch in seawater entry timing with physiological preparedness (Marschall et al. 2011; Stich et al. 2016). We have documented that the observed delays (~48 hours at an upstream dam) also correlate with lower survival at subsequent dams, earlier in the migration. Further exploration of the physiological mechanisms behind this finding and validation through experimentation would be beneficial to the management of this species. Dams in other systems have been seen to potentially delay individuals for up to 9 days (Aarestrup and Koed 2003), and in certain cases (Croze and Larinier 1999) up to 12 days. Meaning that mortality in those systems can be severely affected by the observed effects of delays on latent mortality.

It is notable that survival at Weldon Dam was lower in our study than was observed in previous years (2005–2015) despite a system-wide increase in survival for this period. Recall that in these years, there was a system-wide increase in survival observed in all other reaches—including those with dams. Thus, while cumulative survival for fish released upstream of Weldon Dam in these high discharge years was higher than for past releases, conditions did not alleviate mortality at the Weldon project. Survival at Weldon Dam was consistently low independent of year, release date, or discharge conditions. In fact, survival estimates for the 2016–2019 years were the lowest observed. It is possible that conditions that caused high survival in other reaches of the river might have increased mortality in the Weldon Dam reaches, but that would be unusual. This suggests that the main source of mortality due to this dam may fundamentally differ from other impoundments (Kennedy et al. 2018; Newton et al. 2019; Karppinen et al. 2021). The high survival through the other dams may be a result of lower delays, lower predation in the head-pond of the dam, or higher spill (higher spill may result in higher survival; Fjeldstad et al. 2012). However, all these dams had systems that differed in fish passage, spill, and dimensions, and thus, it’s impossible to speculate which specific characteristics aided in the increased survival. However, understanding the drivers of the increased mortality in Weldon Dam may allow us to understand why all other dams had higher survival.

Weldon Dam consists of a head pond that’s about 5 rkm long, with high mortality occurring both in the head pond and when passing the dam. Total mortality through the entire 6 km reach, including the Weldon Dam, and head pond was between 0.20 and 0.25 in our study, meaning that about a quarter of the fish released upstream of the dam were lost. It may be telling to note that the pattern of highest mortality reversed from the head pond to the dam itself under high flow conditions. Although survival through the dam decreased in 2017–2019 compared to previous years, survival in the head pond increased. As a result, the survival through the entire project was comparable among years.

Importantly, the mortality rate for the Weldon section represents the single most significant risk that smolts face through their entire migration. The loss for this short reach was as great in magnitude as the cumulative risk through the remaining 150 km journey (even with two dams that are

known to be high mortality risks for smolts). Therefore, the causes of the high mortality observed at Weldon Dam and head pond represent critical unknown sources of mortality for the species.

Delays and gill NKA influenced survival, while models that incorporated length or mass did not rank among the top models. The association of elevated gill NKA activity with increased survival is consistent with the observations of [Stich et al. \(2015a\)](#) and represents important confirmation of the role of developmental preparedness in migratory success. Similarly, low levels of gill NKA activity have been linked to delays in seawater entry ([Strand et al. 2011](#)) implying a fitness benefit to the synchrony between physiological development and migratory behavior ([McCormick et al. 1998](#)). While high overall survival during our study is of obvious benefit to the conservation of this species, the lack of mortality provided little opportunity to detect this influence. Because estuary survival was high overall, there was very little variation among years, release groups, or reaches. As a result, exploring the effects of these individual covariates or delay on estuary survival was impossible during the years of this study.

Because Atlantic salmon have complex life cycles that include migration to the sea, and an eventual return as adults to spawn ([McCormick et al. 2013](#); [Armstrong et al. 2018](#)) that makes them difficult to manage at regional and global scales. In such a complex life cycle, with discrete stages, understanding how survival during migration influences overall fitness and adult returns is fundamental for the conservation and recovery of the species. In 2019, the largest number of returning adults since 2011 was observed (1076). This was up from 772 in 2018, and up from an all-time low of fewer than 300 in 2016 and 2014. In 2020, a total of 1426 adult Atlantic salmon returned to the Penobscot River. While these returns remain disappointing fractions of the historic presence of the species in the Penobscot River, an increase in returns that correspond to high smolt survival serves as further evidence of the importance of smolt survival for adult returns. Importantly, it means that actions taken in fresh water can move the needle on recovery.

