

Catchment-wide survival of wild- and hatchery-reared Atlantic salmon smolts in a changing system

Daniel S. Stich, Michael M. Bailey, Christopher M. Holbrook, Michael T. Kinnison, and Joseph D. Zydlewski

Abstract: We developed a hierarchical multistate model to estimate survival of Atlantic salmon (*Salmo salar*) smolts in the Penobscot River, USA, over a decade during which two mainstem dams were removed from the catchment. We investigated effects of (i) environmental factors, (ii) rearing history, and (iii) management actions, including dam removal, turbine shutdown, and installation of new powerhouses. Mean \pm SD smolt survival per kilometre was higher through free-flowing reaches of the catchment ($0.995 \pm 0.004 \cdot \text{km}^{-1}$) than through reaches containing dams that remain in the system ($0.970 \pm 0.019 \cdot \text{km}^{-1}$). We observed maximum survival between 12 and 17 °C and at intermediate discharges ($1200 \text{ m}^3 \cdot \text{s}^{-1}$). Smolt survival increased concurrent with dam removal and decreased following increases in hydropower generation. The greatest increase in smolt survival followed seasonal turbine shutdowns at a dam located on the largest tributary to the Penobscot River, while other shutdowns had little influence. Our model provides a useful tool for assessing changes to survival of migratory species and will be useful for informing stocking plans to maximize numbers of smolts leaving coastal systems.

Résumé : Nous avons élaboré un modèle multi-états hiérarchique pour estimer la survie de saumoneaux de saumon atlantique (*Salmo salar*) dans le fleuve Penobscot (États-Unis) pendant une décennie durant laquelle deux barrages sur le bras principal du fleuve ont été retirés du bassin versant. Nous avons examiné les effets (i) de facteurs ambiants, (ii) de l'historique d'élevage et (iii) des mesures de gestion dont le retrait de barrages, l'arrêt de turbines et l'aménagement de nouvelles centrales électriques. Le taux de survie moyen \pm écart-type par kilomètre des saumoneaux était plus élevé dans les tronçons non régulés du bassin versant ($0.995 \pm 0.004 \cdot \text{km}^{-1}$) que dans les tronçons contenant toujours des barrages ($0.970 \pm 0.019 \cdot \text{km}^{-1}$). Les taux de survie maximums observés étaient entre 12 et 17 °C et à des débits intermédiaires ($1200 \text{ m}^3 \cdot \text{s}^{-1}$). La survie des saumoneaux a augmenté après le retrait des barrages et diminué après des augmentations de la production hydroélectrique. La plus grande augmentation du taux de survie des saumoneaux coïncidait avec des arrêts saisonniers de turbines à un barrage sur le plus grand affluent du fleuve Penobscot, alors que les autres arrêts de turbines n'ont pas eu une grande influence. Notre modèle constitue un outil pour évaluer les variations de la survie d'espèces migratrices et pour éclairer l'élaboration de plans d'empoissonnement dans le but de maximiser le nombre de saumoneaux qui quittent les systèmes côtiers. [Traduit par la Rédaction]

Introduction

Atlantic salmon (*Salmo salar*) stocks in North America diminished beginning in the 1800s, owing to pollution, poor land-use practices, dams, and overfishing (Haines 1992; Parrish et al. 1998). Many of the stocks in the southern range of the species are listed as critically endangered in Canada and the United States. One major driver of reduced Atlantic salmon stock abundances is the effect of ocean conditions on early marine growth (Friedland 1998; Friedland et al. 2000) and survival (Salminen et al. 1995; Friedland et al. 2003a, 2003b). Few options exist for improving marine survival (Hansen et al. 2012; Russell et al. 2012), and therefore a primary goal for recovery of imperiled stocks is to maximize the number of smolts that reach the ocean to offset high mortality there. Changes to links between marine and freshwater ecosystems (Friedland 1998), as well as impediments to passage (such as dams) in migration corridors, can limit population recovery (Parrish et al. 1998; Johnsen et al. 2011).

Migratory delay, physiological impairment (Zydlewski et al. 2010), increased risk of predation (Poe et al. 1991; Blackwell and Juanes 1998), and mortality (Mathur et al. 2000; Keefer et al. 2012) resulting from dam passage can reduce the number of smolts reaching the ocean. Accumulating effects of passing multiple dams can further interfere with migration (Branco et al. 2014; Stich et al. 2015a). This cumulative effect of passing multiple dams can result in elevated mortality during the early marine phase of salmonid migrations in both Pacific (Budy et al. 2002; Schreck et al. 2006) and Atlantic (Stich et al. 2015a) rivers. The magnitude of freshwater mortality occurring from the passage of multiple dams is still not well characterized.

Among extant stocks of Atlantic salmon in the US, the Penobscot River population is the largest, contributing to more than 75% of total US adult returns each year since the 1970s (US Atlantic Salmon Assessment Committee 2014). A major restoration project (the Penobscot River Restoration Project, PRRP), started in 2004 with the goal of balancing hydropower production in the river

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D.S. Stich. Department of Wildlife, Fisheries, and Conservation Biology, 5755 Nutting Hall, University of Maine, Orono, ME 04469, USA.

M.M. Bailey. US Fish and Wildlife Service, Central New England Fishery Resource Office, Nashua, NH 03063, USA.

C.M. Holbrook. US Geological Survey, Great Lakes Science Center Hammond Bay Biological Station, Millersburg, MI 49721, USA.

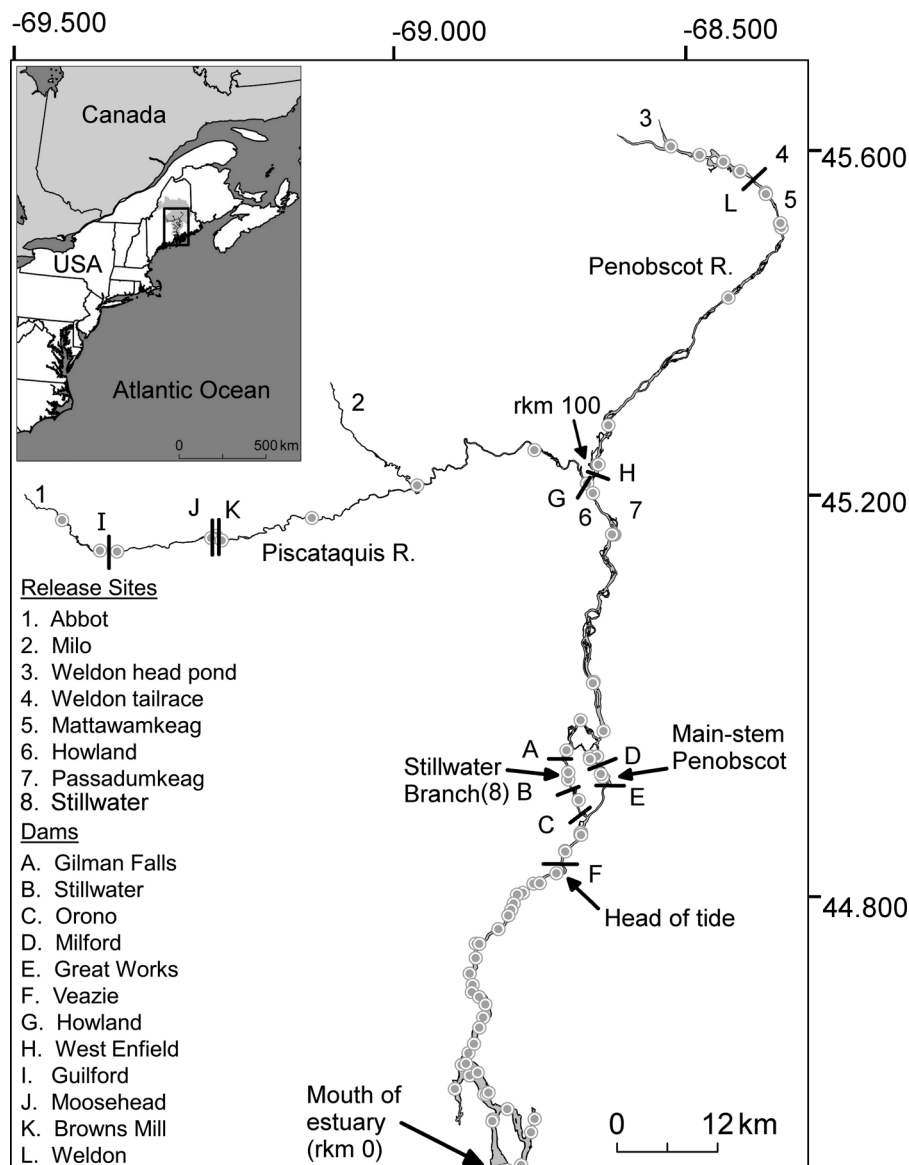
M.T. Kinnison. School of Biology and Ecology, 5751 Murray Hall, University of Maine, Orono, ME 04469, USA.

J.D. Zydlewski. Department of Wildlife, Fisheries, and Conservation Biology, 5755 Nutting Hall, University of Maine, Orono, ME 04469, USA;

US Geological Survey, Maine Cooperative Fish and Wildlife Research Unit, 5755 Nutting Hall, University of Maine, Orono, ME 04469, USA.

Corresponding author: Daniel S. Stich (e-mail: daniel.stich@maine.edu).

