Canadian Journal of Fisheries and Aquatic Sciences

Article

Dams facilitate predation during Atlantic salmon (*Salmo salar*) smolt migration

Matthew A. Mensinger[a], **James P. Hawkes**[b], **Graham S. Goulette**[b], **Alessio Mortelliti**[a,c], **Erik J. Blomberg**[a], and **Joseph D. Zydlewski**[d,a]

[a]Department of Wildlife, Fisheries, and Conservation Biology, University of Maine, Orono, ME, 04469, USA; [b]NOAA National Marine Fisheries Service, Maine Field Station, 17 Godfrey Drive, Orono, ME, 04473, USA; [c]Department of Life Sciences, University of Trieste, Edificio M, Via Licio Giorgieri 10, Trieste 34127, Italy; [d]U.S. Geological Survey, Maine Cooperative Fish and Wildlife Research Unit, University of Maine, Orono, ME 04469, USA

Corresponding author: **Matthew A. Mensinger** (email: matthew.mensinger@maine.edu)

Abstract

Diadromous fish populations have incurred precipitous declines across the globe. Among many stressors, these species are threatened by anthropogenic barriers that impede movement, alter riverine habitat, and augment predator communities. In this study, we used acoustic transmitters ($n = 220$) with predation and temperature sensors to characterize Atlantic salmon (*Salmo salar*) smolt predation risk in the Penobscot River, Maine, USA. Across two seasons, we documented 79 predation events through a 170 km migratory pathway, which included three hydropower projects and a large estuary. We detected tagged smolts that were predated by fish ($n = 42$), marine mammals ($n = 28$), and birds ($n = 9$). Using a multistate mark-recapture framework, we estimated that 46% of smolts were predated during downstream migration, which accounted for at least 55% of all mortality. Relative predation risk was greatest through impoundments and the lower estuary, where on average, predation rates were 4.8-fold and 9.0-fold greater than free-flowing reaches, respectively. These results suggest that predation pressure on Atlantic salmon smolts is exacerbated by hydropower projects and that predation in the lower estuary may be greater than expected.

Key words: predation, salmon, dams, telemetry, migration

Introduction

Human-mediated changes to river systems (e.g., climate change, habitat degradation, and introduction of non-native species) may alter predator–prey dynamics (Alexander et al. 2015; Thakur et al. 2017; Murphy et al. 2021). Predation pressure that exceeds natural levels often contributes to population decline and inhibits population recovery (Swain and Benoît 2015; Hickerson et al. 2019; Nilsson et al. 2019). The consequences of increased predation pressure may be severe for migratory life stages, which is already a period of naturally high mortality due to energetic demands, physiological costs, and exposure to different predator species (Hinch et al. 2005; Thorstad et al. 2012*b*; Osterback et al. 2013; Brönmark et al. 2014). Dams may augment predation risk for migrating fish by: (1) imposing delays that increase exposure time to novel predators (Caudill et al. 2007; Mensinger et al. 2021), (2) supporting large populations and congregations of predators in impoundments (Pelicice and Agostinho 2009; Murphy et al. 2019), and (3) creating bottlenecks at dam outflows where predators may aggregate to prey on injured and disoriented fish (Koed et al. 2002; Andrews et al. 2019). Given that over 93% of global river volume is expected to be fragmented by dams and other barriers in the next decade (Grill et al. 2015), migrating fish will continue to encounter these challenges into the future. Therefore, a better understanding of the relationship between dams and predation risk may provide critical information to recover, conserve, and manage migratory fish populations.

Elevated predation risk is a major concern for diadromous salmonids given their social and ecological importance (Lewis et al. 2019; Mortelliti 2023) and population declines (Noakes et al. 2000; Waldman and Quinn 2022). These fishes are highly susceptible to predation during smolt migration when they encounter a suite of novel predator species (Osterback et al. 2013; Gibson et al. 2015; Flávio et al. 2021). The smolt stage also represents a final opportunity for direct management action before fish enter the expansive marine environment where monitoring is more challenging. As such, smolts have been the focus of long-term research efforts to characterize risks associated with this life stage (e.g., McMichael et al. 2010; Stich et al. 2015*a*; Buchanan et al. 2018). While many studies assume predators are a major driver of in-river mortality, comparatively few have distinguished predation from other mortality sources.

Some tagging studies have identified fates of individual fish by recovering tags at terrestrial kill (Sortland et al. 2023;

Babey et al. 2020) and rookery sites (Hawkes et al. 2013; Osterback et al. 2013) or inferring predation from migration histories (Beland et al. 2001; Gibson et al. 2015). However, these projects are often limited in their ability to characterize predation at large spatial contexts, from multiple taxa, and across all tagged individuals. The recent development of acid-sensitive acoustic predation transmitters offers additional clarity when determining the disposition of tagged fish (Halfyard et al. 2017; Schultz et al. 2017). These tags transmit a different signal when exposed to an acidic environment (e.g., stomach acid of a predator), allowing researchers to detect predated individuals in situ (Daniels et al. 2019; Klinard et al. 2021; Lennox et al. 2021). Here we use acoustic predation transmitters to characterize Atlantic salmon (*Salmo salar*) smolt predation risk through a modified river system to better understand how dams augment predation pressure.

The Gulf of Maine Distinct Population Segment of Atlantic salmon (*Salmo salar*) is listed as endangered under the U.S. Endangered Species Act (USFWS and NOAA 2009). Since their original listing in 2000, fewer than 1500 adult fish return to US waters annually, representing <1% of estimated historical abundance (Saunders et al. 2006; USASAC 2023). More than 80% of these fish return to the Penobscot River, which has been the focus of considerable research and restoration efforts. Since 1970, over 25 million hatchery-reared smolts have been released into the watershed to supplement low, natural reproduction, yet fewer than 0.1% of these smolts return as adults (USASAC 2023). These low return rates occur in a system with 14 federally regulated hydropower projects and dozens of additional, smaller anthropogenic barriers (Hall et al. 2011; Maine DEP 2014; Stevens et al. 2019). Therefore, the Penobscot River represents an ideal area to investigate the relationship between predation and dams for juvenile salmon.

In addition to direct and latent influences of dam passage (Holbrook et al. 2011; Stich et al. 2015*b*, 2015*a*; Molina-Moctezuma et al. 2022), facilitated predation is often discussed as a potential contributor to Atlantic salmon smolt mortality in the Penobscot River. In Maine, smolts have been consumed by double-crested cormorants (*Phalacrocorax auritus*, Blackwell et al. 1997; Hawkes et al. 2013), striped bass (*Morone saxatilis*, Beland et al. 2001), chain pickerel (*Esox niger*, van den Ende 1993), and smallmouth bass (*Micropterus dolomieu*, Mensinger, *unpublished data*). Other potential predators include seals (*Pinnipedia sp.*), and a suite of piscivorous birds (e.g., gulls *Larus sp.*, common loon *Gavia immer*, mergansers *Mergus sp.*), all of which prey upon juvenile salmonids in other systems (Kålås et al. 1993; Osterback et al. 2013; Thomas et al. 2017; Daniels et al. 2018). Despite this perceived predation risk, there remains relatively little information on the extent of predation pressure incurred by Atlantic salmon smolts in the northeast United States. Therefore, by equipping smolts with acoustic predation transmitters and tracking migration through the main stem of the Penobscot River, we aim to (i) identify predator taxa, (ii) quantify and characterize predation risk in the context of overall survival, and (iii) locate areas of high mortality due to predation. We hypothesized that avian and fish predators would impose the highest predation pressure and that risk would be elevated near dams. Identifying sources of mortality during smolt migration represents a critical next step to maximize escapement into the marine environment and would have major implications for Atlantic salmon recovery.

Methods

Fish tagging, release, and tracking

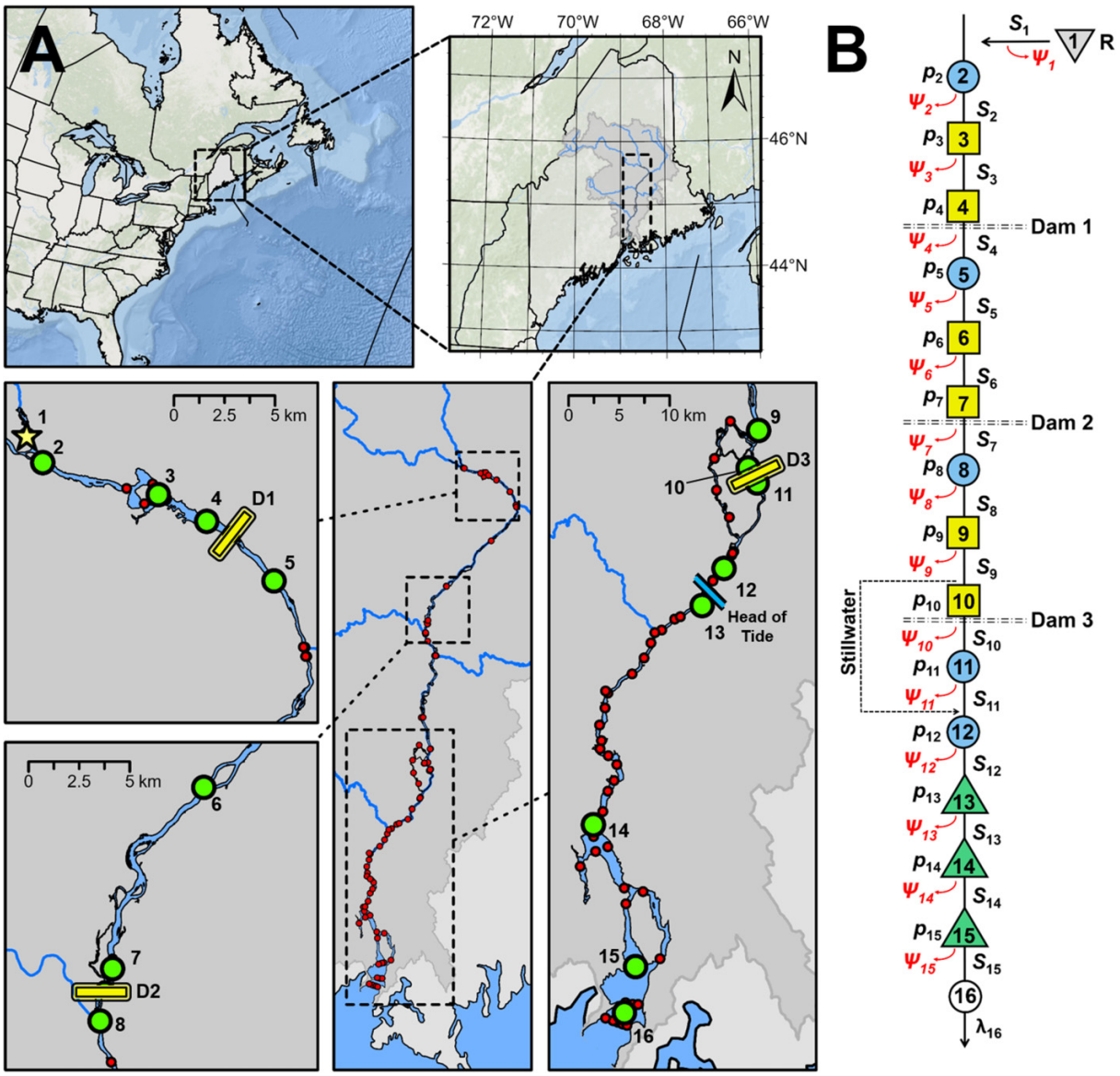
All Atlantic salmon smolts used in this study were hatchery-reared at the U.S. Fish and Wildlife Service (USFWS) Green Lake National Fish Hatchery in Ellsworth, Maine. Smolts were grown from eggs produced from a combination hatchery and naturally reared adult salmon from annual Penobscot River returns. Tagging occurred at the hatchery in late April to align with the natural migratory window for smolts in the region (Kocik et al. 2009; Frechette et al. 2022). We selected fish that demonstrated clear visual signs of smoltification (e.g., silvering, absence of parr marks, McCormick et al. 1998) and were >45 g such that tag weight in air (1.7 g) was <4% of smolt body mass. Before surgery, fish were anesthetized in tricaine methanesulfonate (MS-222 100 mg·L^{-1}, buffered with 2.5 mM $NaHCO_3$, pH = 7.0). Then we recorded fork length (mm) and body mass (g) and surgically implanted each fish with an acoustic predation transmitter (Innovasea, V7DT-2x) through a small incision in the peritoneal cavity and closed the wound with two braided, absorbable sutures (Ethicon Inc., VICRYL 4–0). Fish recovered in a 500 L tank for at least 1 h prior to transport.

