

# Initiation of migration and movement rates of Atlantic salmon smolts in fresh water

Daniel S. Stich, Michael T. Kinnison, John F. Kocik, and Joseph D. Zydlewski

**Abstract:** Timing of ocean entry is critical for marine survival of both hatchery and wild Atlantic salmon (*Salmo salar*) smolts. Management practices and barriers to migration such as dams may constrain timing of smolt migrations resulting in suboptimal performance at saltwater entry. We modeled influences of stocking location, smolt development, and environmental conditions on (i) initiation of migration by hatchery-reared smolts and (ii) movement rate of hatchery- and wild-reared Atlantic salmon smolts in the Penobscot River, Maine, USA, from 2005 through 2014 using acoustic telemetry data. We also compared movement rates in free-flowing reaches with rates in reaches with hydropower dams and head ponds. We compared movement rates before and after (1) removal of two mainstem dams and (2) construction of new powerhouses. Initiation of movement by hatchery fish was influenced by smolt development, stocking location, and environmental conditions. Smolts with the greatest gill  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase (NKA) activity initiated migration 24 h sooner than fish with the lowest gill NKA activity. Fish with the greatest cumulative thermal experience initiated migration 5 days earlier than those with lowest cumulative thermal experience. Smolts released furthest from the ocean initiated migration earlier than those released downstream, but movement rate increased by fivefold closer to the ocean, indicating behavioral trade-offs between initiation and movement rate. Dams had a strong effect on movement rate. Movement rate increased from 2.8 to  $5.4 \text{ km}\cdot\text{h}^{-1}$  in reaches where dams were removed, but decreased from  $2.1$  to  $0.1 \text{ km}\cdot\text{h}^{-1}$  in reaches where new powerhouses were constructed. Movement rate varied throughout the migratory period and was inversely related to temperature. Fish moved slower at extreme high or low discharge. Responses in fish movement rates to dam removal indicate the potential scope of recovery for these activities.

**Résumé :** Le moment de l'entrée en mer joue un rôle clé dans la survie en mer des saumoneaux de saumon atlantique (*Salmo salar*) tant sauvages qu'issus d'écloseries. Les pratiques de gestion et obstacles à la migration, tels que les barrages, peuvent restreindre le moment de la migration des saumoneaux, entraînant une performance moins qu'optimale à l'entrée en eau salée. Nous avons modélisé les influences du lieu d'empoissonnement, du développement des saumoneaux et des conditions ambiantes sur (i) le début de la migration par les saumoneaux élevés en écloseries et (ii) la vitesse des déplacements de saumoneaux élevés en écloseries et à l'état sauvage dans le fleuve Penobscot (Maine, États-Unis), de 2005 à 2014, à la lumière de données de télémétrie acoustique. Nous avons également comparé les vitesses de déplacement dans des tronçons non régulés et des tronçons contenant des barrages hydroélectriques et des réservoirs de barrage. Nous avons comparé les vitesses de déplacement avant et après (1) le retrait de deux barrages sur le bras principal et (2) la construction de nouvelles centrales électriques. Le début des déplacements par les poissons issus d'écloseries était influencé par le développement des saumoneaux, le lieu d'empoissonnement et les conditions ambiantes. Les saumoneaux présentant la plus forte activité de la  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase (NKA) dans les branchies commençaient leur migration 24 heures plus tôt que les poissons avec la plus faible activité de la NKA dans les branchies. Les poissons caractérisés par la plus importante expérience thermique cumulative commençaient à migrer 5 jours plus tôt que ceux avec la plus faible expérience thermique cumulative. Les saumoneaux relâchés le plus loin de l'océan commençaient à migrer plus tôt que ceux relâchés plus en aval, mais la vitesse de déplacement quintuplait plus près de l'océan, indiquant des compromis comportementaux entre l'initiation et la vitesse des déplacements. Les barrages exerçaient une forte influence sur la vitesse de déplacement, cette dernière augmentant de  $2.8$  à  $5.4 \text{ km}\cdot\text{h}^{-1}$  dans les tronçons dont des barrages ont été retirés, mais diminuant de  $2.1$  à  $0.1 \text{ km}\cdot\text{h}^{-1}$  dans les tronçons où de nouvelles centrales électriques ont été construites. La vitesse de déplacement variait tout au long de la période de migration et était inversement reliée à la température. Les poissons se déplaçaient plus lentement à débits extrêmes forts ou faibles. Les réactions au retrait de barrages reflétées dans les vitesses de déplacement des poissons indiquent l'ampleur potentielle du rétablissement associée à ces activités. [Traduit par la Rédaction]

## Introduction

Seaward migration through freshwater and estuarine habitats to ocean feeding grounds represents a critical transition in the life history of anadromous fishes (Zydlewski and Wilkie 2013). In Atlantic salmon (*Salmo salar*) smolts, migration is associated with high predation risk (Blackwell et al. 1997; Kocik et al. 2009; Hawkes

et al. 2013), dynamic environments (Thorstad et al. 2012), and new food sources (Haugland et al. 2006). Seaward migration by smolts occurs in four primary phases: initiation, downstream migration (fresh water), estuary passage, and early marine migration (McCormick 2013). A building body of evidence suggests ocean temperatures play a critical role in the success of early marine migrants

Received 23 December 2014. Accepted 11 May 2015.