Fig. 1. Map of the Penobscot River catchment, showing location in North America (inset), locations of acoustic receivers (grey circles), release sites for acoustically tagged fish throughout the river, and locations of dams (bold lines). Not shown are 40+ acoustic receivers deployed from the mouth of the estuary to the ocean.



with the restoration of diadromous fishes (11 species). Major changes in hydropower generation have occurred in the Penobscot River since 2009 as part of the PRRP (Day 2006). Specific details of changes to hydropower dam operations and downstream fish passage resulting from combined effects of dam removal and hydropower reallocation in the Penobscot River were described by the Federal Energy Regulatory Commission (Federal Energy Regulatory Commission 2004, 2009) and the National Marine Fisheries Service (National Marine Fisheries Service 2012a, 2012b).

Starting in spring 2010, generating turbines at Howland (Fig. 1), Great Works (Fig. 1), and Veazie (Fig. 1) dams were shut down during the smolt migration each year until the removal of Great Works Dam in summer 2012 and the removal of Veazie Dam during summer 2013 as part of the species protection plan (National Marine Fisheries Service 2012a). Seasonal (7 May through 20 May) nighttime shut-downs were continued at Howland Dam. Hydropower generation at Milford Dam (Fig. 1) increased in spring 2012 with the addition of two turbines. Concurrent with these actions, hydropower generation at

the Stillwater (Fig. 1) and Orono (Fig. 1) dams was increased by raising head pond elevation (Federal Energy Regulatory Commission 2005). A secondary powerhouse was constructed at both Stillwater and Orono dams during 2013, which approximately doubled the generating capacity of each facility prior to the 2014 smolt migration (National Marine Fisheries Service 2012b).

The goal of this study was to use a multi-annual data set to assess the effects of tributary-specific management actions on the number of smolts reaching the ocean in the largest extant population of Atlantic salmon in the US and determine what contribution freshwater reaches in the Penobscot River made to the total mortality within that stock from 2005 through 2014. Therefore, the primary objective of this study was to estimate survival of smolts throughout the Penobscot River and its tributaries using hierarchical, multi-state (MS) mark-recapture models from 8 years of smolt migrations before and after changes to hydropower projects in the catchment. As a secondary objective, we evaluated effects of environmental variables (e.g., discharge) and hydropower operations on smolt survival.

Methods

Study site

Although the Penobscot River stock of Atlantic salmon is the largest in the US, abundance has been low since the middle to late 20th century (Trinko Lake et al. 2012), being further diminished in recent years. As part of the species' recovery plan, Atlantic salmon is stocked throughout the catchment at egg, fry, parr, and smolt life stages (US Atlantic Salmon Assessment Committee 2014). Egg and fry plantings occur in headwater streams and contribute proportionally few fish, in combination with wild spawning, to the smolt run each spring (US Atlantic Salmon Assessment Committee 2014). Most migrating smolts are 18-month-old, hatchery-reared smolts stocked in the main stem. As a result, the majority of the adult run (~83%) is made up of hatchery-stocked smolts with few naturally reared counterparts (US Atlantic Salmon Assessment Committee 2012).

All Atlantic salmon (stocked or naturally reared) in the upper Penobscot River enter the main stem at river kilometre (rkm) 100 during migration, passing the Howland Dam (Fig. 1) or West Enfield Dam (Fig. 1) near the confluence of the upper Penobscot River and the Piscataquis River. Smolts approach the Marsh Island hydropower complex at rkm 60, where most (88%) remain in the main stem to the east, and the remainder (12%) use the Stillwater Branch to the west (Fig. 1) before entering the estuary (Stich et al. 2014).

On the east side of Marsh Island (Penobscot River) smolts passed two dams (Great Works and Milford dams) until the removal of the Great Works Dam (Fig. 1) in 2012 and Veazie Dam in 2013. Previous estimates of annual survival through Great Works Dam (98%) and Veazie Dam (99%) were high relative to other dams in the Penobscot, and thus little improvement (1%) in smolt survival is anticipated in that reach of the main stem as a result of dam removal (Holbrook et al. 2011; Stich et al. 2014). Cumulative survival during migration through the Stillwater Branch (96%), on the west side of Marsh Island, historically has been higher than cumulative survival through the main stem (88%), owing largely to relatively low survival at Milford Dam (91%; Fig. 1). Based on historically high downstream survival of migrating smolts, survival through Stillwater and Orono dams in the Stillwater Branch is not expected to increase with the doubling of hydropower generation at those facilities (Stich et al. 2014). Changes in survival through Milford Dam following addition of two generating turbines and increased head pond height are less predictable. Use of the Stillwater Branch by smolts increases with discharge (Stich et al. 2014), and as such cumulative survival of smolts through the lower river could change based on flow diversion and use of the Stillwater Branch by smolts as well.

Acoustic tagging and releases

From 2005 through 2014 smolts were acoustically tagged ($n = 2056$; Table 1) and released into the Penobscot catchment at locations ranging from 63 to 187 rkm (Fig. 1) from the mouth of the estuary, of which 1823 smolts were subsequently relocated using acoustic telemetry. Of the relocated fish, 1504 were hatchery-reared smolts from the US Fish and Wildlife Service (USFWS) Green Lake National Fish Hatchery (GLNFH), and the remaining 319 were wild-reared smolts captured in the Piscataquis River at rotary screw traps run by the Maine Department of Marine Resources in Abbot or in the Penobscot River at the Weldon Dam smolt bypass trap (Table 1). Acoustic tagging methods were described in detail by Holbrook et al. (2011) and Stich et al. (2014); identical procedures were used in all years from 2005 through 2014 of the present study. Briefly, smolts were anaesthetized using a 100 mg·L⁻¹ solution of MS-222 (buffered with 20 mmol NaHCO₃; pH = 7.0). A small (1 cm) incision was made slightly offset from the ventral line and 1 cm posterior to the pectoral fin girdle. An acoustic tag was inserted and the incision was closed with two simple, interrupted knots using 4-0 absorbable vicryl sutures (Ethicon, Somerville,

Table 1. Data summary for acoustically tagged Atlantic salmon smolts released in the Penobscot River, 2005–2014, showing number of fish relocated from release group (n), and within-release groups, means of accumulated thermal units (ATUs), discharge experienced during migration (Q , m³·s⁻¹), photoperiod at release (PP, hours), and daily temperature experienced during migration (T , °C).

Year	Origin	Release site	n	ATU	Q	PP	T
2005	Hatchery	Howland	103 (150)	262	1416	13.9	7.8
		Mattawamkeag	10 (40)	221	1058	13.4	5.9
		Milo	85 (85)	268	1407	13.9	7.5
2006	Hatchery	Weldon	34 (60)	417	1014	15.2	11.1
		Milo	66 (72)	316	401	13.9	8.3
		Weldon	135 (146)	333	489	13.9	9.2
2009	Hatchery	Weldon	46 (73)	346	454	14.5	13.3
		Milo	96 (100)	387	689	14.2	10.4
		Passadumkeag	97 (100)	378	728	14.1	10.1
2010	Wild	Abbot	74 (75)	376	297	14.3	14.0
		Weldon Head Pond	65 (74)	447	283	14.5	13.5
		Milo	100 (100)	364	351	13.9	10.1
2011	Hatchery	Passadumkeag	98 (100)	364	359	13.9	9.7
		Abbot	74 (75)	241	1068	14.7	10.9
		Weldon Head Pond	26 (60)	390	743	15.2	15.0
2012	Hatchery	Milo	88 (100)	228	1195	14.0	7.4
		Passadumkeag	97 (100)	239	1231	14.0	8.1
		Abbot	72 (72)	336	670	13.8	8.8
2013	Hatchery	Weldon Head Pond	84 (85)	336	620	13.8	8.7
		Abbot	70 (75)	253	715	13.5	6.7
		Weldon Head Pond	80 (82)	253	665	13.5	7.4
2014	Hatchery	Abbot	68 (75)	338	950	14.3	8.7
		Weldon Head Pond	80 (82)	338	900	14.3	9.0
		Stillwater	75 (75)	338	1005	14.3	8.3

Note: The number in the parentheses under n is initial size of release group.

New Jersey, USA). Model V7 acoustic tags (Amirix Vemco Ltd., Halifax, Nova Scotia, Canada) with a pinger sound pressure level of 136 dB re 1 μ Pa at 1 m were used in 2005 and for wild fish in 2011. Expected battery life of V7 tags was 69–80 days. In all other years, model V9 acoustic tags (Amirix Vemco Ltd.) with battery life of 80–82 days and sound pressure level of 151 dB re 1 μ Pa at 1 m were used.