Each year, we released all fish simultaneously in the East Branch of the Penobscot River in Medway, Maine, 165 km upstream of the river's mouth ("rkm" hereafter, ~2 h transport time post-surgery, Fig. 1A). This site allowed us to monitor smolt movement through the three main-stem hydropower projects at Weldon (152rkm), West Enfield (102rkm), and Milford (62rkm) dams. We tracked fish migration with a static array of more than 100 acoustic receivers (Innovasea, VR2W, VR2Tx, and VR2AR) deployed from the release site through the estuary (-8rkm). Individual receivers were allocated among >50 long-term acoustic monitoring sites (see Molina-Moctezuma et al. 2022) that are concentrated upstream and downstream of hydropower projects. To locate tags deposited beyond the range of stationary receivers, we searched for transmitters with a mobile receiver (Innovasea, VR100). Active tracking started 25 days post-release, which is beyond the expected migratory period for tagged smolts in the system (Stich et al. 2015*b*). Starting 3 km upstream of the release site, we traversed (by canoe, kayak, motor boat, or on-foot) likely migratory routes in the study area and stopped every 0.5–1 km for a minimum of 60s to listen for tags. Active tracking in the estuary was conducted within 2 h of high tide to allow for greater detection ranges within tidal environments.

Tag programing and identifying predation events

Transmitters contained a temperature and predation sensor, each of which emitted a unique combination of 69 kHz pings to transmit tag identifiers and sensor values. In 2021, each tag was programmed to emit a 137 dB 69 kHz signal once

Fig. 1. (A) Overview of the study area in the Penobscot River Watershed, Maine, USA. Lower middle inset represents main stem of the Penobscot River. The yellow star represents the release site, and numbered green circles represent receiver stations used in the mark-recapture model. Small, red circles represent individual acoustic receivers. D1–3, Weldon, West Enfield, and Milford dams, respectively. Map was produced using Geographic Information Systems software (ArcGIS Pro, Esri) with National Hydrography Dataset and Watershed Boundary Dataset spatial data (Jones et al., 2022; U.S. Geological Survey 2019). Basemap: Esri, GEBCO, Garmin, NaturalVue. Map projection: NAD 1983 UTM Zone 19 N. (B) Conceptual model of the study area in a multistate mark-recapture framework. Shapes, stations (i.e., capture occasions) where individual smolts were characterized as alive, predated, or not detected, and colours represent reach type in the next downstream interval (solid, black lines). Grey inverted pyramid, release site (R) to Station 2; blue circles, free-flowing river reaches; yellow squares, hydropower projects; green triangles, estuary; white circle, open-interval (where λ represents the product of survival and detection beyond this final receiver station). *p*, detection probability at each station; *S*, survival probability between stations; Ψ, the probability that a smolt is predated between stations. Dam 1–3, Weldon, West Enfield, and Milford dams, respectively. Stillwater, exit and re-entry of fish migrating through the Stillwater River.



every 20–40 s over an estimated 56 day tag life. The same sequence was used for the first 25 days in 2022, but then transmitted a higher powered (141 dB) signal every 60–80 s for an additional 23 days before expiration. This switch in emittance occurred after migration and was used to maximize the detection of predated fish during active searches. Given the tag battery life more than doubles the expected migration duration, the potential risk of premature tag failure was assumed to be negligible. The predation sensor is designed to trigger after prolonged contact with stomach acid (usually within 9 h of exposure, Halfyard et al. 2017). Once the tag is triggered, the transmitted data from the predation sensor indicates the

time since triggering (in hours). This also causes the temperature sensor to permanently transmit the temperature (±0.5 °C, range = 0–40 °C) of the environment in which the predation sensor was triggered (i.e., the digestive system of the predator species), regardless of when the tag is detected.

We used temperature data to distinguish ectothermic from endothermic predators.

Because the average internal body temperature of potential avian predators in the system (e.g., double-crested cormorant, common loon) is ≥39 °C, we assumed sensors that exceeded this threshold were predated by birds (Enstipp et al. 2006; Kenow et al. 2021). Alternatively, internal temperatures of mammalian predators in the Penobscot River (e.g., North American river otter *Lontra canadensis,* harbor porpoise *Phocoena phocoena.,* harbor seal *Phoca vitulina*, and grey seal *Halichoerus grypus*) fall between 36 and 39 °C (Gaskin et al. 1974; Boily and Lavigne 1996; Spelman et al. 1997; Hansen and Lavigne 1997). Therefore, we assumed that tags <39 °C and ≥30 °C were predated by mammals, and that triggered tags <30 °C were predated by fish. Overall, we defined predated smolts by detection of triggered predation sensors or if the temperature sensor exceeded 30 °C to account for smolts that were consumed by endothermic predators, but with untriggered predation sensors. Because the internal temperature of smolts and potential predatory fishes reflect ambient river temperatures, we were unable to identify smolts that were predated by these species if the sensors failed to trigger.

Estimating predation risk

We used a multistate mark-recapture model to estimate predation rates through the study system. This framework is frequently used in analyses of survival, where detection probability (p) is estimated at each capture occasion and apparent survival (S, "survival" hereafter) and state-change probabilities (Ψ) are estimated for each interval ("reach" hereafter). For migrating fish, Ψ often reflects path choice (e.g., Holbrook et al. 2011; Stich et al. 2015*a*; Buchanan et al. 2018), but can be used to characterize migration status (Lewandoski et al. 2018) and movement between environments (Frank et al. 2012; Mayfield et al. 2019). In this study, we considered predated fish to have entered a permanent alternative state.

We created capture histories comprising 16 capture occasions ("stations" hereafter) in the study area (Fig. 1). These stations consisted of a subset of acoustic monitoring sites and allowed us to characterize predation risk through areas of interest while also conserving model parameters. We assumed unidirectional, downstream movement, and we used the last detection at a given station to classify each smolt as alive ("s"), predated ("d"), or not-detected (0) at each capture occasion. All fish were alive and appeared healthy upon release, so we assigned each fish an "s" at Station 1. Smolts that were detected as predated between stations (e.g., during active searches or with supplemental receivers) were classified as predated at the next downstream station. We assumed that predation locations occurred near the first detection of a predated tag, unless there was clear evidence of predator-facilitated transport (e.g., avian predation). In this circumstance, we assumed predation occurred near the last living (i.e., non-predated) detection. Once a smolt was detected as predated at a capture occasion, all detections at downstream stations were assigned a "0." Additionally, ~15% of surviving smolts migrate though the Stillwater River and bypass the Milford Dam hydropower project (Molina-Moctezuma et al. 2022). Our relatively low sample size and the complexity of the predation parameter prevented us from reliably modeling an additional state change for these fish. Therefore, we censored individuals from the capture history when they were unavailable for detection (i.e., at Stations 10 and 11) until they reentered the Penobscot River just upstream of Station 12 (Fig. 1B).

Model parameters and selection

We assessed the goodness-of-fit of the unconstrained global model by estimating median $\hat{c}$ in Program MARK (White and Burnham 1999). This revealed that our model was slightly over-dispersed ($\hat{c}$ = 1.36, 95% Confidence Interval, CI = 1.29–1.42), so we used quasi-Akaike information criterion adjusted for sample size ($QAIC_c$) to evaluate relative support among models (Burnham and Anderson 2002). Competing hypotheses regarding the structure of detection, survival, and predation parameters were assessed using the *RMark* package (Laake 2013) in *Program R* (R Core Team 2021).

We first evaluated support for spatially explicit models that allowed estimates to vary by reach (for S and Ψ) and station (for p, Fig. 1B). For S, we controlled for variable reach lengths when creating the design matrix in *RMark* such that survival estimates reflected survival per 1 km (S_{km}), and we fixed survival to zero at all downstream reaches once individuals transitioned to a predated state. Using this approach, S represents the probability of surviving a reach given the smolt is not predated, and 1-S yields the probability of latent mortality. Starting with the most general reach-specific survival structure, we assessed whether smolts migrating through dammed (S_4, S_7, S_{10}) and estuarine reaches (S_{13}-S_{15}) incurred differential survival relative to free-flowing river reaches. We evaluated support for models that allowed for either (1) different survival estimates at each dam (i.e., $S_4 \neq S_7, \neq S_{10}$) or (2) similar estimates across all dams (i.e., $S_4 = S_7 = S_{10}$), while tidal reaches were treated equally (i.e., $S_{13} = S_{14} = S_{15}$). In all constrained survival models, we controlled for post-release mortality (Erhardt and Tiffan 2018) by allowing survival to differ through S_1.