Acknowledgments

This work includes data from previous publications from Christopher Holbrook, Dan Stich, Michael Kinnison, and Michael Bailey. Substantial contributions were made to this work by C. Gardner (Department of Wildlife, Fisheries, and Conservation Biology, University of Maine). Field and logistic support was provided by B. Heres, K. Job, J. Kocik, S. Vogel, and M. Mensinger (Department of Wildlife, Fisheries, and Conservation Biology, University of Maine), as well as K. Lachapelle (School of Marine Sciences, University of Maine). The US Fish and Wildlife Service Green Lake National Fish Hatchery provided juvenile Atlantic salmon and was instrumental in facilitating the marking and stocking of hatchery reared smolts for this and other work. Maine DMR is responsible for the capture of adult salmon. This work was done in coordination and cooperation with NOAA Fisheries Northeast Fisheries Science Center and Maine Department of Marine Resources. Any use of trade, firm, or product names is for

descriptive purposes only and does not imply endorsement by the US Government. This work was conducted under the University of Maine Institutional Animal Care and Use Committee protocols numbers A2014-10-04 and A2017-10-02.

Article information

History dates

Received: 22 March 2022

Accepted: 15 August 2022

Accepted manuscript online: 29 August 2022

Version of record online: 11 November 2022

Copyright

© 2022 The Author(s). Permission for reuse (free in most cases) can be obtained from [copyright.com](https://creativecommons.org/licenses/by/4.0/).

Data availability statement

At the time of publication, data were not publicly available from NOAA.

Author information

Author ORCIDs

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

Author notes

Joseph D. Zydlewski served as an Associate Editor at the time of manuscript review and acceptance; peer review and editorial decisions regarding this manuscript were handled by Martin Krkošek.

Author contributions

AM-M contributed with data curation, formal analysis, investigation, methodology, visualization, and writing of the original draft.

DSS contributed with data curation, investigation, methodology, supervision, and writing (review and editing).

JDZ contributed with conceptualization, funding acquisition, methodology, project administration, resources, supervision, and writing (review and editing).

Competing interests

The authors declare there are no competing interests.

Funding statement

This research was supported by The National Oceanic and Atmospheric Administration “Species Recovery Grants to States Program” (Section 6) through grant number NA16NMF4720065; Kruger Inc. (no grant number); The American Recovery and Reinvestment Act and NOAA Open Rivers Initiative through the Penobscot River Restoration Trust and NMFS (no grant number); The Nature Conservancy (no grant number); National Fish and Wildlife Foundation (no grant number); Maine Department of Marine Resources (no grant number); and in-kind support was provided by the US

Geological Survey, Maine Cooperative Fish and Wildlife Research Unit.

Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/CJFAS-2022-0055>.