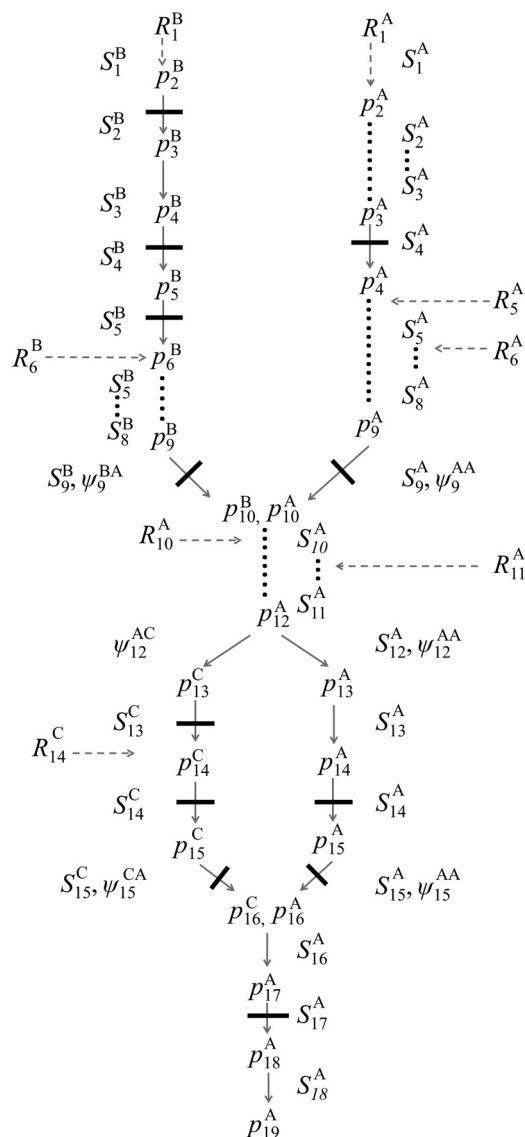
Acoustic array

Smolts were tracked using an array of stationary VR2 and VR2-W acoustic receivers (Amirix Vemco Ltd.). The array was deployed prior to tagging each year cooperatively among the United States Geological Survey (USGS) Maine Cooperative Fish and Wildlife Research Unit, the University of Maine, and the National Oceanic and Atmospheric Administration (NOAA). Coverage extended from rkm 187 in the Piscataquis River and rkm 165 in the East Branch of the Penobscot River to the mouth of Penobscot Bay (rkm -45; Fig. 1). Numbers and locations of acoustic receivers used varied during the study years, and as such we restricted our analysis to locations that were common to most years. Acoustic receivers were deployed on the river bottom with 45 kg concrete anchors in the freshwater and estuary reaches, while receivers in the bay were tethered 10 m below the surface. Multiple receivers were deployed across the river to achieve cross-sectional coverage where needed; smolt detections at these locations were pooled for statistical analyses. For the purpose of this study, all acoustic receivers from the second location downstream of Veazie Dam (rkm 43.5) to the bay were pooled as a terminal detection event.

Multistate (MS) survival model

Survival was estimated in the Penobscot River 2005–2014 using MS mark-recapture models (Fig. 2). Spatially explicit capture histories were created for each smolt using detections at acoustic receivers during one-way downstream migration (Fig. 2). To accommodate two upstream sources (Piscataquis River and East Branch) and two migration routes through the Marsh Island com-

Fig. 2. Schematic representation of multistate mark-recapture models used to estimate apparent survival (S), probability of detection (p), and state-transition probabilities (ψ) of acoustically tagged Atlantic salmon smolts within each reach of the mainstem Penobscot River (A), the Piscataquis River (B), and the Stillwater Branch (C). The symbol “R” represents release events that occurred at location t within state h . Bold lines represent dams.



plex, three “states” were used, in addition to a nondetected (dead) state. Detection in the Penobscot River (A), Piscataquis River (B), or Stillwater Branch (C) defined the state occupied by fish (Fig. 2). Fish were assigned a zero (0) for locations at which they were not detected, meaning that they may not have reached that location (owing to death or ceased migration) or that they passed that location undetected. Within each state, apparent survival (S), probability of detection (p), and probability of movement into the other two states (ψ) were estimated. Survival estimated from these models is “apparent” rather than “true” survival (confirmation of dead fish is generally not possible), but we use the term “survival” throughout for simplicity.

Parameters of MS models were estimated using a hierarchical (state-space) modeling framework (Calvert et al. 2009) in WinBUGS (Lunn et al. 2000) from the “R2WinBUGS” package (Sturtz et al. 2005) in R (version 3.1.0; R Core Team 2014). The use of MS models

Table 2. State-process matrix showing probability that an individual occupies state h' at interval $t + 1$ given the true state h of the individual at interval t , the probability of surviving interval t , and the probability of changing states immediately before $t + 1$.

True state at t	True state at $t + 1$			
	Penobscot (A)	Piscataquis (B)	Stillwater (C)	Dead (0)
Penobscot (A)	$S_t^A (1 - \psi_t^{AC})$	0	$S_t^A (1 - \psi_t^{AA})$	$1 - S_t^A$
Piscataquis (B)	$S_t^B (1 - \psi_t^{BB})$	$S_t^B (1 - \psi_t^{BA})$	0	$1 - S_t^B$
Stillwater (C)	$S_t^C (1 - \psi_t^{CC})$	0	$S_t^C (1 - \psi_t^{CA})$	$1 - S_t^C$
Dead (0)	0	0	0	1

Note: The matrix is reduced from its general form to reflect parameter constraints imposed by biological constraints of the system and the downstream nature of Atlantic salmon smolt migrations.

allows for separate estimation of S and ψ while accounting for imperfect detection. The probability of detecting a smolt was contingent upon the state occupied by fish and probability of survival within that state. The state occupied by fish was conditional on the probability of moving between states in the previous interval, as well as on the initial state occupied, which was known (stocking location). Therefore, the likelihood for MS models incorporated components describing the state and the observation processes.

In the state matrix of the MS models (Table 2), the probability of occupying a given state (h') at a given location ($t + 1$) was based on the state of an individual (i) at the previous location (t), the probability of survival in state h during interval t (S_t^h), and the probability of moving from one state (h) to another (h') immediately prior to location $t + 1$, given survival during interval t ($\psi_t^{h,h'}$). Because of this, the state-process model was conditioned on the state at first observation (stocking tributary was known; see Fig. 2). As such, the likelihood used in the state-process model was defined (see Kéry and Schaub 2011) by the following component equations:

$$(1) \quad z_{i,f_i} = fh_i$$

and

$$(2) \quad z_{i,t+1}|z_{i,t} \sim \text{categorical}(\Omega_{z_{i,t},1,\dots,H,i,t})$$

where $z_{i,t}$ was the true state of each individual i at interval t , and f was the state (h) of each fish at first encounter. The probability of an individual's true state was a categorical distribution described by the four-dimensional array Ω (Table 2) in which the first dimension corresponded with the true state z at location t , the second dimension was the vector of true states ($1, \dots, H$) at location $t + 1$, the third dimension was the individual fish (i), and the fourth dimension represented location t (see Kéry and Schaub 2011 for a general structure).

Detection probability (p) was estimated separately for each location in each state (p_t^h) in the MS models (Fig. 2). The likelihood for the observation process, conditional on the state of individual i , was defined as follows (see Kéry and Schaub 2011):

$$(3) \quad y_{i,t}|z_{i,t} \sim \text{categorical}(\Theta_{z_{i,t},1,\dots,O,i,t})$$

where y was the observed state of individual i at location t given the true state of that individual at location t , and y was defined to have a categorical distribution described by the four-dimensional array Θ (Table 3). The first dimension of Θ corresponded with the vector of true states, the second dimension was the vector of observed states (O), the third dimension was the individual (i), and the fourth dimension was location t (see Kéry and Schaub 2011).

Table 3. Observation-process matrix showing the probability of Atlantic salmon being detected in a given state at location t conditional on the true state of individuals at location t .

True state at t	Observation at t			
	Penobscot (A)	Piscataquis (B)	Stillwater (C)	Not detected
Penobscot (A)	p_t^A	0	0	$1 - p_t^A$
Piscataquis (B)	0	p_t^B	0	$1 - p_t^B$
Stillwater (C)	0	0	p_t^C	$1 - p_t^C$
Dead (0)	0	0	0	1

Note: States of individuals were assumed to be known without error given that they were detected.

General MS model

In the most general MS model structures, animals are allowed to transition among all states during every interval. In reality, there are physical constraints to this structure when modeling survival of smolts during downstream migration through a river. In these models, we assume that migration occurs in one direction (downstream), and thus some states can only be occupied by individuals during some intervals (see Fig. 2). Within the state- and observation-process matrices, constraints were imposed on survival, state transition, and detection probabilities based on physical constraints of the study system (Table 2) to produce a “general” model structure (Fig. 3). First, we did not allow downstream-migrating fish to transition to the Piscataquis River (B) from the Penobscot River (A) or the Stillwater Branch (C) during any interval, so $\psi_{t-1,t}^{AB}$ and $\psi_{t-1,t}^{CB}$ were fixed to zero for all reaches (Fig. 2; Table 2).

We assumed smolts that failed to move downstream represented mortality even if this was not confirmed, because failed migrants typically make little to no population contribution because of high overwinter mortality (Horton et al. 2009). The only interval during which fish could move from the Piscataquis River into the Penobscot was $t = 9$ when the probability of transition was 1 given that fish survived (i.e., $\psi_{1,...,8}^{BA} = 0$, $\psi_9^{BA} = 1$, and $\psi_{10,...,19}^{BA} = 0$), and no fish could move from the Piscataquis River directly into the Stillwater Branch ($\psi_{1,...,19}^{CA} = 0$) given the intervening mainstem Penobscot River. It was impossible to detect a fish in the Piscataquis River (state B) after $t = 8$; therefore, $S_{10,...,19}^B$ and $p_{9,...,19}^B$ were fixed to 1. The only interval during which fish could move from the Penobscot River (state A) into the Stillwater Branch was at $t = 12$; therefore, $\psi_{1,...,11}^{AC}$ and $\psi_{13,...,19}^{AC}$ were fixed to 0. Fish could be located in the Stillwater Branch only when $t = 12, \dots, 14$; therefore, $p_{1,...,11}^C$, $p_{15,...,19}^C$, $S_{1,...,12}^C$, and $S_{16,...,19}^C$ all were fixed to 1. Probability of fish moving from the Stillwater Branch into the mainstem Penobscot River after interval $t = 15$ was fixed to 1 given survival during interval $t = 15$.