Unlike S, we were unable to apply differences in reach length to Ψ using *RMark*. This prevented us from modeling predation risk across a common scale (i.e., $\Psi \cdot km^{-1}$) as a component of the model likelihood, which would also complicate evaluating the relative performance of more constrained models through model selection. Therefore, we only considered the most general spatial model (i.e., all reaches allowed independent estimates of Ψ) for this parameter. Because the transition from a living to predated state ($\Psi_{s\rightarrow d}$, "Ψ" hereafter) is unidirectional and permanent, we fixed the reciprocal transition probability (i.e., $\Psi_{d\rightarrow s}$) to zero. Using this approach, Ψ represents the probability that a smolt is predated before entering the next interval, and predated fish also explicitly do not contribute to estimates of S, Ψ, or p as-

Table 1. Summary of Atlantic salmon (*Salmo salar*) smolt predation observations by year.

Year	Release date	*N*	Fork length (mm)	Mass (g)	Fish	Bird	Mammal	Unknown
2021	April 28	72	191 (166–220)	74 (46–109)	16	4	12	10
2022	April 26	148	200 (177–220)	81 (57–117)	26	5	16	42

Note: Fork length and Mass represented mean values with ranges in parentheses. *N*, smolts released each year; Fish, Bird, and Mammal, detected predation events from each taxon; Unknown, smolts that incurred mortality from unknown sources.

sociated with downstream reaches or receiver stations. This framework also prevents us from modeling state-specific *p*, because we did not have repeated detections for predated smolts. Therefore, we assumed predated and non-predated tags had similar recapture probabilities, given that they were still available for detection. Under this parametrization, *p* provides the joint probability of detecting an individual upriver from (via mobile tracking) or at each receiver station. Given inherent variability among monitoring stations (e.g., discharge, receiver coverage, and river width), we also only considered the most general spatial model for *p* (i.e., allowing for different estimates of *p* at each receiver station).

All spatially explicit combinations of *S*, *p*, and Ψ were first evaluated with and without a group effect (additive and interactive) of release year. General spatial models were considered supported if they improved support by >2.00 $\Delta QAIC_c$ against the null, and more-constrained survival models were supported if they improved support against the general model using the same criteria. We considered year effects to be supported if they were included within one of the best-supported models (i.e., $\Delta QAIC_c < 2.00$) and the 95% confidence interval (CI) of the year effect did not include zero. The best-supported spatial/year model combination was retained to evaluate the influence of individual-based variables (i.e., fork length, Fulton's condition factor, "condition," hereafter) for *S* and Ψ. A covariate was supported if the 95% CI of the effect excluded zero and it was included in a model with $\Delta QAIC_c < 2.00$. We used estimates from the best-supported model to derive *post-hoc* calculations of reach-specific predation rates (Ψ_{km}) using the following formula:

$$(1) \qquad \Psi_{km} = 1 - (1 - \Psi)^{\left(\frac{1}{L}\right)}$$

where Ψ is the reach-specific predation probability and *L* is the reach length (km). We used scaled estimates for *S* and Ψ to estimate cumulative probabilities. Cumulative survival (*c.surv*) through the study area is given as follows:

$$(2) \qquad c.surv = \prod_{r=2}^{15} (S_r \times (1 - \Psi_r))$$

where Ψ_r is the probability of predation through each reach, *r*, and S_r represents the probability of a smolt surviving each reach given that it was not predated. We further estimated cumulative predation (*c.pred*) through the study area as follows:

$$(3) \qquad c.pred = 1 - \left(\prod_{r=2}^{15} (1 - \Psi_r)\right)$$

Together eq. 2 and eq. 3 allowed us to estimate the proportion of all mortality attributed to predation (also defined as the probably of predation given mortality) as follows:

$$(4) \qquad p(\text{pred}|\text{mort}) = \frac{c.pred}{(1 - c.surv) + c.pred}$$

We excluded S_1 and Ψ_1 from all cumulative estimates to control for the potential of increased mortality risk post-release, and we used the Delta method (Powell 2007) to propagate error for these estimates using the *emdbook* package (Bolker 2020).

Results

We released 220 smolts over two seasons in the Penobscot River and identified 79 individuals that were predated before passing the most downstream receiver station (Station 16, Table 1). We detected 18 predated tags solely through active tracking, while the remaining tags were identified by stationary receivers ($n = 38$) or both methods ($n = 23$). Predatory fishes posed the greatest predation risk overall (53% of observed predation events) and accounted for 87% of predated tags detected in the upper river (Table 2, Fig. 2). Mammals were the predominant predator in the lower section of the river, where they consumed 88% of tags predated in these reaches. Of the predation events by endothermic predators ($n = 37$), four tags never triggered and smolt fate was determined only by temperature sensors. On average, this suggests that ~90% of predation sensors triggered successfully.

We removed one fish from the mark-recapture analysis because the transmitter did not appear to activate until Station 8. The best-supported parameterization of *p* allowed for different detection probabilities at each station between years (Table 2). Detection probabilities varied at individual locations (range = 0.31–1.00), but averaged 0.88 across all stations (Table S1). The most-supported survival model indicated that migrating smolts incurred similar losses through each dam that were consistently greater than free-flowing reaches. An additive effect of release year was also included in this model, which suggested that survival throughout the study area was lower in 2022 ($\beta = -0.89$, -1.64 to -0.14 95% CI). We did not find support for an effect of fork length or condition on survival or predation risk.

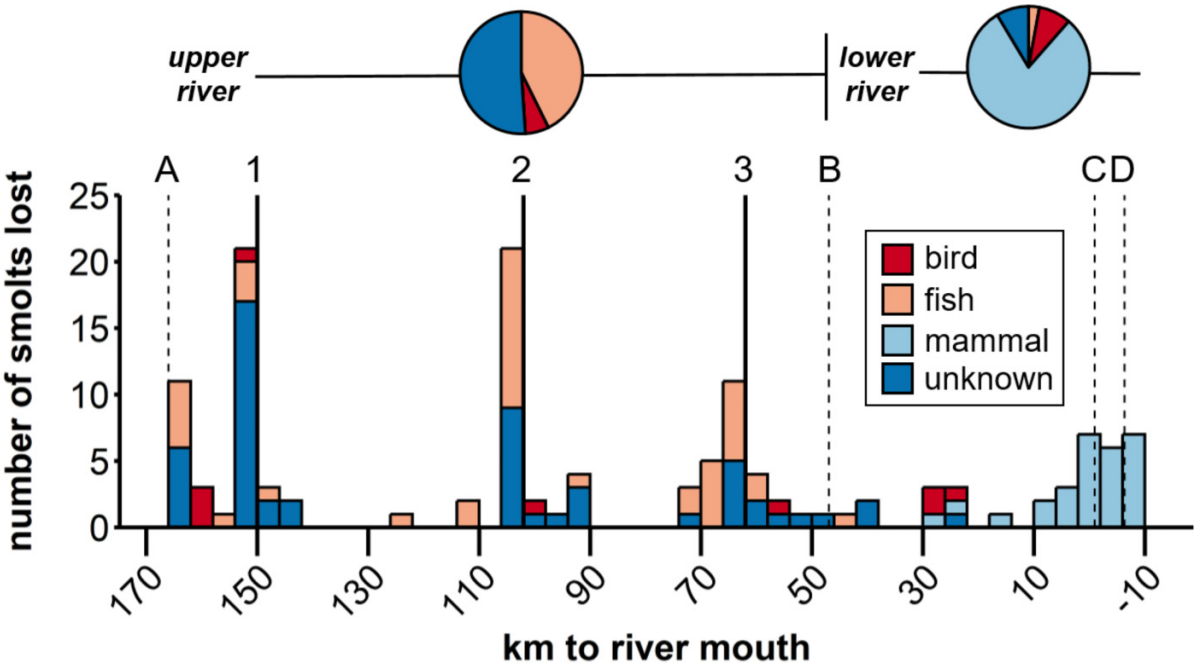
The annual predation probability through the study system was 0.46 (95% CI: 0.39–0.54, Fig. 3) and was similar between years. When we allowed predation to contribute to overall mortality, the cumulative probability of survival was 0.40 (0.30–0.50) in 2021 and 0.26 (0.19–0.34) in 2022. Predation accounted for 55% (46–64%) of all mortality and a greater

Table 2. Relative performance of a subset of supported multistate mark-recapture models to evaluate predation risk during Atlantic salmon (*Salmo salar*) smolt migration.

S	p	Ψ	K	$\Delta QAIC_c$
dams + river + year	station × year	reach	49	0.00
dams + river	station × year	reach	48	1.66
dam 1 + dam 2 + dam 3 + river	station × year	reach	50	11.87
reach	station × year	reach	60	18.49
reach	station + year	reach	46	24.92
reach	station	reach	45	52.34
null	station	reach	31	66.17
reach	station	null	31	71.68
null	station	null	17	74.32
reach	null	reach	31	219.45
reach	null	null	17	241.97
null	null	reach	17	257.49
null	null	null	3	270.39

S, structure of survival parameter; *p*, structure of detection of parameter; Ψ, structure of predation parameter; dams, same estimate across three hydropower projects; dam 1–3, different estimates for each hydropower project, river, same estimate across undammed reaches; reach, reach-dependent estimates for intervals between stations; year, release year; null, intercept-only model; station, different estimate for each receiver station; *K*, number of parameters estimated in each model; $\Delta QAIC_c$, difference in quasi-Akaike's information criterion (adjusted for sample size) from the most supported model.