References

- Aarestrup, K., and Koed, A. 2003. Survival of migrating sea trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) smolts negotiating weirs in small danish rivers. *Ecol. Freshw. Fish.* **12**(3): 169–176. Wiley Online Library. doi:[10.1034/j.1600-0633.2003.00027.x](https://doi.org/10.1034/j.1600-0633.2003.00027.x).
- Aas, O., Einum, S., Klemetsen, A., and Skurdal, J. (Editors). 2011. *Atlantic Salmon Ecology*. Blackwell, Chichester; Ames, IA.
- Armstrong, J.D., McKelvey, S., Smith, G.W., Rycroft, P., and Fryer, R.J. 2018. Effects of individual variation in length, condition and run-time on return rates of wild-reared Atlantic salmon *Salmo salar* smolts: survival of *Salmo salar*. *J. Fish Biol.* **92**(3): 569–578. doi:[10.1111/jfb.13548](https://doi.org/10.1111/jfb.13548).
- Burnham, K.P. (Editor). 1987. *Design and Analysis Methods for Fish Survival Experiments based on Release-Recapture*. American Fisheries Society, Bethesda, MD.
- Burnham, K.P., and Anderson, D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. 2nd ed. Springer, New York.
- Caudill, C.C., Daigle, W.R., Keefer, M.L., Boggs, C.T., Jepson, M.A. Burke, B.J., et al. 2007. Slow dam passage in adult Columbia river salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent mortality? *Can. J. Fish. Aquat. Sci.* **64**(7): 979–995. doi:[10.1139/f07-065](https://doi.org/10.1139/f07-065).
- Chaput, G. 2012. Overview of the status of Atlantic salmon (*Salmo salar*) in the north Atlantic and trends in marine mortality. *ICES J. Mar. Sci.* **69**(9): 1538–1548. doi:[10.1093/icesjms/fss013](https://doi.org/10.1093/icesjms/fss013).
- Croze, O., and Larinier, M. 1999. A study of Atlantic salmon (*Salmo salar* L.) smolt behaviour at the Pointis hydroelectric powerhouse water intake on the Garonne river and an estimate of downstream migration over the Rodere dam (Haute Garonne, France). *Bull. Francais Pêche Piscic. Fr.* **72**: 353–354.
- Evans, D.H., Claiborne, J.B., and Currie, S. (Editors). 2014. *The Physiology of Fishes*. Fourth ed. CRC Press, Boca Raton, FL.
- Fjeldstad, H.P., and Uglem, I. 2012. A concept for improving Atlantic salmon *Salmo salar* smolt migration past hydro power intakes. *J. Fish Biol.* **81**: 642–663. doi:[10.1111/j.1095-8649.2012.03363.x](https://doi.org/10.1111/j.1095-8649.2012.03363.x).
- Fletcher, D.J. 2012. Estimating overdispersion when fitting a generalized linear model to sparse data. *Biometrika*, **99**(1): 230–237. doi:[10.1093/biomet/asr083](https://doi.org/10.1093/biomet/asr083).
- Hawkes, J., Goullete, G., Molina-Moctezuma, A., Atkinson, E., and Cox, O. 2019. Supplementation of Atlantic salmon in the southern extent of their range: evaluation of age-1 hatchery smolt stocking in a small coastal watershed North Pacific Anadromous Fish Commission Technical Report No. 15: 197–199. doi:[10.23849/npafctr15/197.199](https://doi.org/10.23849/npafctr15/197.199).
- Holbrook, C.M., Zydlewski, J., Gorsky, D., Shepard, S.L., and Kinnison, M.T. 2009. Movements of prespaw adult Atlantic salmon near hydroelectric dams in the lower Penobscot River, Maine. *North Am. J. Fish. Manag.* **29**(2): 495–505. doi:[10.1577/M08-042.1](https://doi.org/10.1577/M08-042.1).
- Holbrook, C.M., Kinnison, M.T., and Zydlewski, J. 2011. Survival of migrating Atlantic salmon smolts through the Penobscot River, Maine: a prerecovery assessment. *Trans. Am. Fish. Soc.* **140**(5): 1255–1268. doi:[10.1080/00028487.2011.618356](https://doi.org/10.1080/00028487.2011.618356).
- Hvidsten, N.A., and Lund, R.A. 1988. Predation on hatchery-reared and wild smolts of Atlantic salmon, *Salmo salar* L., in the estuary of River Orkla Norway. *J. Fish Biol.* **33**(1): 121–126. doi:[10.1111/j.1095-8649.1988.tb05453.x](https://doi.org/10.1111/j.1095-8649.1988.tb05453.x).
- Izzo, L.K., Maynard, G.A., and Zydlewski, J. 2016. Upstream movements of Atlantic salmon in the lower Penobscot River, Maine following two dam removals and fish passage modifications. *Mar. Coast. Fish.* **8**(1): 448–461. doi:[10.1080/19425120.2016.1185063](https://doi.org/10.1080/19425120.2016.1185063).
- Jensen, A., and Johnsen, B. 1999. The functional relationship between peak spring floods and survival and growth of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). *Funct. Ecol.* **13**(6): 778–785. Wiley Online Library. doi:[10.1046/j.1365-2435.1999.00358.x](https://doi.org/10.1046/j.1365-2435.1999.00358.x).