Based on the constraints imposed above, the only state-transition probability estimated within MS models was the probability of moving into the Stillwater Branch from the Penobscot River during interval $t = 12$ (ψ_{12}^{AC}), and this parameter was assigned a uniform prior distribution between 0 and 1. Similarly, survival through intervals for which no constraint was applied ($S_{1,...,19}^A$, $S_{1,...,9}^B$, and $S_{13,...,15}^C$) and detection probabilities that were not constrained ($p_{1,...,19}^A$, $p_{1,...,8}^B$, and $p_{12,...,14}^C$) were assigned uniform prior distributions between 0 and 1.

Base model

We modified the general model by including the size of acoustic transmitters as a group-level covariate of detection probability, and we used an individual detection covariate for discharge, resulting in the “base model” that was used to estimate reach-specific survival across years. For the detection model, discharge was defined as the mean discharge experienced by each smolt during downstream migration, as measured at West Enfield Dam

(Fig. 1). All subsequent models modified the structure of this base model (Fig. 3). Acoustic tag model ($V7 = 0$, $V9 = 1$) was included as a fixed effect (β_1) in the observation model. Because we previously have found that larger (i.e., louder) tags (V9) were easier to detect than smaller (V7) tags (Stich et al. 2015a), we used a “flat” prior distribution for the effect of tag type defined as a uniform distribution between 0 and 1, $U(0, 1)$. Similarly, we have observed an inverse relationship between freshwater discharge (Q) and detection. The prior for this covariate effect (β_2) was defined as for tag type. Each of these priors was then transformed on the logit scale for estimation, resulting in a normal prior distribution for each coefficient on the logit scale ($N(0, 1.8)$). For all locations (t) at which detection (p_t^h) was not fixed to 1, the posterior probability (\hat{p}_t^h) was modeled as a function of fixed effects (β_j) of tag model (Tag _{i}) used and discharge (Q_i) for individual fish (i) using a logit link function as

$$(4) \quad \text{logit}(\hat{p}_t^h) = \beta_0 + \beta_1 \times \text{Tag}_i + \beta_2 \times Q_i$$

Parameter estimation

We used Markov chain Monte Carlo (MCMC) methods to estimate survival, state-transition, and detection probabilities for the base model and all extensions thereof. We ran three Markov chains for each parameter in each model and chose random starting values for each individual chain from the prior distribution of each parameter. We used a burn-in of 3000 samples and then sampled another 30 000 values from the posterior distribution of each parameter, keeping every third sample to reduce autocorrelation between samples and to increase the number of independent samples (effective sample size; Kruschke 2011). This resulted in a total of 1000 burn-in samples in each chain and 10 000 samples from the posterior distribution of each chain for each parameter estimated, yielding a total of 30 000 samples from which to construct the posterior distribution of each parameter. We assessed convergence of Markov chains using the Gelman and Rubin convergence diagnostic ($\hat{r} \approx 1.00$ at convergence). We monitored the number of independent samples from the posterior distribution of each parameter (effective sample size) to ensure adequate sampling (Kruschke 2011).

Unless otherwise specified, survival estimates are presented as posterior mean (95% credible interval (CRI)) in the results. To standardize survival as a per-kilometre rate ($\hat{S}_{D_i}^h$), reach survival (\hat{S}_t^h) through each interval (t) in each state (h) was raised to the power of one divided by interval length (D_t , km) to which the estimate corresponded (as $(\hat{S}_t^h)^{1/D_t}$). This approach allowed direct comparisons of the posterior distributions of estimated survival within each interval for all models developed in this study despite the fact that reaches varied in total distance.

Estimating cumulative survival from the base model

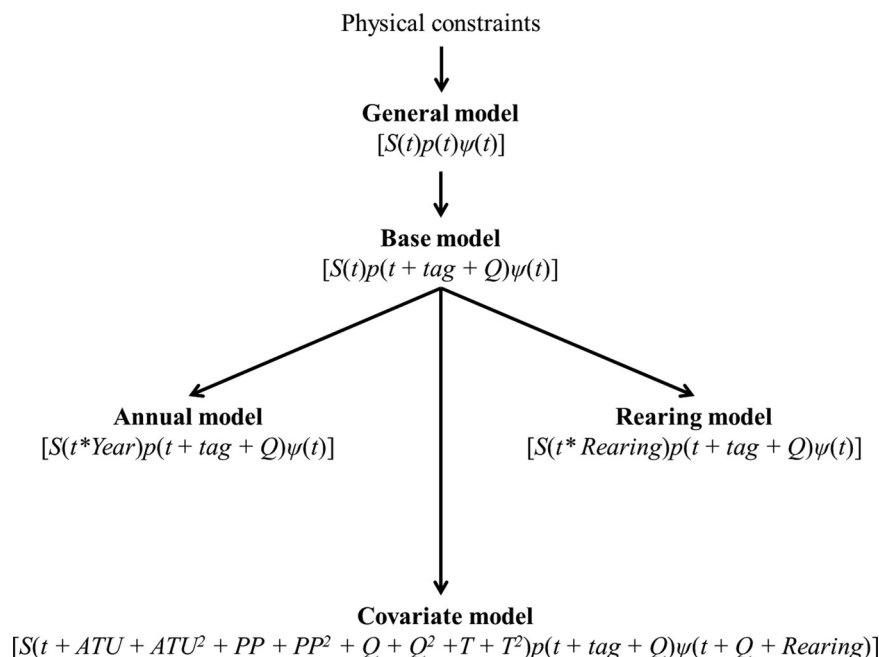
We calculated cumulative survival of Atlantic salmon smolts from the Piscataquis River to the estuary for each MCMC simulation from the base model using per-kilometre survival through each interval as

$$(5) \quad \hat{S}_{\text{Piscataquis}} = \prod_{t=1}^9 \hat{S}_t^B \times \prod_{t=10}^{12} \hat{S}_t^A \times \left[(1 - \psi_{12}^{AC}) \times \prod_{t=15}^{17} \hat{S}_t^A + \psi_{12}^{AC} \times \prod_{t=13}^{15} \hat{S}_t^C \right] \times \prod_{t=16}^{17} \hat{S}_t^A$$

Cumulative survival of smolts migrating from the upper main stem of the Penobscot River to the estuary was calculated from the posterior distributions of per-kilometre survival in a similar fashion:

$$(6) \quad \hat{S}_{\text{Main stem}} = \prod_{t=1}^{12} \hat{S}_t^A \times \left[(1 - \psi_{12}^{AC}) \times \prod_{t=15}^{17} \hat{S}_t^A + \psi_{12}^{AC} \times \prod_{t=13}^{15} \hat{S}_t^C \right] \times \prod_{t=16}^{17} \hat{S}_t^A$$

Fig. 3. Schematic of model development for multistate (MS) mark–recapture models used to estimate interval-specific (indicated by t) survival and detection probabilities, as well as proportional use of the Stillwater Branch by Atlantic salmon smolts in the Penobscot River catchment during 2005–2014. The general MS model structure is given at the top and is extended to include effects of tag model (tag) and discharge (Q) on detection probability (base model). The base model was further extended to estimate (i) annual survival (Annual model) and effects of rearing history on survival (Rearing model) and (ii) linear and quadratic fixed effects of discharge, accumulated thermal units (ATU), photoperiod (PP), and temperature (T) on survival, as well as effects of discharge and rearing history on use of the Stillwater Branch. Note that the general model was not fit to the data, but provided the framework for all subsequent model structures.



To determine the cumulative effects of dam passage on the number of smolts arriving in the estuary, we compared cumulative survival derived from the above equations with the expected survival through the system in the absence of dams. To do this, we replaced estimated survival through intervals containing dams or head ponds associated with dams with the mean of estimated survival through all intervals that did not contain dams or head ponds, for each MCMC simulation, to account for uncertainty in the free-flowing survival estimates. While we recognize that reaches near to specific dams could also have been used for this purpose, we have noticed no apparent trend in survival throughout the system based on previous research (Holbrook et al. 2011; Stich et al. 2014) or during the present study, and the approach we took incorporates uncertainty about survival in the free-flowing reaches of the system. For the sake of comparison, an average survival rate was estimated for (i) free-flowing reaches in the system and (ii) reaches containing dams for each MCMC simulation.

Environmental covariates

We extended the base model to include effects of date (photoperiod), discharge, and temperature experienced by individual smolts on survival (Fig. 3). Photoperiod on the release date for each fish was calculated from latitudes in the watershed and day of year for detections. Daily temperature and discharge data were obtained from the US Geological Survey river gage at West Enfield Dam. Discharge and temperature covariates were calculated for each fish as the mean daily average of the covariate from the time of release to the final detection. Because of the potential for collinearity and confounding among explanatory variables, we examined correlations between explanatory variables prior to analysis. Given that none of the variables were strongly correlated ($r < 0.60$ for all variable comparisons), we felt comfortable moving forward with the analysis without modification. Similarly, post hoc analysis of correlations between coefficient estimates from MCMC samples indicated that most parameter estimates were uncorre-

lated, and none were so strongly correlated as to be problematic for estimation.