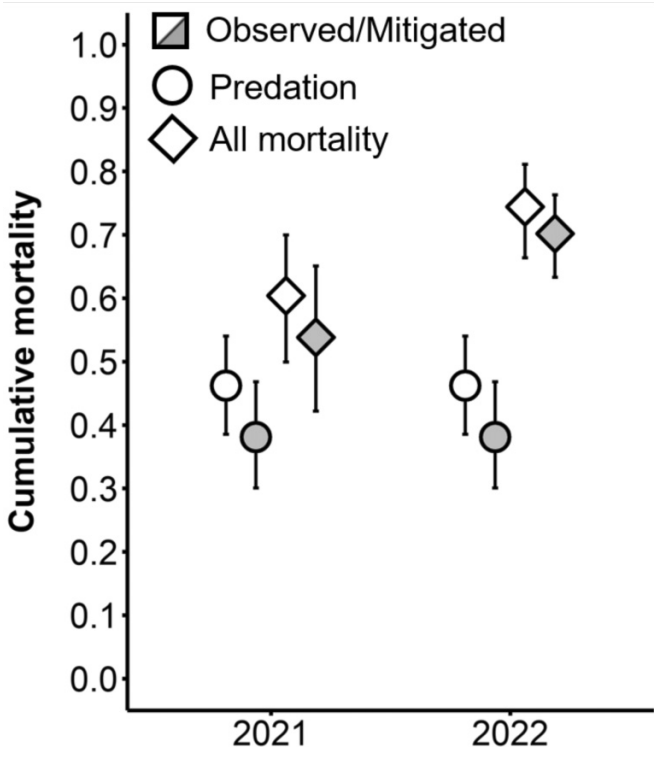
Fig. 2. Locations of apparent migratory failure binned in 4 km sections. Red, orange, and light blue bars represent the location where Atlantic salmon (*Salmo salar*) smolts were detected as predated by birds, fish, and mammals, respectively. Dark blue bars represent the point of final detection of fish that were not detected as predated or as living smolt downstream of 0 river kilometers (rkm). Numbered, solid lines delineate areas upstream (left) and downstream (right) of Weldon (1), West Enfield (2), and Milford (3) dams. Dashed lines represent the release site (A), head of tide (B), and seal haulouts at Odom's Ledge (C), and Fort Point Ledge (D). Pie charts represent the proportional losses by fate between the upper and lower Penobscot River, delineated by the head of tide.



proportion of smolt losses in 2021 (0.64, 0.48–0.76) than 2022 (0.47, 0.40–0.54)

Predation risk was greater through hydropower projects and the estuary compared to free-flowing river reaches (Fig. 4A). Of the predation events detected near dams, 93% (n = 27) occurred in the headpond (Fig. 2). On average, predation rates were 4.8-fold greater through dammed (0.0063 km^{-1}, 0.0043–0.0092 km^{-1}) than free-flowing river sections

Fig. 3. Cumulative Atlantic salmon (*Salmo salar*) smolt mortality by release year. Circles, cumulative probability that a smolt is predated; diamonds, cumulative probability that a smolt does not survive. Shaded points assume that average predation rates through impounded reaches are replaced with those of free-flowing river sections. Error bars represent 95% confidence limits.



(0.0013 km^{-1}, 0.0008–0.0022 km^{-1}, Fig. 4A). The greatest proportional loss occurred through West Enfield Dam where the predation probability was 0.09 (0.05–0.14) annually. Of the dammed reaches, the greatest relative risk occurred at Milford Dam, where the average predation rate (0.0105 km^{-1}, 0.0053–0.0206 km^{-1}) was 8.0-fold greater than free-flowing river sections. Across the three hydropower projects, both cumulative and relative predation risk was lowest for smolts moving through Weldon Dam, where the probability of predation was 0.02 (0.01–0.05). Overall, we estimated that the cumulative probability of a smolt being predated while moving through a hydropower project at 0.16 (0.11–0.23, Fig. 4B). If the average predation rate through dammed reaches was equal to free-flowing reaches, we would expect the cumulative predation probability to decrease from 0.46 to 0.38 (0.30–0.47), which would result in an increase in system-wide survival from 0.40 to 0.46 (0.35–0.58) in 2021 and from 0.26 to 0.30 (0.24–0.37) in 2022 (Fig. 3).

Of the 120 smolts that survived to the Penobscot River estuary, 27% (n = 32) were detected as predated before leaving the study area. The results from the mark-recapture model suggested that a similar proportion (0.27, 0.12–0.38) of surviving smolts were predated in this area. Overall, the estuary represented the greatest proportional loss of any general (i.e., release, dammed, estuarine, free-flowing) reach type (Fig. 4B). Most losses occurred in the lower estuary, where the estimated predation probability was 0.23 (0.16–0.32) between Stations 14 and 16. Estuary-wide, the average relative risk (0.0064 km^{-1}, 0.0045–0.0091 km^{-1}) was 4.9-fold greater than that of free-flowing river sections, and this difference increased to 9.0-fold in the lower estuary (0.0119 km^{-1}, 0.0081–0.0177 km^{-1}). While free-flowing river sections consisted of 50% of the study area, cumulative predation probability was lowest through these reaches (0.12, 0.07–0.18).

Discussion

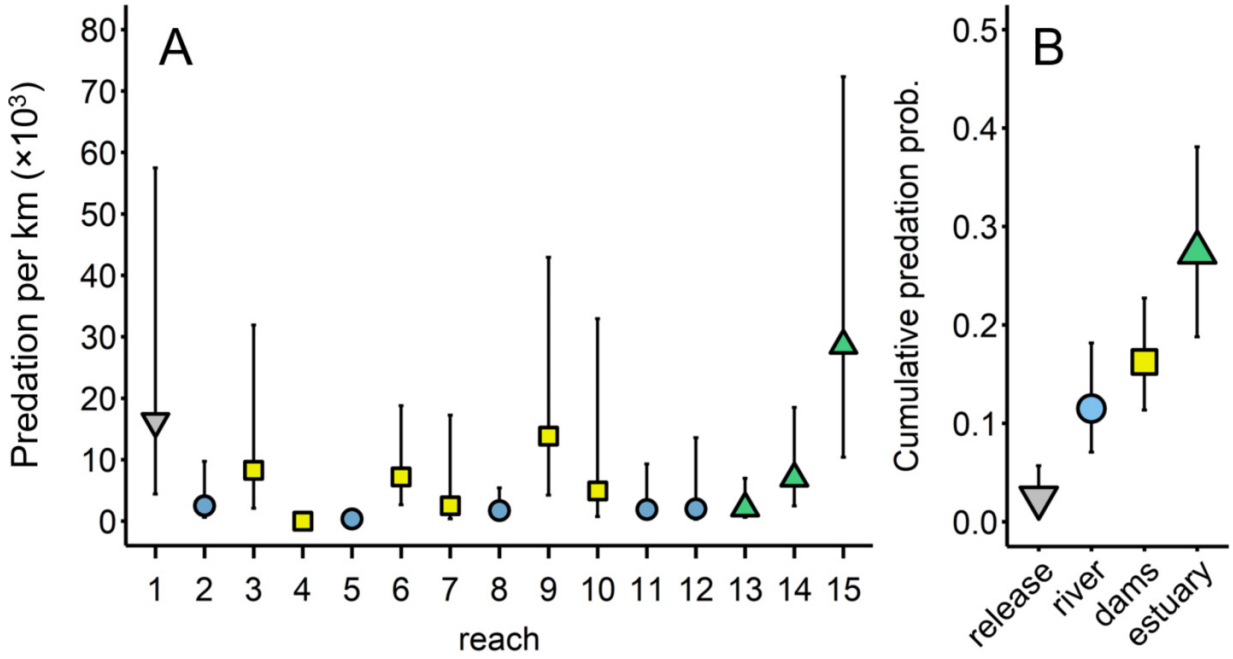
We show that migrating Atlantic salmon smolts are predated by a suite of predator taxa during migration and that risk is exacerbated near hydropower projects and the lower Penobscot River estuary. Smolts incurred predation from avian, fish, and mammalian species during the ~170 km migration from release to marine entry. Over two field seasons, we identified 79 smolts that were predated before moving through the study area, which we estimated represented at least 55% of annual mortality. Collectively, this study is among the first to characterize and quantify in situ predation risk throughout a major Atlantic salmon smolt migration corridor and is one of the most comprehensive assessments of smolt predation risk conducted in the region.

Predation near dams

Our study demonstrated that predation risk was elevated near dams, and that predators may consume nearly 9% of migrating smolts at a single hydropower project. Over 80% of predated tags recovered near dams were detected in the impoundment and were attributed to fish predators. Our findings are corroborated by other downstream passage studies that show Atlantic salmon smolts incur lower survival when migrating through reservoirs (Jepsen et al. 1998; Havn et al. 2018; Molina-Moctezuma et al. 2022). Though not evaluated in this study, we assume that elevated predation in these areas is due to a combination of increased exposure time from dam-induced migratory delay (Molina-Moctezuma et al. 2022), aggregations of predatory fishes (Jepsen et al. 2000), and foraging pressure by diving water birds (Modde et al. 1996).

Predation risk varied between the three hydropower projects. The majority of smolts (18 out of 32) whose final detection was upstream of West Enfield or Milford Dam were detected as predated. While cumulative predation loss was greatest at West Enfield Damjpe (~9%), relative risk was greatest through Milford Dam where predation rates were 8-fold greater than free-flowing river sections. When also accounting for undetected predation events, our results suggest that predation is a leading source of mortality through these projects. The Weldon Dam hydropower project is considered one of the riskiest areas in the Penobscot River for migrating smolts, where up to 25% of individuals have died in a single season (Stich et al. 2015*a*; Molina-Moctezuma et al. 2022). Therefore, we expected predation risk to parallel these losses. While the average mortality through Weldon Dam was relatively high, ranging from ~8% to 16% between years, we estimated that only ~2% of smolts were predated in this area.

Fig. 4. Atlantic salmon (*Salmo salar*) smolt predation risk by reach type. (A) Relative predation rates through 15 intervals. Coloured shapes represent release (grey inverted pyramid), free-flowing river (blue circles), dammed (yellow squares), and estuarine (green triangles) reaches. (B) Cumulative predation probability through each reach type. Error bars represent 95% confidence limits.



Therefore, there is a large proportion of unexplained mortality that occurs through this project (Fig. 2). While the predation estimates account for some undetected predation events by modelling detection probabilities, this approach assumes the tags are still available (i.e., in the river) for detection.

Acoustic tags deposited in close proximity to hydropower dams are also difficult to detect given increased ambient noise, tag entrainment in dam structures, and our ability to safely approach facilities during mobile tracking. Ultimately, we are unable to disentangle whether the unknown mortality through Weldon Dam is the result of undetected predation (discussed later) or lethal injuries sustained during dam passage (e.g., turbine strikes, spillway falls, impingement, Algera et al. 2020).

Estuarine predation

We estimated that ~27% of smolts were predated through the Penobscot River estuary. Most of these events (26 out of 32) occurred in the lower estuary through a 22 km area downstream of Station 14. This is congruent with a gradual decrease in survival observed by previous studies as smolts progress towards the marine environment (Renkawitz et al. 2012; Stich et al. 2015*b*). However, the extent of marine mammal predation pressure observed in our study was substantial and unexpected. Overall, 13% of smolts tagged in this study were consumed by marine mammals and these events accounted for 88% of detected estuarine predation. Harbor porpoises are present in the river and may account for some marine mammal predation events, but there is little empirical evidence to suggest smolt predation by this species (Gibson and Atkinson 2003). Alternatively, we assume that the majority of marine mammal predation is from grey and harbor seals, as seals are known predators on juvenile Pacific salmonids (Clements et al. 2012; Thomas et al. 2017). In this study, the majority of mammal predation events were observed within 3 km of known seal haulouts at Odom's Ledge ($n = 8$, 1rkm) and Fort Point Ledge ($n = 13$, -6rkm, Figs. 1A, 2), where up to 65 seals have been spotted on a single occasion (Leach 2020). However, we expected the increased biomass of adult clupeids (e.g., *Alosa sp.*) migrating upstream to serve as a prey buffer for smolts migrating through the estuary (O'Malley et al. 2017), so were surprised by the degree of seal predation observed in this study during a time of increased prey availability. This may be the result of sub-lethal effects incurred earlier in migration (e.g., during dam passage, Stich et al. 2015*b*) or the "dinner-bell" effect, where marine mammals hear and selectively prey on acoustically tagged fish (Stansbury et al. 2015; Wargo Rub and Sandford 2020). The latter scenario has yet to be evaluated in the Northeast US, but if substantiated, may bias predation risk for untagged smolts.