- Karppinen, P., Hynninen, M., Vehanen, T., and Vähä, J.-P. 2021. Variations in migration behaviour and mortality of Atlantic salmon smolts in four different hydroelectric facilities. *Fish. Manag. Ecol.* **28**(3): 253–267. doi:[10.1111/fme.12486](https://doi.org/10.1111/fme.12486).
- Keefer, M.L., Taylor, G.A., Garletts, D.F., Helms, C.K., Gauthier, G.A., Pierce, T.M., and Caudill, C.C. 2012. Reservoir entrapment and dam passage mortality of juvenile Chinook salmon in the Middle Fork Willamette River: Chinook salmon entrapment and mortality. *Ecol. Freshw. Fish.* **21**(2): 222–234. doi:[10.1111/j.1600-0633.2011.00540.x](https://doi.org/10.1111/j.1600-0633.2011.00540.x).
- Kennedy, R.J., Rosell, R., Millane, M., Doherty, D., and Allen, M. 2018. Migration and survival of Atlantic salmon *Salmo salar* smolts in a large natural lake. *J. Fish Biol.* **93**(1): 134–137. Wiley Online Library. doi:[10.1111/jfb.13676](https://doi.org/10.1111/jfb.13676).
- Klemetsen, A., Amundsen, P.-A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F., and Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic Charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecol. Freshw. Fish.* **12**(1): 1–59. doi:[10.1034/j.1600-0633.2003.00010.x](https://doi.org/10.1034/j.1600-0633.2003.00010.x).
- Kocik, J.F., Hawkes, J.P., and Sheehan, T.F. 2009. Assessing estuarine and coastal migration and survival of wild Atlantic salmon smolts from the Narraguagus River, Maine using ultrasonic telemetry. In *Challenges for Diadromous Fishes in a Dynamic Global Environment*, Symposium 69 American Fisheries Society. Edited by A. Haro, K.L. Smith, R.A. Rulifson, C.M. Moffitt and R.J. Klauda. p. 19.
- Laake, J.L. 2013. Rmark: an r interface for analysis of capture-recapture data with mark. AFSC Processed Rep 2013-01, Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv.
- Lawrence, E.R., Kuparinen, A., and Hutchings, J.A. 2016. Influence of dams on population persistence in Atlantic salmon (*Salmo salar*). *Can. J. Zool.* **94**(5): 329–338. doi:[10.1139/cjz-2015-0195](https://doi.org/10.1139/cjz-2015-0195).
- Lebreton, J.-D., Burnham, K.P., Clobert, J., and Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**(1): 67–118. doi:[10.2307/2937171](https://doi.org/10.2307/2937171).
- Marshall, E.A., Mather, M.E., Parrish, D.L., Allison, G.W., and McMenemy, J.R. 2011. Migration delays caused by anthropogenic barriers: modeling dams, temperature, and success of migrating salmon smolts. *Ecol. Appl.* **21**(8): 3014–3031. doi:[10.1890/10-0593.1](https://doi.org/10.1890/10-0593.1).
- McCormick, S.D. 1993. Methods for nonlethal gill biopsy and measurement of Na⁺,K⁺-ATPase activity. *Can. J. Fish. Aquat. Sci.* **50**(3): 656–658. doi:[10.1139/f93-075](https://doi.org/10.1139/f93-075).
- McCormick, S.D. 1994. Ontogeny and evolution of salinity tolerance in anadromous salmonids: hormones and heterochrony. *Estuaries*, **17**(1): 26. doi:[10.2307/1352332](https://doi.org/10.2307/1352332).
- McCormick, S.D., Hansen, L.P., Quinn, T.P., and Saunders, R.L. 1998. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* **55**(S1): 77–92. doi:[10.1139/d98-011](https://doi.org/10.1139/d98-011).
- McCormick, S.D., Sheehan, T.F., Björnsson, B.T., Lipsky, C., Kocik, J.F., Regish, A.M., and O'Dea, M.F. 2013. Physiological and endocrine changes in Atlantic salmon smolts during hatchery rearing, downstream migration, and ocean entry. *Can. J. Fish. Aquat. Sci.* **70**(1): 105–118. doi:[10.1139/cjfas-2012-0151](https://doi.org/10.1139/cjfas-2012-0151).
- Molina-Moctezuma, A., Peterson, E., and Zydlewski, J.D. 2021. Movement, survival, and delays of Atlantic salmon smolts in the Piscataquis River, Maine, USA. *Trans. Am. Fish. Soc.* **150**(3): 345–360. doi:[10.1002/tafs.10289](https://doi.org/10.1002/tafs.10289).
- Moring, J.R., Marancik, J., and Griffiths, F. 1995. Changes in stocking strategies for Atlantic salmon restoration and rehabilitation in Maine, 1871–1993. *Am. Fish. Soc. Symp.* **15**: 38–46.
- Music, P.A., Hawkes, J.P., and Cooperman, M.S. 2010. Magnitude and causes of smolt mortality in rotary screw traps: an Atlantic salmon case study. *N. Am. J. Fish. Manag.* **30**(3): 713–722. doi:[10.1577/M09-181.1](https://doi.org/10.1577/M09-181.1).
- National Research Council (U.S.) 2004. *Atlantic Salmon in Maine*. National Academies Press, Washington, D.C.
- Newton, M., Barry, J., Dodd, J.A., Lucas, M.C., Boylan, P., and Adams, C.E. 2019. A test of the cumulative effect of river weirs on downstream migration success, speed and mortality of Atlantic salmon (*Salmo salar*)