Prior distributions for survival in the base model were modified to incorporate these factors in a “covariate model” (Fig. 3). As above, the prior distribution on survival in each interval within each state (S_t^h) was uniform between 0 and 1 (i.e., $U(0, 1)$), such that survival (\hat{S}_t^h) was modeled as a function of interval (t) and individual fish (i) using a logit link function to estimate the fixed effect (β_j) of the j th covariate (X_{ij}) as

$$(7) \quad \text{logit}(\hat{S}_t^h) = \beta_0 + \sum_{j=1}^{k=8} \beta_j \times X_{ij}, \dots, \beta_k \times X_{ik}$$

The prior distribution for each of the β_j was constructed as a logit-transformation of a uniform distribution ($U(0, 1)$) that was used to constrain the values to the probability scale. This resulted in a normal prior distribution for each coefficient on the logit scale ($N(0, 1.8)$). All covariates were standardized prior to analysis to speed model convergence and facilitate comparison between effects. We first ran a full additive model that included linear and quadratic terms each for (i) photoperiod, (ii) discharge, (iii) temperature, and (iv) the accumulated thermal units (ATUs) experienced by smolts from 1 January to tagging (sensu Sykes et al. 2009). These factors have been identified as major drivers of smolt migrations (see McCormick et al. 1998). Our rationale for including second-order terms for each of the environmental covariates was that there theoretically is some threshold after which effects on smolt survival might reverse or asymptote during migration. To understand the influence of each covariate on survival, we used Gibbs variable selection (Tenan et al. 2014) to estimate the probability that each covariate coefficient was included in the true model.

We ran the covariate model once (using settings described above) and used the posterior distributions for the coefficient estimates from the first run as priors to run the model a second time and estimate a probability that each covariate was retained (Tenan et al. 2014). To characterize the sensitivity of parameter inclusion probabilities, and hence our inferences, to choice of prior (Tenan et al. 2014), we also conducted Gibbs variable selection using flat priors ($U(0, 1)$) transformed to produce a normal distribution with mean 0 on the logit scale for all model coefficients instead of the estimates from the first model run. A binary indicator variable, gamma, for each coefficient was incorporated in the regression function to include (gamma = 1) or exclude (gamma = 0) each covariate coefficient from the model at each MCMC iteration. A flat Bernoulli ($p = 0.5$) distribution was used as the prior probability of each γ_j . The probability of each covariate being in the model (i.e., parameter inclusion probability) was then calculated as the posterior mean of gamma (see Tenan et al. 2014):

$$(8) \quad \text{logit}(\hat{\delta}_i^h) = \beta_0 + \sum_{j=1}^{k=8} \gamma_j \times \beta_j \times X_{ij}, \dots, \gamma_k \times \beta_k \times X_{ik}$$

We used the same variable-selection process described above to investigate influences of discharge and rearing history on the probability of using the Stillwater Branch (ψ_{12}^{AC}) as a migration route through the lower river. The prior on ψ_{12}^{AC} was uniform between 0 and 1 ($U(0, 1)$) and was transformed to produce a normally distributed prior on the logit scale. The effects of discharge and rearing history were estimated as

$$(9) \quad \text{logit}(\hat{\psi}_{12}^{\text{AC}}) = \beta_0 + \sum_{j=1}^{k=2} \gamma_j \times \beta_j \times X_{ij}, \dots, \gamma_k \times \beta_k \times X_{ik}$$

Rearing history

We extended the base model to estimate mean survival for hatchery- and wild-reared fish across years to assess influence of rearing history (Fig. 3). Because we were unsure how survival might vary, we estimated survival probability in each reach for each rearing history. Based on consideration of model size and estimability of parameters, we did not include environmental covariates in this “rearing model”, with the exception of detection covariates (tag and discharge). The prior distributions for survival probabilities in the base model were therefore modified to allow independent estimation of survival for hatchery and wild fish (i.e., group-specific survival in each reach). Because there were no other covariates in the survival model, this could be accomplished on the probability scale by the use of a fixed group effect (see Kéry and Schaub 2011). Although we recognize the potential for confounding of this effect with annual variability (not included in this model) owing to lack of balance in release groups, our objective for this model was to determine whether gross differences existed between rearing histories considering uncertainty involved with year-to-year variation.

Tracking changes in annual survival

The efficacy of management and conservation activities within the Penobscot River to increase smolt survival was assessed by extending the base model to estimate survival separately for each year (Fig. 3). We included acoustic tag model and discharge as covariates in the detection model for this “annual model” and estimated detection across years because we did not foresee sources of detection heterogeneity other than these variables. We compared per-kilometre rates of survival in years preceding man-

agement actions to per-kilometre rates survival in years following those actions. We examined effects of three types of management: (i) dam removals at Great Works Dam (2012) and Veazie Dam (2013); (ii) turbine shutdowns during the smolt migration at Howland (2010–2014), Great Works (2010–2012), and Veazie dams (2010–2013); and (iii) increases in hydropower generation at Milford (2012–2014), Orono (spring 2013–2014), and Stillwater dams (2013–2014). To calculate effects of management actions, we subtracted average estimated survival in years following management actions from average survival in years preceding management actions for each of the reaches in question. To incorporate uncertainty in these estimates, this was done for each MCMC simulation, resulting in 30 000 estimates of the change in survival following each of the management actions. To improve inferences about the effects of management actions, we contrast changes through impacted reaches with changes in estimated survival through the nearest free-flowing reaches of river during the same periods.

Results

Base model

Detection probability was higher for smolts tagged with the larger (model V9) acoustic tags than the smaller (model V7) tags according to the base model (Table 4). Detection probability for the larger tag was 73% (95% CRI = 71%–76%) greater than the smaller tag. Detection probability also decreased with increasing discharge. Over the range of discharge (212–2164 m³·s⁻¹), detection probability decreased from 0.81 (0.80–0.82) to 0.028 (0.023–0.034).

Survival of smolts in free-flowing (i.e., unimpounded) reaches of the river was high across years. Mean survival through all free-flowing reaches across years was 0.995·km⁻¹ (0.987–0.999·km⁻¹). Survival through reaches containing dams was notably lower than survival through unimpounded reaches or reaches that contained head ponds in most cases (Fig. 4). Survival rates through some reaches containing dams were as much as 0.05 lower per kilometre than through unimpounded reaches (see online supplementary material, Table S1¹).

Cumulative mortality was high during migration from the most upstream reaches of the catchment to the estuary. Cumulative survival to the mouth of the estuary was 0.459 (0.422–0.497) for fish emigrating from the upper Penobscot River (rkm 165) and was 0.486 (0.449–0.522) for fish emigrating from the upper Piscataquis River (rkm 187). This resulted in an average cumulative survival of 0.473 (0.428–0.517) for smolts emigrating from the river. Most losses occurred through reaches of the freshwater system associated with dams that, in terms of coverage in the system, represent a minority of the study river (Fig. 4). For reference, reaches containing dams in the Penobscot River accounted for 32 rkm of the more than 250 rkm through which survival was estimated in the present study or about 15% of the total study system.

When survival through intervals containing dams and head ponds was replaced with mean survival through free-flowing intervals, cumulative survival of smolts from the Piscataquis River was 0.609 (0.555–0.661), and cumulative survival of smolts from the upper main stem of the Penobscot River was 0.600 (0.539–0.657). These results indicate a decrease in cumulative survival probability of 0.12 (20% reduction) for smolts from the Piscataquis River and a decrease in cumulative survival probability of 0.15 (25% reduction) for smolts from the mainstem Penobscot River due to the effects of dams and head ponds associated with dams.

Rearing model

Based on comparisons of survival from wild- and hatchery-reared smolts, there was little difference in survival among rear-

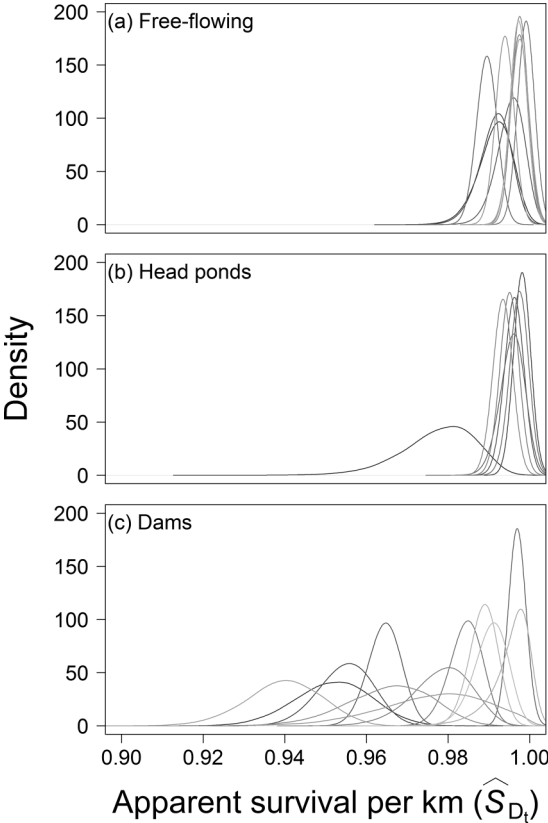
¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0573>.

Table 4. Mean and 95% credible intervals (CRIs) for each of the covariates used to model detection probability, apparent survival, and the probability of transitioning into the Stillwater Branch from the mainstem Penobscot River (ψ_{12}^{AC}) during migration through the lower river by Atlantic salmon smolts.

Parameter modeled	Covariate	Mean	SD	2.5%	97.5%	iPIP	uPIP
Detection (p)	Tag model	1.007	0.066	0.878	1.139	1.000	1.000
	Discharge	-0.988	0.026	-1.039	-0.937	1.000	0.998
Survival (S)	Discharge	1.392	0.086	1.224	1.565	1.000	0.989
	Discharge ²	-0.536	0.037	-0.609	-0.463	1.000	0.964
	ATU	0.182	0.077	0.030	0.333	0.425	0.237
	ATU ²	0.064	0.036	-0.006	0.134	0.317	0.088
	Photoperiod	-0.977	0.086	-1.147	-0.808	1.000	0.904
	Photoperiod ²	-0.001	0.030	-0.059	0.058	0.129	0.031
	Temperature	1.676	0.082	1.514	1.837	1.000	0.997
	Temperature ²	-0.279	0.020	-0.319	-0.240	1.000	0.995
Transition to stillwater (ψ_{12}^{AC})	Discharge	0.159	0.090	-0.190	0.336	0.630	0.449
	Rearing history	-0.282	0.238	-0.741	0.198	0.183	0.144

Note: Coefficient estimates are from the “covariate model”. Parameter inclusion probability (PIP) is given for each covariate separately for covariate models using informative (iPIP) and unininformative (uPIP) priors on survival, detection, transition, and covariate effects.