Research beyond the Penobscot River suggests that striped bass may exert heavy predation pressure during smolt migration (Beland et al. 2001; Gibson et al. 2015; Daniels et al. 2018). Although the Penobscot River's striped bass population has increased following dam-removals (Watson et al. 2018), they were not a major smolt predator in this study. We only observed three fish predation events in striped bass habitat (i.e., downstream of Milford Dam) and none of these transmitter histories displayed movements characteristic of striped bass foraging patterns (Beland et al. 2001; Gibson et al. 2015; Daniels et al. 2018). In both years, striped bass were first encountered at the Milford Dam fish lift in early June

(MDMR 2021, 2022 *unpublished data*), after surviving smolts had moved through the study area. Due to early (mid-April) stocking efforts, hatchery-reared smolts may be more likely to avoid striped bass predation relative to wild-reared fish that migrate later in the season (Frechette et al. 2022).

Cumulative predation risk and unknown fates

We estimated that cumulative predation probability in our study system averaged 46% annually. This estimate falls within the range of other smolt studies (30%–59%) that used predation transmitters (Daniels et al. 2019; Notte et al. 2022; Hanssen et al. 2022). Unlike these studies, we were unable to tag naturally emigrating smolts in our study because of low population densities and an absence of rotary screw trapping efforts in the Penobscot River watershed during study years. Research from other systems suggests differential predation risk between naturally and hatchery-reared salmonids (Fresh et al. 2003; Fritts et al. 2007), but long-term monitoring in the Penobscot River suggests similar survival between these groups (Stich et al. 2015*a*). Future research in the watershed may benefit from incorporating smolt origin into predation risk assessments. Given intense hatchery supplementation efforts for this population, the estimates in this study are representative of the vast majority of smolts migrating through the system and we assume reflect the relative risk for naturally reared smolts.

Notably, neither cumulative survival nor predation estimates include the relatively high mortality (~3.5% annual average) observed between the release site and the first receiver station (Fig. 4A). Five smolts were predated in this reach alone, and three individuals were not detected after release (Fig. 2). This elevated post-stocking mortality is consistent with other research (Erhardt and Tiffan 2018; Klinard et al. 2019; Gatch et al. 2022). In our study, we assume this is caused by opportunistic predation on recovering and acclimating smolts and is not reflective of true predation risk through this river section. Therefore, our results support previous findings that describe the importance of accounting for post-release losses to avoid overestimating mortality.

The predation estimates presented in this study account for imperfect recovery of predated tags that remain available for detection. There was an 11% difference between tagged smolts that were detected as predated (35% excluding release interval) and our cumulative predation estimate (46%). Therefore, we would expect that ~23 smolts were predated, deposited somewhere in river, but were never detected. We assume that most of these undetected predation events were from predatory fishes, given that these tags likely remain in the river, and the majority of smolts with unknown fates were last detected in areas of increased fish predation (Fig. 2). When accounting for both observed and undetected predation events, we estimate there were ~30 smolts that incurred mortality from unknown sources. In addition to injuries associated with dam passage, tags that are transported to terrestrial environments by avian and mammalian predators may account for some additional unexplained mortality. Because these predation events result in permanent tag removal from the system, they are analogous to permanent emigration in a standard capture-mark-recapture study design, and are not likely to be captured by the detection parameter (Williams et al. 2002). Predation events preceding terrestrial tag deposition are most likely incorporated into estimates of S rather than Ψ in our modelling framework, and therefore the apparent cumulative predation estimates presented in this study may underestimate true predation risk.

In the Penobscot River, predators such as river otters and water birds represent the most likely mechanism for terrestrial deposition. Radio telemetry studies show that otters may predate and deposit tagged fish along riverbanks (Aarestrup et al. 2005; Babey et al. 2020; Flávio et al. 2021) which are then undetectable using acoustic telemetry alone. While we have yet to find definitive evidence of otter predation in the Penobscot River, they may help explain some smolt losses in the upper river (Fig. 2). Ultimately, we assume that diving water birds are responsible for most terrestrial tag transport, and thus may be a substantial source of latent predation. We recovered nine smolts that were consumed by avian predators during this study. While these tags were deposited in the river, research in the Columbia River system suggests that terrestrial deposition by avian predators are species specific but range from 15% to 71% (Hostetter et al. 2015). Applying these rates to our study, anywhere from 2 to 22 smolts could have been excreted on land, which may account for some of the unknown fates of fish last detected in impoundments (Fig. 2).

We assume that double-crested cormorants are responsible for the majority of avian predation events in this study. Cormorants (*Phalacrocoracidae sp.*) impose substantial predation pressure on migrating smolts in other systems (Sebring et al. 2013; Jepsen et al. 2019). Historically, the Penobscot River has supported a population of more than 1000 double-crested cormorants and they are frequently observed foraging near hydropower projects and throughout the estuary. Previous research on this population suggests they prey opportunistically on Atlantic salmon smolts (Blackwell et al. 1997), and one of our tags was recovered within 50 m of a cormorant rookery near Sandy Point (1rkm). Three additional tags were predated in the estuary near known cormorant foraging locations (Justin Stevens, Maine Sea Grant, *oral communication,* 2023), one of which was deposited in the Milford Dam impoundment (~40 km upstream). In addition to cormorants, we frequently observed common loons and common mergansers in reaches between the release site and Weldon Dam. These species may account for the fate of three bird-predated tags recovered within a 200 m area between Stations 2 and 3 (161rkm, Fig. 2). When considering recovery of predated tags and those unavailable for detection, our study suggests that at least 7% of smolts tagged in this study were consumed by avian predators, which may increase if we could determine the fates of all smolts.

In addition to terrestrial deposition, the mechanics of the acid-sensitive predation transmitters used in this study may add additional uncertainty to predation estimates. First, there is a delay between a predation event and when the predation sensor is triggered. Laboratory trials on similar transmitters suggest the magnitude of this delay is highly variable (1–78 h) and is temperature dependent (Halfyard et al. 2017;

Lennox et al. 2021). Absent of clear evidence of predator-facilitated transport, we assumed that predation events occurred in the same reach where the tag was first detected as predated. Therefore, lags in trigger time may cause some tags to be detected in different reaches than they were consumed, a risk exacerbated by highly mobile predators (e.g., seals, striped bass). While, this potential location-bias may change reach-specific predation estimates, we expect system-wide estimates to remain unchanged. Second, predation sensors may fail to trigger after consumption. Although we did not explicitly evaluate trigger-success, corroboration with temperature sensor data suggests the predation sensors triggered on ~90% of endothermic predation events, which was similar to rates reported by Halfyard et al. 2017 (95%). Therefore, a small proportion of smolts with unknown dispositions may have been consumed by predatory fishes, but the predation sensor never triggered. Third, predation sensors may trigger in the absence of the predation event. This is most likely to occur soon after dam passage when dead or moribund fish are susceptible to scavengers (Gadomski and Hall-Griswold 1992; Tiller et al. 2004; Havn et al. 2018). Despite relatively high detection in these areas (average $p = \sim$80%), we observed comparatively few predation events downstream of dams (Fig. 2). It is also unlikely that predation sensors would be triggered prior to predation events. This type of false-positive is most likely to occur after prolonged exposure to warm water temperatures (Halfyard et al. 2017; Slusher et al. 2021). Ambient water temperatures during this study (10 °C) were lower than trials that evaluated tag performance (12–24 °C), and therefore we expect the prevalence of false-positives to be minimal in this study.

Cumulative smolt mortality

We estimated that at least 55% of all mortality incurred by smolts in this study was predation-dependent. When combined with unknown sources of mortality, the average cumulative survival through the study area was 33%. Given the elevated predation risk near dams, we imagined a scenario in which predation rates through hydropower projects were reduced to the baseline predation expected through free-flowing reaches (Fig. 3). Under the conditions associated with this thought-experiment, cumulative survival through the study area increased by 6% in 2021 and 4% in 2022. While this increase may seem trivial, such improvements may substantially increase the number of smolts entering the marine environment.

Overall, the average cumulative survival estimated in this study is less than those reported from fish released at the same location (46%–62%, Stich et al. 2015*a*; Molina-Moctezuma et al. 2022). This may be for the following reasons, both of which our study design prevented us from reliably assessing. First, prior research in the Penobscot River indicated that smolt survival is optimized when river discharge exceeds 1000$m^3 \cdot s^{-1}$ (Stich et al. 2015*a*; Molina-Moctezuma et al. 2022). However, migrating smolts in this study did not experience flows beyond 850 $m^3 \cdot s^{-1}$ in either year (taken from the U.S. Geological Survey stream gage site 01034500, U.S. Geological Survey 2023). Higher flows reduce migration time, especially through impoundments, which may limit exposure to predators. Second, this difference may stem from explicitly including disposition in our analysis and reflect predation bias in past research (Gibson et al. 2015; Daniels et al. 2019). Predation-naïve mark-recapture studies may overestimate survival by failing to account for predated individuals that remain available for detection. Historical bias in this system may be most realized in the lower estuary, where predated smolts are detected as alive at the most downstream receiver stations (i.e., presenting as living fish). This scenario may also help explain greater estuarine mortality than previously reported in the system (Holbrook et al. 2011; Stich et al. 2015*b*; Molina-Moctezuma et al. 2022).

Implications for Atlantic salmon conservation

Our results suggest that predation is the leading source of mortality during Atlantic salmon smolt migration. While this is often speculated, we quantified predation risk throughout the main stem of the Penobscot River, the last stronghold of sea-run Atlantic salmon in the United States. While some mortality is expected during this life stage, it is important to understand how much mortality is sustainable. This study offers greater insights to the sources of mortality, which represents a critical step in developing recovery efforts. Given the heterogeneity of predation risk during migration, mitigation efforts may differ across contexts.