- smolts: an empirical study. *Ecol. Freshw. Fish.* **28**(1): 176–186. Wiley Online Library. doi:[10.1111/eff.12441](https://doi.org/10.1111/eff.12441).
- Nieland, J.L., Sheehan, T.F., and Saunders, R. 2015. Assessing demographic effects of dams on diadromous fish: a case study for Atlantic salmon in the Penobscot River, Maine. *ICES J. Mar. Sci.* **72**(8): 2423–2437. doi:[10.1093/icesjms/fsv083](https://doi.org/10.1093/icesjms/fsv083).
- Norrgård, J.R., Greenberg, L.A., Piccolo, J.J., Schmitz, M., and Bergman, E. 2013. Multiplicative loss of landlocked Atlantic salmon *Salmo salar* L. smolts during downstream migration through multiple dams: migration of landlocked salmon smolts. *River Res. Appl.* **29**(10): 1306–1317. doi:[10.1002/rra.2616](https://doi.org/10.1002/rra.2616).
- Opperman, J.J., Royte, J., Banks, J., Rose Day, L., and Apse, C. 2011. The Penobscot River, Maine, USA: a basin-scale approach to balancing power generation and ecosystem restoration. *Ecol. Soc.* **16**(3):7. doi:[10.5751/ES-04117-160307](https://doi.org/10.5751/ES-04117-160307).
- Pardo, S.A., and Hutchings, J.A. 2020. Estimating marine survival of Atlantic salmon using an inverse matrix approach. *PLoS ONE*, **15**(5): e0232407. doi:[10.1371/journal.pone.0232407](https://doi.org/10.1371/journal.pone.0232407).
- Parrish, D.L., Behnke, R.J., Gephart, S.R., McCormick, S.D., and Reeves, G.H. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? *Can. J. Fish. Aquat. Sci.* **55**(S1): 281–287. doi:[10.1139/d98-012](https://doi.org/10.1139/d98-012).
- Poe, T.P., Hansel, H.C., Vigg, S., Palmer, D.E., and Prendergast, L.A. 1991. Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day reservoir, Columbia River. *Trans. Am. Fish. Soc.* **120**(4): 405–420. doi:[10.1577/1548-8659\(1991\)120\(0405:FOPFOO\)2.3.CO;2](https://doi.org/10.1577/1548-8659(1991)120(0405:FOPFOO)2.3.CO;2).
- R Core Team. 2019. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available from: <http://www.R-project.org/>.
- Rubenstein, S.R. 2021. *Energetic Impacts of Passage Delays in Migrating Adult Atlantic Salmon*(Master of Science). The University of Maine. Available from: <https://digitalcommons.library.umaine.edu/etd/3468> [accessed 23 November 2021].
- Saunders, R., Hachey, M.A., and Fay, C.W. 2006. Maine's diadromous fish community: past, present, and implications for Atlantic salmon recovery. *Fisheries*, **31**(11): 537–547. doi:[10.1577/1548-8446\(2006\)31\[537:MDFC\]2.0.CO;2](https://doi.org/10.1577/1548-8446(2006)31[537:MDFC]2.0.CO;2).
- Smith, P., Krohn, R.I., Hermanson, G.T., Mallia, A.K., Gartner, F.H. Provenzano, M.D., et al. 1985. Measurement of protein using bicinchoninic acid. *Anal. Biochem.* **150**(1): 76–85. Elsevier. doi:[10.1016/0003-2697\(85\)90442-7](https://doi.org/10.1016/0003-2697(85)90442-7).