Fig. 4. Density plots for posterior distributions of estimated survival of Atlantic salmon smolts through (a) reaches that do not contain impoundments or head ponds, (b) reaches that contained head ponds, and (c) reaches of the river that contained dams.



ing histories (Table S2¹). In general, the trend in survival estimates for hatchery and wild fish was similar (Fig. 5), with survival at dams generally low relative to free-flowing reaches of the river. Additionally, in most cases, estimated survival for hatchery and wild fish were also quite similar within reaches. However, in the Stillwater Branch, where all reaches contained dams, survival of hatchery-reared fish was similar to free-flowing reaches, while survival of wild fish was lower at two of the dams (Fig. 5).

Covariate model

Mean probability of using the Stillwater Branch was 0.113 (0.096–0.131) among years and was influenced by environmental condi-

tions. Use of the Stillwater Branch increased with increasing discharge. Although the 95% CRI for the effect of discharge contained zero, there was a relatively high probability (0.62) that the effect of discharge was included in the best model (Table 4). Conversely, there was little support for differential use of the Stillwater Branch between rearing histories (inclusion probability = 0.18; Table 4).

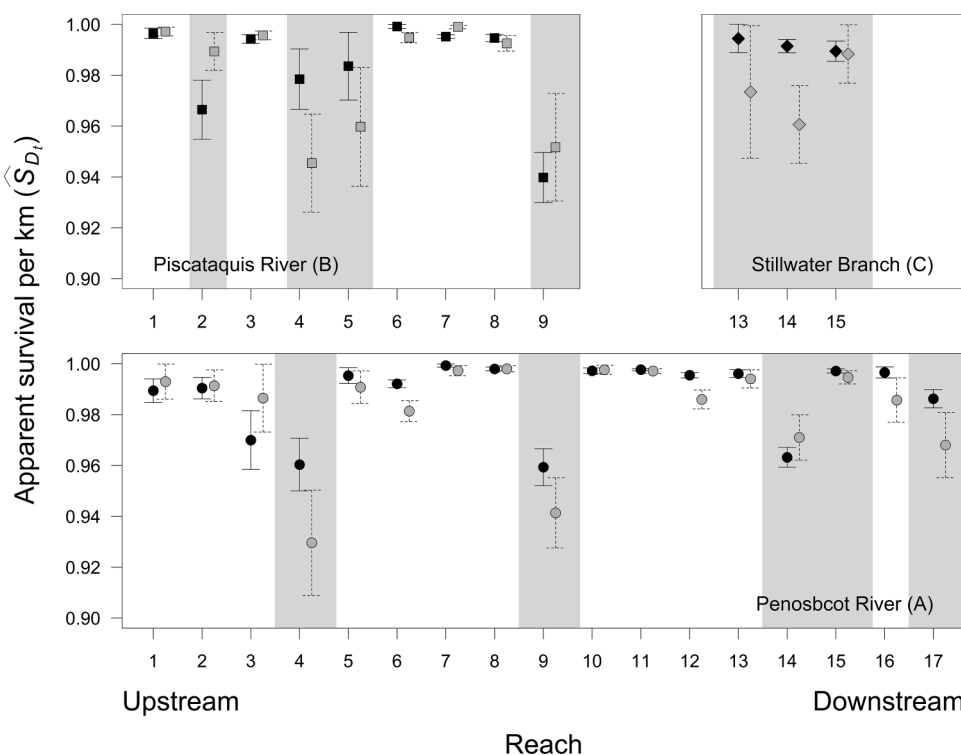
Smolt survival increased with increasing discharge until about 1200 m³·s⁻¹ (Fig. 6a), but decreased at discharges higher than that. Over the range of observed discharge (212–2164 m³·s⁻¹), survival increased from 0.034 (0.032–0.036) at the lowest discharge to 0.712 (0.649–0.790) at intermediate discharge of about 1200 m³·s⁻¹ (Fig. 6a). The estimated regression coefficients for the first- and second-order terms used to estimate effects of discharge on survival both excluded zero, suggesting that both were important predictors of survival (Table 4). Inclusion probabilities for these terms also indicated both were supported (Table 4).

ATUs experienced by Atlantic salmon smolts prior to tagging were positively related to survival (Fig. 6b). Fish that experienced the greatest ATU (warmer development period) had 47% higher survival (mean = 0.686, 95% CRI = 0.510–0.822) than fish experiencing the lowest ATU (mean = 0.467, 95% CRI = 0.449–0.485). Although the 95% CRI of the coefficient for linear effect of ATU did not contain zero, the probability that the variable was included in the best model was less than 0.50 (Table 4). The 95% CRI for the quadratic term contained zero, and there was a low probability of inclusion for the quadratic term (0.32), suggesting that a quadratic effect of ATU on survival was not strongly supported (Table 4).

We found strong evidence for a relationship between smolt survival and mean water temperature experienced during migration (Fig. 6d). Survival was lowest (approximately zero) at temperatures below 5 °C, after which survival increased rapidly until reaching 0.93 (0.86–0.97) near 12 °C. Survival remained high with increasing temperature from about 12 °C to about 19 °C, after which smolt survival began to decrease again (Fig. 6d). Both the linear and quadratic effects of temperature were strongly supported based on lack overlap of coefficients with zero, and the high probability that both terms were included in the model (Table 4).

Smolts migrating during longer photoperiod had lower survival than those migrating at shorter photoperiods (Fig. 6c). Survival decreased from 0.865 (0.853–0.878) when photoperiod was shortest in the earliest part of the smolt run to about 0.044 (0.015–0.123) when photoperiod was longest in the latest part of the run (Fig. 6c). The estimated coefficient for the quadratic effect of photoperiod on survival was essentially centered at zero, and the 95% CRI overlapped zero considerably (Table 4). The inclusion probability for the quadratic effect (0.129) indicated low probabil-

Fig. 5. Mean (\pm SD) estimated apparent survival (per kilometre) of hatchery- (black symbols) and wild-reared (gray symbols) Atlantic salmon smolts through discrete reaches of the Penobscot River catchment in all years (2005–2014) from release locations to the head of tide in the Penobscot River (circles, state A), the Piscataquis River (squares, state B), and the Stillwater Branch (diamonds, state C). Reach numbers and states correspond to parameters in the model schematic (Fig. 2), as well as those in Table S2¹. Gray panels indicate reaches containing dams.



ity that the term was included in the model (Table 4). Conversely, both the 95% CRI of the regression coefficient and the inclusion probability indicated strong support for inclusion of the linear term (Table 4).

Changes in annual survival following management actions from the annual model

The removal of Great Works Dam in 2012 and Veazie Dam in 2013 increased smolt survival, but the increase was small. The result was an increase of 0.005 in smolt survival following removal of Great Works Dam and an increase of 0.014 following removal of Veazie Dam (Fig. 7). Although these changes are small, it is noteworthy that survival at each of these dams was already high prior to dam removal (Table S3¹), and thus there was little room for increased survival at these dams. At Great Works Dam, survival increased despite slight decreases in nearby free-flowing reaches during the same period (Fig. 7). Conversely, the change in survival following the removal of Veazie Dam appeared to mirror changes through the nearest free-flowing reach (Fig. 7).

Seasonal shutdowns of hydropower generation at three facilities in the Penobscot River were varied in efficacy. At Howland Dam, a marked increase in smolt survival (+0.078) coincided with shutdowns in 2010 (Fig. 7). This change was also quite pronounced in comparison with the modest increases in estimated survival through the nearest free-flowing reach during that time period (Fig. 7). However, the results of shutdowns at Veazie (2010–2013) and Great Works dams (2010–2012) were more ambiguous. Minimal increase in survival followed turbine shutdown at Great Works Dam (+0.001), but survival at Veazie Dam appeared to decrease (−0.014) slightly following implementation (Fig. 7). Similar to the removal of these dams, smolt survival through Great Works Dam increased despite reduced survival through the nearest free-flowing river reach, whereas smolt survival at Veazie Dam ap-

peared to follow the same decreasing pattern as the nearest free-flowing reach (Fig. 7).