Dams facilitate predation and timely passage may be as important as safe passage. Management actions (e.g., flow manipulation) that allow smolts to move quickly through impoundments and locate safe, downstream passage may help alleviate predation risk in these areas (Cavallo et al. 2013; Courter et al. 2016; Frechette et al. 2022). Such actions may be most effective when paired with predator control measures that reduce the predator densities encountered by migrating smolts. For predatory fishes, this may include active predator removal (Cavallo et al. 2013; Michel et al. 2020), increased angling pressure, or reservoir draining (Murphy et al. 2019). Non-lethal harassment of double-crested cormorants may also minimize risk in these areas (Hawkes et al. 2013). However, it may be worth considering whether these actions are sustainable and that compensatory effects from the remaining predator communities do not outweigh potential gains (Beamesderfer 2000).

Increasing survival in the Penobscot River estuary may be challenging given the legal protections afforded to marine mammals and spatial extent of predation risk in this area. In the absence of predator control, actions that allow smolts to move under naturally decreased predation risk may be effective. In the Penobscot River, the majority of hatchery-reared smolts are released in early-April downstream of Milford Dam (Frechette et al. 2022), allowing them to move unimpeded into the estuary (13.3 km downstream). Therefore, predation risk may be mitigated with strategic releases based on diel cycle, (Vollset et al. 2017), water temperature (Karppinen et al. 2014; Nobriga et al. 2021), location (Thorstad et al. 2012*a*), and predator densities (Furey et al. 2016). Such synchrony is disturbed for wild-reared smolts that must pass multiple dams before estuarine arrival, where delays may result in migrat-

ing under suboptimal environmental conditions (Holbrook et al. 2011; Stich et al. 2015*b*; Molina-Moctezuma et al. 2022). This scenario further emphasizes the importance of efficient dam passage, which may help alleviate predation risk system wide. Ultimately, mitigating smolt predation risk that occurs beyond natural levels may represent a critical hurdle in Atlantic salmon recovery.

Acknowledgements

This project could not have been completed without the help of many graduate students and technicians in the Zydlewski and Mortelliti labs. Smolts were provided by the USFWS Green Lake National Fish Hatchery and hatchery staff were instrumental in facilitating fish tagging and transport. This manuscript was greatly improved through comments from Daniel Stich and two anonymous reviewers. 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 done in coordination and cooperation with NOAA Fisheries Northeast Fisheries Science Center and conducted under the University of Maine Institutional Animal Care and Use Committee protocol A2022-02-01.

Article information

History dates

Received: 19 June 2023
Accepted: 13 September 2023
Version of record online: 16 November 2023

Copyright

Data availability

At the time of publication, data were not publically available from NOAA Fisheries Northeast Fisheries Science Center. Data and code used in this study are available from the corresponding author upon reasonable request.

Author information

Author ORCIDs

Matthew A. Mensinger https://orcid.org/0000-0002-0873-4696
Alessio Mortelliti https://orcid.org/0000-0003-0480-6100
Erik J. Blomberg https://orcid.org/0000-0002-0810-5523
Joseph D. Zydlewski https://orcid.org/0000-0002-2255-2303

Author notes

Joseph D. Zydlewski served as an Associate Editor at the Canadian Journal of Fisheries and Aquatic Sciences at the time of manuscript review and acceptance and did not handle peer review and editorial decisions regarding this manuscript.

Author contributions

Conceptualization: MAM, JPH, GSG, AM, JDZ
Data curation: MAM, JPH, GSG
Formal analysis: MAM, EJB
Funding acquisition: MAM, JDZ
Investigation: MAM, JPH, GSG, AM
Methodology: MAM, JPH, GSG, AM, EJB, JDZ
Project administration: MAM, JPH, GSG, AM, JDZ
Resources: JDZ, JPH, GSG
Supervision: AM, JDZ
Validation: MAM, EJB
Visualization: MAM
Writing – original draft: MAM
Writing – review & editing: JPH, GSG, AM, EJB, JDZ

Funding information

Financial support for this research was provided by NOAA (NA19OAR4320074), West Enfield Fisheries Management Fund, and the University of Maine. Field and logistic support was provided by the University of Maine Department of Wildlife, Fisheries, and Conservation Biology. In-kind support was provided by the U.S. 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-2023-0175.

References

Aarestrup, K., Jepsen, N., Koed, A., and Pedersen, S. 2005. Movement and mortality of stocked brown trout in a stream. J. Fish Biol. **66**(3): 721–728. doi:10.1111/j.0022-1112.2005.00634.x.

Alexander, M.E., Kaiser, H., Weyl, O.L.F., and Dick, J.T.A. 2015. Habitat simplification increases the impact of a freshwater invasive fish. Environ. Biol. Fish. **98**(2): 477–486. doi:10.1007/s10641-014-0278-z.

Algera, D.A., Rytwinski, T., Taylor, J.J., Bennett, J.R., Smokorowski, K.E., Harrison, P.M., et al. 2020. What are the relative risks of mortality and injury for fish during downstream passage at hydroelectric dams in temperate regions? A systematic review. Environ. Evid. **9**(1): 3. doi:10.1186/s13750-020-0184-0.

Andrews, S.N., Hirtle, S.V., Linnansaari, T., and Curry, R.A. 2019. Consumption of Atlantic salmon smolt by striped bass: a review of the predator–prey encounter and implications for the design of effective sampling strategies. Fishes **4**(4): 50. doi:10.3390/fishes4040050.

Babey, C.N., Gantner, N., Williamson, C.J., Spendlow, I.E., and Shrimpton, J.M. 2020. Evidence of predation of juvenile white sturgeon (*Acipenser transmontanus*) by North American river otter (*Lontra canadensis*) in the Nechako River, British Columbia, Canada. J. Appl. Ichthyol. **36**(6): 780–784. doi:10.1111/jai.14114.

Beamesderfer, R.C.P. 2000. Managing fish predators and competitors: deciding when intervention is effective and appropriate. Fisheries, **25**(6): 18–23. doi:10.1577/1548-8446(2000)025⟨0018:MFPACD⟩2.0.CO;2.

Beland, K.F., Kocik, J.F., vandeSande, J., and Sheehan, T.F. 2001. Striped bass predation upon Atlantic salmon smolts in Maine. Northeastern Nat. **8**(3): 267–274. doi:10.1656/1092-6194(2001)008[0267:SBPUAS]2.0.CO;2.

Blackwell, B.F., Krohn, W.B., Dube, N.R., and Godin, A.J. 1997. Spring prey use by double-crested cormorants on the Penobscot River, Maine, USA. Colonial Waterbirds, **20**(1): 77. doi:10.2307/1521766.

Boily, P., and Lavigne, D.M. 1996. Thermoregulation of juvenile grey seals, *Halichoerus grypus*, in air. Can. J. Zool. **74**(2): 201–208. doi:10.1139/z96-025.

Bolker, B. 2020. emdbook: ecological models and data in R.

Brönmark, C., Hulthén, K., Nilsson, P.A., Skov, C., Hansson, L.-A., Brodersen, J., and Chapman, B.B. 2014. There and back again: migra-

tion in freshwater fishes. Can. J. Zool. **92**(6): 467–479. doi:10.1139/cjz-2012-0277.

Buchanan, R.A., Brandes, P.L., and Skalski, J.R. 2018. Survival of juvenile fall-run chinook salmon through the San Joaquin River Delta, California, 2010-2015. North Am. J. Fish Manage. **38**(3): 663–679. doi:10.1002/nafm.10063.

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.

Cavallo, B., Merz, J., and Setka, J. 2013. Effects of predator and flow manipulation on Chinook salmon (*Oncorhynchus tshawytscha*) survival in an imperiled estuary. Environ. Biol. Fish **96**(2–3): 393–403. doi:10.1007/s10641-012-9993-5.

Clements, S., Stahl, T., and Schreck, C.B. 2012. A comparison of the behavior and survival of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) in a small estuary system. Aquaculture, **362–363**: 148–157. doi:10.1016/j.aquaculture.2011.11.029.

Courter, I.I., Garrison, T.M., Kock, T.J., Perry, R.W., Child, D.B., and Hubble, J.D. 2016. Benefits of prescribed flows for salmon smolt survival enhancement vary longitudinally in a highly managed river system: benefits of prescribed flows for salmon survival. River Res. Appl. **32**(10): 1999–2008. doi:10.1002/rra.3066.

Daniels, J., Chaput, G., and Carr, J. 2018. Estimating consumption rate of Atlantic salmon smolts (*Salmo salar*) by striped bass (*Morone saxatilis*) in the Miramichi River estuary using acoustic telemetry. Can. J. Fish Aquat. Sci **75**(11): 1811–1822. doi:10.1139/cjfas-2017-0373.

Daniels, J., Sutton, S., Webber, D., and Carr, J. 2019. Extent of predation bias present in migration survival and timing of Atlantic salmon smolt (*Salmo salar*) as suggested by a novel acoustic tag. Anim. Biotelemetry, **7**(1): 16. doi:10.1186/s40317-019-0178-2.

Enstipp, M.R., Grémillet, D., and Jones, D.R. 2006. The effects of depth, temperature and food ingestion on the foraging energetics of a diving endotherm, the double-crested cormorant (*Phalacrocorax auritus*). J. Exp. Biol. **209**(5): 845–859. doi:10.1242/jeb.02064. PMID: 16481574.

Erhardt, J.M., and Tiffan, K.F. 2018. Post-release predation mortality of age-0 hatchery-reared Chinook salmon from non-native smallmouth bass in the Snake River. Fish Manag. Ecol. **25**(6): 474–487. doi:10.1111/fme.12322.

Flávio, H., Caballero, P., Jepsen, N., and Aarestrup, K. 2021. Atlantic salmon living on the edge: smolt behaviour and survival during seaward migration in River Minho. Ecol. Freshw Fish **30**(1): 61–72. doi:10.1111/eff.12564.

Frank, B.M., Gimenez, O., and Baret, P.V. 2012. Assessing brown trout (*Salmo trutta*) spawning movements with multistate capture–recapture models: a case study in a fully controlled Belgian brook. Can. J. Fish Aquat. Sci. **69**(6): 1091–1104. doi:10.1139/f2012-041.

Frechette, D.M., Hawkes, J.P., and Kocik, J.F. 2022. Managing for Atlantic Salmon smolt run timing variability in a changing climate. N. American J. Fish Manag. nafm.10868. doi:10.1002/nafm.10868.

Fresh, K.L., Schroder, S.L., and Carr, M.I. 2003. Predation by Northern pikeminnow on hatchery and wild coho salmon smolts in the Chehalis River, Washington. N. Am. J. Fish. Manag. **23**(4): 1257–1264. doi:10.1577/M02-030.

Fritts, A.L., Scott, J.L., and Pearsons, T.N. 2007. The effects of domestication on the relative vulnerability of hatchery and wild origin spring Chinook salmon (*Oncorhynchus tshawytscha*) to predation. Can. J. Fish. Aquat. Sci. **64**(5): 813–818. doi:10.1139/f07-057.