- Stich, D.S., Bailey, M.M., and Zydlewski, J.D. 2014. Survival of atlantic salmon *Salmo salar* smolts through a hydropower complex: smolt survival through a hydropower complex. *J. Fish Biol.* **85**(4): 1074–1096. doi:[10.1111/jfb.12483](https://doi.org/10.1111/jfb.12483).
- Stich, D.S., Bailey, M.M., Holbrook, C.M., Kinnison, M.T., and Zydlewski, J.D. 2015a. Catchment-wide survival of wild- and hatchery-reared Atlantic salmon smolts in a changing system. *Can. J. Fish. Aquat. Sci.* **72**(9): 1352–1365. doi:[10.1139/cjfas-2014-0573](https://doi.org/10.1139/cjfas-2014-0573).
- Stich, D.S., Kinnison, M.T., Kocik, J.F., and Zydlewski, J.D. 2015b. Initiation of migration and movement rates of Atlantic salmon smolts in fresh water. *Can. J. Fish. Aquat. Sci.* **72**(9): 1339–1351. doi:[10.1139/cjfas-2014-0570](https://doi.org/10.1139/cjfas-2014-0570).
- Stich, D.S., Zydlewski, G.B., Kocik, J.F., and Zydlewski, J.D. 2015c. Linking behavior, physiology, and survival of Atlantic salmon smolts during estuary migration. *Mar. Coast. Fish.* **7**(1): 68–86. doi:[10.1080/19425120.2015.1007185](https://doi.org/10.1080/19425120.2015.1007185).
- Stich, D.S., Zydlewski, G.B., and Zydlewski, J.D. 2016. Physiological preparedness and performance of atlantic salmon *Salmo salar* smolts in relation to behavioural salinity preferences and thresholds: salinity preference of *Salmo salar*. *J. Fish Biol.* **88**(2): 595–617. doi:[10.1111/jfb.12853](https://doi.org/10.1111/jfb.12853).
- Strand, J.E.T., Davidsen, J.G., Jorgensen, E.H., and Rikardsen, A.H. 2011. Seaward migrating atlantic salmon smolts with low levels of gill Na⁺, K⁺ -ATPase activity; is sea entry delayed? *Environ. Biol. Fishes*, **90**(3): 317–321. doi:[10.1007/s10641-010-9737-3](https://doi.org/10.1007/s10641-010-9737-3).
- Taylor, E.B., and McPhail, J.D. 1985. Variation in burst and prolonged swimming performance among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. *Can. J. Fish. Aquat. Sci.* **42**(12): 2029–2033. doi:[10.1139/f85-250](https://doi.org/10.1139/f85-250).
- United States Atlantic Salmon Assessment Committee. 2019. *Annual Report of The U.S. Atlantic Salmon Assessment Committee 2019*. United States Atlantic Salmon Assessment Committee. Available from: <https://www.nefsc.noaa.gov/USASAC/Reports/USASAC2013-Report%202325-2012-Activities.pdf> [accessed 5 March 2018].
- USGS. 2019. USGS 01031500 Piscataquis River near Dover-Foxcroft, Maine. Available from: <https://waterdata.usgs.gov> [accessed 10 October 2019].
- White, G.C., and Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**(sup1): S120–S139. doi:[10.1080/00063659909477239](https://doi.org/10.1080/00063659909477239).

Copyright of Canadian Journal of Fisheries & Aquatic Sciences is the property of Canadian Science Publishing and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.