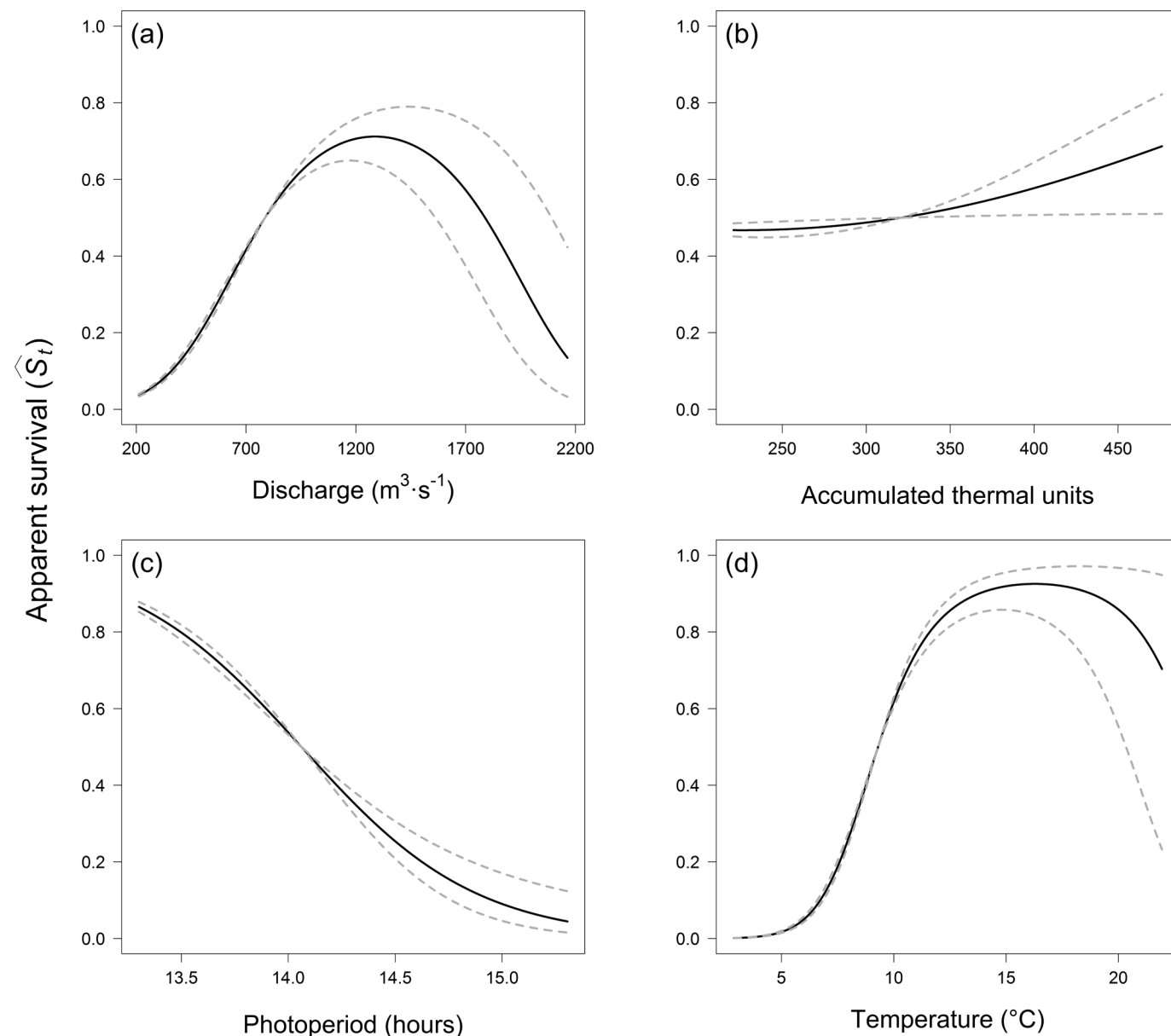
Changes to survival also were minimal but negative (−0.017) at Milford Dam following increases in head pond height and addition of two turbines (Fig. 7). The change in distribution for survival closely mimicked changes in survival through the nearest free-flowing reach of river (Fig. 7). Survival also decreased following construction of two new powerhouses (2013) and increased generation (2014) at Stillwater (−0.040) and Orono dams (−0.039) in the Stillwater Branch. However, when survival was estimated separately for each year in the Stillwater Branch, there was a high degree of uncertainty in the estimates for most years prior to 2013 based on the small number of tagged smolts that used that migratory route (Table S3¹). The patterns in survival through Stillwater and Orono dams followed patterns in decreasing survival through the nearest free-flowing reaches of river (Fig. 7); however, median survival through the dams decreased to a much greater extent and was much more variable than survival through the free-flowing reaches.

Discussion

Effects of dams and changes in the hydrosystem

Dams remain the single largest impediment to successful migration of Atlantic salmon in freshwater systems throughout the world (Parrish et al. 1998). In the Penobscot River, survival through dams was reduced relative to free-flowing reaches of the system. Mortality at dams can occur as a result of increased exposure to predators through migratory delay (Poe et al. 1991; Keefer et al. 2012) or physical injury during passage (Stier and Kynard 1986; Mathur et al. 2000). Smolts can incur delayed mortality from dam passage because of physical injuries (Music et al. 2011) that impair osmoregulatory ability in estuaries (Zydlewski et al. 2010)

Fig. 6. Relationships between environmental covariates and apparent survival of Atlantic salmon smolts in the Penobscot River, Maine, USA, showing effects of (a) discharge, (b) accumulated thermal units from 1 January to release date, (c) photoperiod (day length), and (d) water temperature in the river during migration.



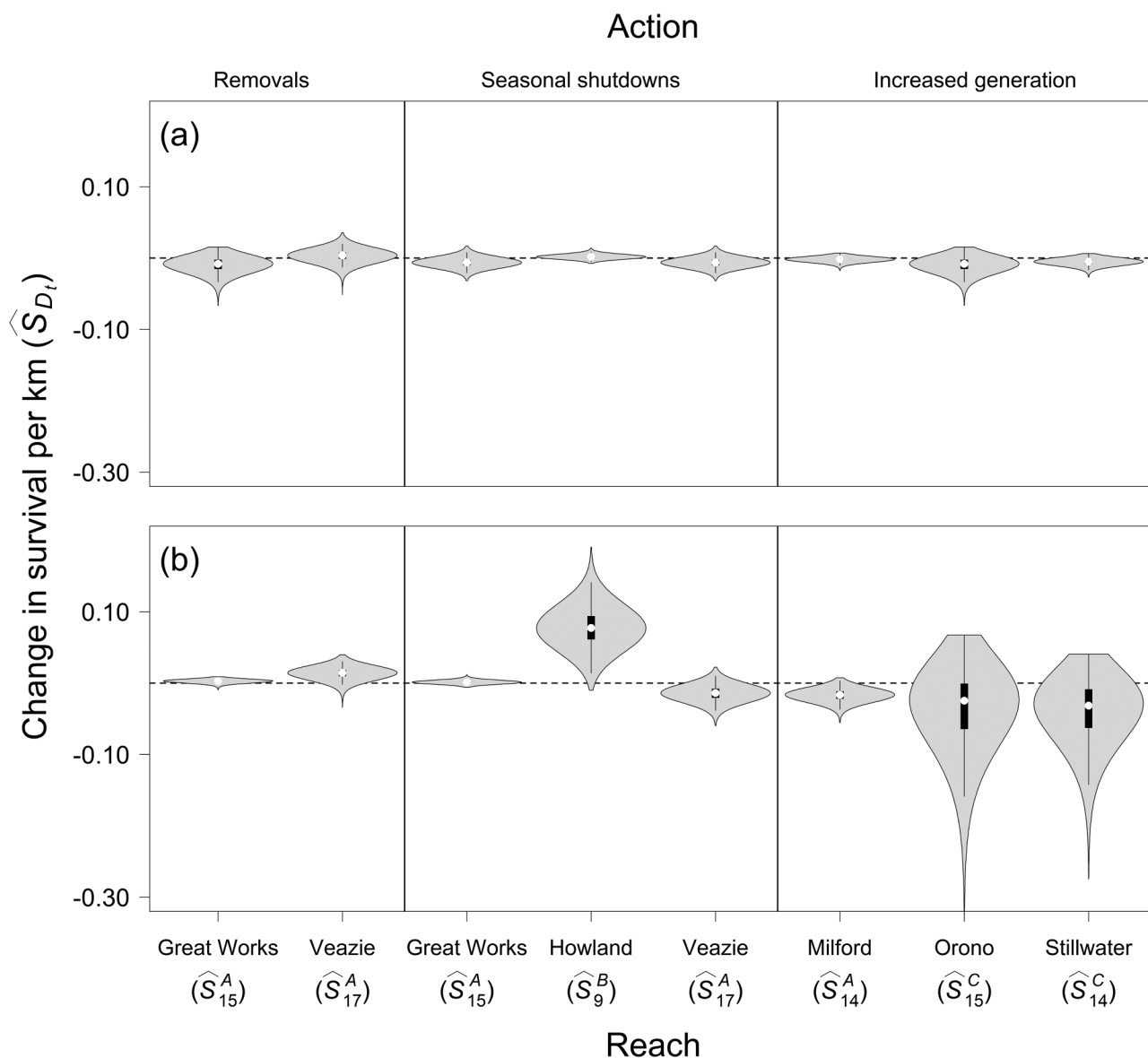
where predation is high (Hawkes et al. 2013), resulting in dam-related estuary mortality (Budy et al. 2002; Schaller et al. 2014; Stich et al. 2015a).

The mean cumulative probability of survival (0.47) of Atlantic salmon smolts during emigration from upper reaches to the estuary in the Penobscot River demonstrates that a large proportion of this population is lost during the freshwater phase of the smolt migration each year. The passage of dams in this system results in a cumulative decrease of 0.13 in the probability of smolt survival compared with what might be expected in a free-flowing system (0.60). Dams contribute to a 30% reduction in survival incurred during this freshwater migration. These results indicate that ongoing recovery and management activities (such as dam removal and improvements to fish passage) continue to have demonstrated potential to increase the number of fish entering the estuary.

A growing body of evidence demonstrates the utility of assessing proposed changes to regulated hydrosystems at both catch-

ment and local-project scales to balance multiple uses of river systems (Ziv et al. 2012; Null et al. 2014). Ongoing management and restoration activities in the Penobscot River have the potential to increase survival of smolts during freshwater and estuary migration through dam removal and seasonal turbine shutdowns (Fig. 7). The removal of mainstem dams in the river increased the per-kilometre rate of smolt survival through the lower river. Because survival was previously high around these facilities (Holbrook et al. 2011; Stich et al. 2014), the increases in survival at Great Works and Veazie Dams to levels seen in other free-flowing river reaches suggests that dam removal has some benefit, even if modest. Veazie Dam was the lower-most dam, and all smolts had to pass it prior to removal, so any change at this facility demonstrates the potential to enhance recovery of Atlantic salmon (a change of 0.01 in survival translates to a difference of several thousand fish).