Furey, N.B., Hinch, S.G., Bass, A.L., Middleton, C.T., Minke-Martin, V., and Lotto, A.G. 2016. Predator swamping reduces predation risk during nocturnal migration of juvenile salmon in a high-mortality landscape. J. Anim. Ecol. **85**(4): 948–959. doi:10.1111/1365-2656.12528. PMID: 27159553.

Gadomski, D.M., and Hall-Griswold, J.A. 1992. Predation by Northern squawfish on live and dead juvenile chinook salmon. Trans. Am. Fish. Soc. **121**(5): 680–685. doi:10.1577/1548-8659(1992)121⟨0680:PBNSOL⟩2.3.CO;2.

Gaskin, D.E., Arnold, P.W., and Blair, B.A. 1974. Phocoena phocoena. Gluconeog.: Its Regul. Mamm. Species(42): 1–8. [American Society of Mammalogists, Oxford University Press].

Gatch, A.J., Furgal, S.L., Gorsky, D., Marsden, J.E., Biesinger, Z.F., and Lantry, B.F. 2022. Evaluation of post-stocking dispersal and mortality of juvenile lake trout salvelinus namaycush in Lake Ontario using acoustic telemetry. J. Great Lakes Res. **48**(2): 572–580. doi:10.1016/j.jglr.2022.01.014.

Gibson, A.J.F., Halfyard, E.A., Bradford, R.G., Stokesbury, M.J.W., and Redden, A.M. 2015. Effects of predation on telemetry-based survival estimates: insights from a study on endangered Atlantic salmon smolts. Can J Fish Aquat Sci **72**(5): 728–741. doi:10.1139/cjfas-2014-0245.

R.N. Gibson and R.J.A. Atkinson(*Editors*). 2003. Oceanography and marine biology: an annual review. **Vol. 41**. Taylor & Francis, London; New York. Available from http://www.myilibrary.com?id=2296 [accessed 27 January 2023].

Grill, G., Lehner, B., Lumsdon, A.E., MacDonald, G.K., Zarfl, C., and Reidy Liermann, C. 2015. An index-based framework for assessing patterns and trends in river fragmentation and flow regulation by global dams at multiple scales. Environ. Res. Lett. **10**(1): 015001. doi:10.1088/1748-9326/10/1/015001.

Halfyard, E.A., Webber, D., Del Papa, J., Leadley, T., Kessel, S.T., Colborne, S.F., and Fisk, A.T. 2017. Evaluation of an acoustic telemetry transmitter designed to identify predation events. Methods Ecol. Evol. **8**(9): 1063–1071. doi:10.1111/2041-210X.12726.

Hall, C.J., Jordaan, A., and Frisk, M.G. 2011. The historic influence of dams on diadromous fish habitat with a focus on river herring and hydrologic longitudinal connectivity. Landscape Ecol. **26**(1): 95–107. doi:10.1007/s10980-010-9539-1.

Hansen, S., and Lavigne, D.M. 1997. Ontogeny of the thermal limits in the harbor seal (*Phoca vitulina*). Physiol. Zool. **70**(1): 85–92. doi:10.1086/639549. PMID: 9231380.

Hanssen, E.M., Vollset, K.W., Salvanes, A.G.V., Barlaup, B., Whoriskey, K., Isaksen, T.E., et al. 2022. Acoustic telemetry predation sensors reveal the tribulations of Atlantic salmon (*Salmo salar*) smolts migrating through lakes. Ecol. Freshw. Fish. **31**(2): 424–437. doi:10.1111/eff.12641.

Havn, T.B., Thorstad, E.B., Teichert, M.A.K., Sæther, S.A., Heermann, L., Hedger, R.D., et al. 2018. Hydropower-related mortality and behaviour of Atlantic salmon smolts in the River Sieg, a German tributary to the Rhine. Hydrobiologia, **805**(1): 273–290. doi:10.1007/s10750-017-3311-3.

Hawkes, J.P., Saunders, R., Vashon, A.D., and Cooperman, M.S. 2013. Assessing efficacy of non-lethal harassment of double-crested cormorants to improve Atlantic salmon smolt survival. Northeast. Nat. **20**(1): 1–18. doi:10.1656/045.020.0101.

Hickerson, B.T., Maitland, B.M., and Walters, A.W. 2019. Effects of multiple nonnative fish on an imperiled cyprinid, hornyhead chub. Trans. Am. Fish. Soc. **148**(6): 1132–1145. doi:10.1002/tafs.10203.

Hinch, S.G., Cooke, S.J., Healey, M.C., and Farrell, A.P., (Tony). 2005. Behavioural physiology of fish migrations: salmon as a model approach. *In* Fish physiology. *Edited by* K.A. Sloman, R.W. Wilson and S. Balshine. Elsevier, Amsterdam. pp. 239–295. doi:10.1016/S1546-5098(05)24007-4.

Holbrook, C.M., Kinnison, M.T., and Zydlewski, J. 2011. Survival of migrating Atlantic Salmon smolts through the Penobscot River, Maine: a prerestoration assessment. Trans. Am. Fish. Soc. **140**(5): 1255–1268. doi:10.1080/00028487.2011.618356.

Hostetter, N.J., Evans, A.F., Cramer, B.M., Collis, K., Lyons, D.E., and Roby, D.D. 2015. Quantifying avian predation on fish populations: integrating predator-specific deposition probabilities in tag recovery studies. Trans. Am. Fish. Soc. **144**(2): 410–422. doi:10.1080/00028487.2014.988882.

Jepsen, N., Aarestrup, K., Økland, F., and Rasmussen, G. 1998. Survival of radio-tagged Atlantic salmon (*Salmo salar L.*) and trout (*Salmo trutta L.*) smolts passing a reservoir during seaward migration. Hydrobiologia, **371/372**: 347–353. doi:10.1023/A:1017047527478.

Jepsen, N., Flávio, H., and Koed, A. 2019. The impact of cormorant predation on Atlantic salmon and Sea trout smolt survival. Fish. Manag. Ecol. **26**(2): 183–186. doi:10.1111/fme.12329.

Jepsen, N., Pedersen, S., and Thorstad, E. 2000. Behavioural interactions between prey (trout smolts) and predators (pike and pikeperch) in an impounded river. Regul. Rivers: Res. Mgmt. **16**(2): 189–198.

doi:10.1002/(SICI)1099-1646(200003/04)16:2⟨189::AID-RRR570⟩3.0.CO;2-N.

Jones, K.A., Niknami, L.S., Buto, S.G., and Decker, D. 2022. Federal standards and procedures for the national Watershed Boundary Dataset (WBD). 5th ed. U.S. Geol. Surv. Tech. Methods, **11-A3**: 54. doi:10.3133/tm11A3.

Kålås, J.A., Heggberget, T.G., Bjørn, P.A., and Reitan, O. 1993. Feeding behaviour and diet of goosanders (*Mergus merganser*) in relation to salmonid seaward migration. Aquat. Living Resour. **6**(1): 31–38. EDP Sciences. doi:10.1051/alr:1993003.

Karppinen, P., Jounela, P., Huusko, R., and Erkinaro, J. 2014. Effects of release timing on migration behaviour and survival of hatchery-reared Atlantic salmon smolts in a regulated river. Ecol. Freshw. Fish **23**(3): 438–452. doi:10.1111/eff.12097.

Kenow, K.P., Fara, L.J., Houdek, S.C., Gray, B.R., Heard, D.J., Meyer, M.W., et al. 2021. Migration patterns and wintering distribution of common loons breeding in the Upper Midwest. J. Avian Biol. **52**(8): jav.02609. doi:10.1111/jav.02609.

Klinard, N.V., Matley, J.K., Fisk, A.T., and Johnson, T.B. 2019. Long-term retention of acoustic telemetry transmitters in temperate predators revealed by predation tags implanted in wild prey fish. J. Fish Biol. **95**(6): 1512–1516. doi:10.1111/jfb.14156. PMID: 31605542.

Klinard, N.V., Matley, J.K., Ivanova, S.V., Larocque, S.M., Fisk, A.T., and Johnson, T.B. 2021. Application of machine learning to identify predators of stocked fish in Lake Ontario: using acoustic telemetry predation tags to inform management. J. Fish Biol. **98**(1): 237–250. doi:10.1111/jfb.14574. PMID: 33015862.

Kocik, J.F., Hawkes, J.P., Sheehan, T.F., Music, P.A., and Beland, K.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. American Fisheries Society, Halifax, Canada. p. 293.

Koed, A., Jepsen, N., Aarestrup, K., and Nielsen, C. 2002. Initial mortality of radio-tagged Atlantic salmon (*Salmo salar L.*) smolt following release downstream of a hydropower station. Hydrobiologia, **483**(1/3): 31–37. doi:10.1023/A:1021390403703.

Laake, J.L. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115. Available from http://www.afsc.noaa.gov/Publications/ProcRpt/PR2013-01.pdf [accessed September 2022].

Leach, L. 2020. Assessing predator risk to diadromous fish conservation in the Penobscot River Estuary. The University of Maine. Orono, ME. Available from https://digitalcommons.library.umaine.edu/etd/3324 [accessed 13 January 2023].

Lennox, R.J., Nilsen, C.I., Nash, A., Hanssen, E.M., Johannesen, H.L., Berhe, S., et al. 2021. Laboratory and field experimental validation of two different predation sensors for instrumenting acoustic transmitters in fisheries research. Fisheries, **46**(11): 565–573. doi:10.1002/fsh.10669.

Lewandoski, S.A., Bishop, M.A., and McKinzie, M.K. 2018. Evaluating Pacific cod migratory behavior and site fidelity in a fjord environment using acoustic telemetry. Can. J. Fish. Aquat. Sci. **75**(11): 2084–2095. doi:10.1139/cjfas-2017-0432.

Lewis, D.J., Dundas, S.J., Kling, D.M., Lew, D.K., and Hacker, S.D. 2019. The non-market benefits of early and partial gains in managing threatened salmon. PLoS ONE, **14**(8): e0220260. doi:10.1371/journal.pone.0220260. PMID: 31412046.

Maine DEP. 2014. Hydropower relicensing. Maine Department of Environmental Protection, Augusta, Maine.

Mayfield, M.P., McMahon, T.E., Rotella, J.J., Gresswell, R.E., Selch, T., Saffel, P., et al. 2019. Application of multistate modeling to estimate salmonid survival and movement in relation to spatial and temporal variation in metal exposure in a mining-impacted river. Can. J. Fish. Aquat. Sci. **76**(11): 2057–2068. doi:10.1139/cjfas-2018-0280.

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.

McMichael, G.A., Eppard, M.B., Carlson, T.J., Carter, J.A., Ebberts, B.D., Brown, R.S., et al. 2010. The juvenile salmon acoustic telemetry system: a new tool. Fisheries, **35**(1): 9–22. doi:10.1577/1548-8446-35.1.9.

Mensinger, M.A., Blomberg, E.J., and Zydlewski, J.D. 2021. The consequences of dam passage for downstream-migrating American eel in the Penobscot River, Maine. Can. J. Fish. Aquat. Sci. doi:10.1139/cjfas-2020-0402.

Michel, C.J., Smith, J.M., Lehman, B.M., Demetras, N.J., Huff, D.D., Brandes, P.L., et al. 2020. Limitations of active removal to manage predatory fish populations. N. Am. J. Fish. Manag. **40**(1): 3–16. doi:10.1002/nafm.10391.

Modde, T., Wasowicz, A.F., and Hepworth, D.K. 1996. Cormorant and grebe predation on rainbow trout stocked in a Southern Utah reservoir. N. Am. J. Fish. Manag. **16**(2): 388–394. doi:10.1577/1548-8675(1996)016⟨0388:CAGPOR⟩2.3.CO;2.

Molina-Moctezuma, A., Stich, D.S., and Zydlewski, J.D. 2022. 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. Can. J. Fish. Aquat. Sci. **79**(12): 2237–2250. doi:10.1139/cjfas-2022-0055.

Mortelliti, A. 2023. The importance of animal behavior for ecosystem services. Trends Ecol. Evol. **38**: 320–333. doi:10.1016/j.tree.2022.10.009.

Murphy, C.A., Romer, J.D., Stertz, K., Arismendi, I., Emig, R., Monzyk, F., and Johnson, S.L. 2021. Damming salmon fry: evidence for predation by non-native warmwater fishes in reservoirs. Ecosphere, **12**(9). doi:10.1002/ecs2.3757.

Murphy, C.A., Taylor, G., Pierce, T., Arismendi, I., and Johnson, S.L. 2019. Short-term reservoir draining to streambed for juvenile salmon passage and non-native fish removal. Ecohydrology, **12**(6):. doi:10.1002/eco.2096. PMID: 31762869.

Nilsson, J., Flink, H., and Tibblin, P. 2019. Predator–prey role reversal may impair the recovery of declining pike populations. J. Anim. Ecol. **88**(6): 927–939. doi:10.1111/1365-2656.12981. PMID: 30895606.

Noakes, D.J., Beamish, R.J., and Kent, M.L. 2000. On the decline of Pacific salmon and speculative links to salmon farming in British Columbia. Aquaculture **183**(3–4):363–386. doi:10.1016/S0044-8486(99)00294-X.

Nobriga, M.L., Michel, C.J., Johnson, R.C., and Wikert, J.D. 2021. Coldwater fish in a warm water world: implications for predation of salmon smolts during estuary transit. Nat. Ecol. Evol. **11**(15): 10381–10395. doi:10.1002/ece3.7840. PMID: 34367582.

Notte, D.V., Lennox, R.J., Hardie, D.C., and Crossin, G.T. 2022. Application of machine learning and acoustic predation tags to classify migration fate of Atlantic salmon smolts. Oecologia, **198**(3): 605–618. doi:10.1007/s00442-022-05138-3. PMID: 35244774.

O'Malley, M.B., Saunders, R., Stevens, J.R., Jech, J.M., and Sheehan, T.F. 2017. Using hydroacoustics to describe pelagic fish distribution in the Penobscot Estuary, Maine. Trans. Am. Fish. Soc. **146**(5): 817–833. doi:10.1080/00028487.2017.1308883.

Osterback, A.-M.K., Frechette, D.M., Shelton, A.O., Hayes, S.A., Bond, M.H., Shaffer, S.A., and Moore, J.W. 2013. High predation on small populations: avian predation on imperiled salmonids. Ecosphere, **4**(9): art116. doi:10.1890/ES13-00100.1.

Pelicice, F.M., and Agostinho, A.A. 2009. Fish fauna destruction after the introduction of a non-native predator (*Cichla kelberi*) in a Neotropical reservoir. Biol. Invasions **11**(8): 1789–1801. doi:10.1007/s10530-008-9358-3.

Powell, L.A. 2007. Approximating variance of demographic parameters using the Delta method: a reference for Avian biologists. Condor, **109**(4): 949–954. doi:10.1093/condor/109.4.949.

R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org [accessed January 2021].

Renkawitz, M.D., Sheehan, T.F., and Goulette, G.S. 2012. Swimming depth, behavior, and survival of Atlantic Salmon postsmolts in Penobscot Bay, Maine. Trans. Am. Fish. Soc. **141**(5): 1219–1229. doi:10.1080/00028487.2012.688916.

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.

Schultz, A.A., Afentoulis, V.B., Yip, C.J., and Johnson, M.N. 2017. Efficacy of an acoustic tag with predation detection technology. N. Am. J. Fish. Manag. **37**(3): 574–581. doi:10.1080/02755947.2017.1290720.

Sebring, S.H., Carper, M.C., Ledgerwood, R.D., Sandford, B.P., Matthews, G.M., and Evans, A.F. 2013. Relative vulnerability of PIT-tagged

subyearling fall chinook salmon to predation by caspian terns and double-crested cormorants in the Columbia River Estuary. Trans. Am. Fish. Soc. **142**(5): 1321–1334. doi:10.1080/00028487.2013.806952.

Slusher, B., Thomas, M., Peterson, M., and Guignard, J. 2021. V3D Predation Tag Testing. FISHBIO, Oakdale, CA.

Sortland, L.K., Lennox, R.J., Velle, G., Vollset, K.W., and Kambestad, M. 2023. Impacts of predation by Eurasian otters on Atlantic salmon in two Norwegian rivers. Freshw. Biol. **68**(7): 1176–1193. doi:10.1111/fwb.14095.

Spelman, L.H., Jochem, W.J., Sumner, P.W., Redmond, D.P., and Stoskopf, M.K. 1997. Postanesthetic monitoring of core body temperature using telemetry in North American River otters (*Lontra canadensis*). J. Zoo Wildl. Med. **28**(4): 413–417. PMID: 9523635.

Stansbury, A.L., Götz, T., Deecke, V.B., and Janik, V.M. 2015. Grey seals use anthropogenic signals from acoustic tags to locate fish: evidence from a simulated foraging task. Proc. Biol. Sci. **282**(1798): 20141595. doi:10.1098/rspb.2014.1595.

Stevens, J.R., Kocik, J.F., and Sheehan, T.F. 2019. Modeling the impacts of dams and stocking practices on an endangered Atlantic salmon (*Salmo salar*) population in the Penobscot River, Maine, USA. Can. J. Fish. Aquat. Sci. **76**(10): 1795–1807. doi:10.1139/cjfas-2018-0225.

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.

Stich, D.S., Zydlewski, G.B., Kocik, J.F., and Zydlewski, J.D. 2015b. 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.

Swain, D., and Benoît, H. 2015. Extreme increases in natural mortality prevent recovery of collapsed fish populations in a Northwest Atlantic ecosystem. Mar. Ecol. Prog. Ser. **519**: 165–182. doi:10.3354/meps11012.

Thakur, M.P., Künne, T., Griffin, J.N., and Eisenhauer, N. 2017. Warming magnifies predation and reduces prey coexistence in a model litter arthropod system. Proc. Biol. Sci. **284**(1851): 20162570. doi:10.1098/rspb.2016.2570.

Thomas, A.C., Nelson, B.W., Lance, M.M., Deagle, B.E., and Trites, A.W. 2017. Harbour seals target juvenile salmon of conservation concern. Can. J. Fish. Aquat. Sci. **74**(6): 907–921. doi:10.1139/cjfas-2015-0558.

Thorstad, E.B., Uglem, I., Finstad, B., Chittenden, C.M., Nilsen, R., Økland, F., and Bjørn, P.A. 2012a. Stocking location and predation by marine fishes affect survival of hatchery-reared Atlantic salmon smolts: survival and migration of hatchery-reared smolts. Fish. Manag. Ecol. **19**(5): 400–409. doi:10.1111/j.1365-2400.2012.00854.x.

Thorstad, E.B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A.H., and Finstad, B. 2012b. A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. J. Fish. Biol. **81**(2): 500–542. doi:10.1111/j.1095-8649.2012.03370.x. PMID: 22803722.

Tiller, B.L., McKinstry, C.A., Welch, I.D., and Bernhard, J.E. 2004. Assessment of Potential Juvenile Salmon Predation by American White Pelicans in the Vicinity of McNary Dam, 2002-2003. Battelle, Pacific Northwest Division.

U.S. Geological Survey. 2019. National Hydrography Dataset (ver. USGS National Hydrography Dataset Best Resolution (NHD) for Hydrologic Unit (HU) 4 - 2001. Available from https://www.usgs.gov/national-hydrography/access-national-hydrography-products [accessed 2 June 2022].

U.S. Geological Survey. 2023. USGS 01034500 Penobscot River at West Enfield, Maine. Available from https://waterdata.usgs.gov/ [accessed 10 September 2023].

USASAC. 2023. Annual Report of the U.S. Atlantic Salmon Assessment Committee, Report No. 35 - 2022 Activities. United States Atlantic Salmon Assessment Committee.

USFWS, and NOAA. 2009. Endangered and threatened species; determination of endangered status for the Gulf of Maine distinct population segment of Atlantic Salmon. U.S. Fish & Wildlife Service, Washington, DC.

van den Ende, O. 1993. Predation of Atlantic salmon smolts (Salmo salar) by smallmouth bass (*Micropterus dolomieu*) and chain pickerel (*Esox niger*) in the Penobscot River, Maine. MS Thesis. University of Maine, Orono, Maine.

Vollset, K.W., Barlaup, B.T., and Normann, E.S. 2017. Release during night enhances survival of wild Atlantic salmon smolts. Fish. Manag. Ecol. **24**(3): 256–264. doi:10.1111/fme.12230.

Waldman, J.R., and Quinn, T.P. 2022. North American diadromous fishes: drivers of decline and potential for recovery in the Sci. Adv. **8**(4): eabl5486. doi:10.1126/sciadv.abl5486.

Wargo Rub, A., and Sandford, B. 2020. Evidence of a 'dinner bell' effect from acoustic transmitters in adult Chinook salmon. Mar. Ecol. Prog. Ser. **641**: 1–11. doi:10.3354/meps13323.

Watson, J.M., Coghlan, S.M., Zydlewski, J., Hayes, D.B., and Kiraly, I.A. 2018. Dam removal and fish passage improvement influence fish assemblages in the Penobscot River. Maine. Trans Am Fish Soc **147**(3): 525–540. doi:10.1002/tafs.10053.

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.

Williams, B.K., Nichols, J.D., and Conroy, M.J. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, CA.