Fig. 7. Estimated mean (95% CRI) changes in estimated survival through free-flowing reaches of the river (a) during periods corresponding to change in survival of Atlantic salmon smolts through impacted reaches and (b) following three different types of changes (dam removal, seasonal turbine shutdowns during the smolt run, or increased power generation) to dams in the Penobscot River catchment (Great Works, Howland, Milford, Stillwater, and Veazie). Survival parameters in parentheses correspond to parameters in the model schematic (Fig. 2), as well as those in Table S3¹.



Seasonal turbine shutdowns and increases in hydropower generation had dam-specific effects on smolt survival (Fig. 7), but there are some general trends that could inform seasonal management of hydropower and site location for changes to generation in the future. At dams where survival was already high (Great Works and Veazie), turbine shutdown had little (and mixed) influence on smolt survival. However, where survival was low without shutdowns, we observed increases in survival concurrent with this action. These increases were far greater than might have been expected based on changes in survival through free-flowing reaches of river during the same years. Prior to seasonal turbine shutdowns, the probability of survival through the reach containing Howland Dam (range = 0.75–0.92) was among the lowest in the entire catchment (Table S3¹). Concurrent with seasonal turbine shutdowns, survival through the reach containing Howland Dam increased such that it now surpasses survival at small dams further upstream in the Piscataquis River.

Increases in hydropower generation indicated dam-specific responses by smolts. At Milford Dam, survival was historically low relative to free-flowing reaches and other reaches containing dams (Holbrook et al. 2011; Stich et al. 2014). Smolt survival exhibited little change following increases in generation at this facility concurrent with head pond increase and addition of two turbines. Indeed, the change in survival at Milford Dam following increased generation was virtually identical to changes in a nearby free-flowing river reach. Conversely, survival at Stillwater and Orono dams, where survival historically was high (Holbrook et al. 2011; Stich et al. 2014) decreased by 4% at each facility following the addition of a new powerhouse (Fig. 7). The change in survival was much greater and much more variable by comparison to decreases in survival at nearby free-flowing reaches of river. Based on the above results, it is evident that the greatest increases in survival through dam removal and seasonal turbine shutdowns can be achieved at sites where survival is reduced relative to free-

flowing reaches. Conversely, the greatest reductions in survival resultant from increases in hydropower generation can be expected at facilities through which survival is high.

Our results demonstrate that the number of smolts entering the marine environment could be increased through specific stocking strategies. By stocking below dams in the Penobscot River (as was done in 2014), the number of smolts entering salt water is expected to increase by a minimum of about 55% through avoidance of mortality at dams and within free-flowing reaches of the river. This does not include reductions of up to 40% in estuarine and (or) early marine mortality that otherwise result from delayed effects of dam passage (Budy et al. 2002; Schaller et al. 2014; Stich et al. 2015a). The number of smolts exiting the Penobscot Estuary previously has been related to the number of adult returns (Sheehan et al. 2011), so this gain is expected to translate directly to an increased number of returning adult Atlantic salmon. There are potential implications of these management actions on the imprinting and homing of Atlantic salmon, but adult salmon currently need only reach the main stem of the Penobscot River (after which they are taken for captive breeding), and straying of adults is offset by increases in smolt-to-adult survival (Gunnerød et al. 1988). Such a stocking strategy may provide a means of increasing relative adult returns to the Penobscot River in the face of low marine survival until other conservation measures can be enacted in estuary or marine environments (Hansen et al. 2012). In the future, as recovery goals are changed, or in years of higher adult returns, it may be necessary to balance trade-offs in homing to natal streams by returning adults with survival of downstream-migrating smolts. Stocking of smolts higher in the system will likely lead to increased spawning site fidelity and adult migration times in fresh water (Gorsky et al. 2009), but at the cost of reducing the number of smolts reaching the ocean.

Environmental variability in smolt survival

We were able to identify important environmental influences on Atlantic salmon smolt survival in fresh water that can be directly incorporated into the decision-making framework for smolt stocking and the regulatory framework for hydropower dams with respect to smolt passage. Smolt survival was highest early in the run each year, at intermediate discharges, and at temperatures between 10 and 20 °C (Fig. 6). Previous studies have shown that salmon smolts stop moving at temperatures above 20 °C in laboratory experiments (Martin et al. 2012; Zydlewski et al. 2014) and may be considered losses due to high overwinter mortality (Horton et al. 2009). Karppinen et al. (2014) demonstrated that smolts released at temperatures below 10 °C had low survival and moved less compared with smolts released later, at temperatures above 10 °C. Thus, previous research confirms our finding that there is an enhanced period of survival at intermediate temperatures, and the window of temperatures in our study is similar to what has been found in other systems in North America and Europe. In the future, smolt survival could be optimized with respect to temperature by informing decisions about when to stock hatchery-reared smolts.

Low survival of Pacific salmon smolts also has been observed at high temperatures in fresh water (Newman and Rice 2002). Pacific salmon smolt survival also has previously been shown to increase with increasing discharge (Kjelson and Brandes 1989; Newman 2003), but those studies used only flows well below the 50th percentile observed in the present study, even though rivers in which this trend has been documented (e.g., San Joaquin River) are substantially larger than the Penobscot River. This difference is due, in large part, to intensive regulation of the quantity of water that is diverted for human uses in those systems (see Kjelson and Brandes 1989) compared with the Penobscot River, in which most dams are operated as “run-of-river” (National Marine Fisheries Service 2012a, 2012b). However, the data suggest an upper threshold to this relationship, after which further increases in flow re-

duce survival. Thus, our results have uncovered some of the complexities of environmental influences on salmonid smolt survival that may previously have gone unnoticed in other systems or studies of shorter duration. There may be multiple mechanisms that act to decrease survival with further increases in flow beyond a threshold. For example, previous research has shown that smolts generally reduce movement at high flows in the Nechako River in central British Columbia (Sykes et al. 2009). Therefore, it is possible that smolts incur elevated rates of predation naturally owing to increased exposure time. Because the results of our study are observational in nature, and there is some correlation between environmental parameters studied, we are unable to draw conclusions about cause and effect. As such, without further research, the mechanisms behind this relationship remain speculative.

Rearing history and implications for conservation hatcheries

The similarity in survival trends among rearing histories (Fig. 5) suggests that rearing of fish in hatcheries has little influence on survival of out-migrating smolts in the freshwater reaches of this particular system. Because the majority (90%) of smolts leaving the Penobscot River Estuary results from hatchery stocking of smolts (Sheehan et al. 2011), trends in freshwater survival of hatchery-reared smolts likely will be representative of broader population trends until wild smolt production increases. Based on similarities, hatchery-reared smolts provide a useful surrogate for the study of smolt survival in lieu of wild-reared smolts. Wild-reared Atlantic salmon smolts are a precious commodity in most rivers based on multidecadal lows in adult returns (US Atlantic Salmon Assessment Committee 2014). Ultimately, increasing natural reproduction and rearing are the goal of most recovery plans for the species (see National Marine Fisheries Service and US Fish and Wildlife Service 2005). As such, any limitation to trapping, handling, and otherwise interrupting migration of wild smolts can only benefit species recovery.

We do not suggest that hatchery and wild smolts in the Penobscot River or other systems are fully exchangeable or even equivalent in terms of survival, long-term marine performance, or other life-history aspects. In fact, a large number of other studies have documented differential performance of hatchery- and wild-reared smolts globally (e.g., Jonsson et al. 2003; Saloniemi et al. 2004; Jokikokko et al. 2006), and wild fish generally are found to outperform hatchery fish in a variety of ways (Hyvärinen and Rodewald 2013). The similarity in survival among rearing histories in the Penobscot River likely reflects the artificial nature of high mortality associated with dam passage. This result indicates that the cause of mortality from dams is not being mitigated by phenotypic responses of wild-reared smolts and that active management of hydrosystems for maintenance of these stocks will likely be required in the future.

Resource managers may target optimal release timing of hatchery-reared smolts using knowledge about relationships among survival, environmental conditions, and hydropower operations in the system. The findings of this study could be integrated with information about onset of migratory behavior and freshwater movement rates of Atlantic salmon smolts in the Penobscot River (Stich et al. 2015b) and information about smolt physiology, the timing of estuary arrival, and early marine survival in this system (Stich et al. 2015a) to produce models to assist with decisions about hatchery supplementation of this population in the future. Moving into the future, such support tools have the potential to assist in the management and recovery of critically endangered Atlantic salmon stocks throughout the world.

The model developed in this study provides a standardized approach for assessing changes to Atlantic salmon smolt survival in the Penobscot River in the future and can be modified for use with other species or in other systems. By standardizing locations used for estimating survival among years and by standardizing survival estimates within those reaches as per-kilometre rates, the meth-

ods used in this study allowed for direct comparison of survival among reaches and years within the catchment. We were able to compare survival between rearing histories of Atlantic salmon smolts throughout the catchment and identify environmental influences on smolt survival across years. We also were able to compare changes in survival from year to year associated with management and conservation activities catchment-wide and within specific tributaries of the Penobscot River. As such, this framework offers a means to target potential restoration activities (shutdown periods, bypasses, and dam removals) and assess whether they meet their intended goals.

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