Paper handled by Associate Editor Martin Krkošek.

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

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

**J.F. Kocik.** National Oceanic and Atmospheric Administration Northeast Fisheries Science Center, 17 Godfrey Drive Suite 1, Orono, ME 04473, USA.

**J.D. Zydlewski.** 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](mailto:daniel.stich@maine.edu)).

(Friedland 1998; Friedland et al. 2003, 2014), and sea surface temperatures are predictive of the timing of smolt arrival in estuaries throughout the world (Otero et al. 2014). Timing of estuary arrival and ocean entry are important for survival based on match among physiological development (Stich et al. 2015), environmental conditions (Otero et al. 2014), food availability (Haugland et al. 2006), and presence or absence of predators (Hawkes et al. 2013) or other migrants (Svenning et al. 2005). However, the arrival of smolts in the ocean is determined by the integration of cues experienced far (sometimes hundreds of kilometres) from the point of ocean entry (McCormick et al. 1998). As such, these cues play a critical role in determining when smolts initiate migration and how fast these fish move.

Smolting in Atlantic salmon involves synchronous changes in physiology, morphology, and behavior that prepare the salmon for a life at sea (McCormick et al. 1998). Smolting includes, among other changes, increased saltwater tolerance and upregulation of enzymes involved with ion transport (such as gill  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase (NKA) activity). Loss of territoriality, inhibition of positive rheotaxis, and adoption of schooling behavior also are characteristics of smolting (McCormick et al. 1998). Environmental cues, particularly photoperiod, control physiological transformation (McCormick et al. 1987) and onset of migratory behavior (Whalen et al. 1999; Zydlowski et al. 2005; Zydlowski et al. 2014) in hatchery- and wild-reared Atlantic salmon smolts. These processes are adapted for effectively transitioning to the marine environment. Dams can interrupt migration of Atlantic salmon smolts through injury (Stier and Kynard 1986; Mathur et al. 2000; Music et al. 2010) or migratory delay (Holbrook et al. 2011). Delays at dams result in increased risk of predation (Poe et al. 1991; Blackwell and Juanes 1998) or may result in mismatch of physiological preparedness for ocean entry and timing of ocean entry through temperature-related loss of smolt characteristics (McCormick et al. 1999, 2009; Marschall et al. 2011) and high mortality during early marine migration (Petrosky and Schaller 2010). Such an effect has been implicated in substantial dam-related estuary mortality (Stich et al. 2015). Recent dam removals, such as those in the Kennebec and Penobscot rivers (Day 2006) in Maine, USA, allow examination of how dams, in conjunction with other influences, affect migration behavior.

Many rivers with Atlantic salmon rely heavily on stocking for population persistence (United States Atlantic Salmon Assessment Committee 2014). In light of low marine survival, a primary goal of management is to maximize the number of smolts leaving coastal systems (Hansen et al. 2012; Russell et al. 2012). Decisions about where and when to stock hatchery-reared smolts not only influence survival in fresh water based on the presence of dams (Holbrook et al. 2011), but also can influence timing of ocean entry (Otero et al. 2014). The complex relationships among timing, stocking location, and environmental conditions with ecology and survival of smolt migration are poorly characterized. It is possible that behavioral trade-offs exist in the initiation of migration and movement rates of smolts with respect to stocking decisions and environmental conditions.

The goal of this study was to investigate influences of dams, stocking decisions (where and when to stock), and environmental conditions on movement rates of smolts through fresh water and determine how those same factors influence initiation of migration by hatchery-stocked smolts. We had two specific objectives to this end. First, we used acoustic telemetry data from 2005 through 2014 in the Penobscot River to model how movement rate of hatchery- and wild-reared smolts was influenced by (i) presence of dams and head ponds, (ii) distance from the ocean, (iii) environmental conditions (e.g., temperature and discharge), and (iv) characteristics indicative of physiological development. Second, we used telemetry data to model relationships between initiation of

migration behavior by hatchery-reared smolts and stocking conditions, including (1) stocking location, (2) temporal variability in environmental conditions at stocking, and (3) spatial variability in release locations used.

## Methods

### Study site

The Penobscot River (Fig. 1) is the largest river in Maine, USA, and drains an area of approximately 22 000 km<sup>2</sup>. Limited wild spawning of Atlantic salmon occurs in the system, and this is extensively supplemented by annual stocking of eggs and fry in headwater streams (United States Atlantic Salmon Assessment Committee 2014). Because these life stages are not marked, naturally reared hatchery fish are morphologically indistinguishable from wild-spawned fish and all are referred to hereinafter simply as "wild". Peak migration of wild smolts generally occurs during late April and early May each year (United States Atlantic Salmon Assessment Committee 2014).

The remainder of the Penobscot River smolt run is made up of 18-month-old stocked smolts (hereinafter "hatchery" smolts). While exact estimates of the proportion of the Penobscot River smolt run made up by stocked fish is not known, sampling in the bay suggests that more than 90% of the run results from smolt stocking (Sheehan et al. 2011). Consequently, most (~83%) of the spawners that return to the Penobscot River each year result from the stocking of hatchery-reared smolts (United States Atlantic Salmon Assessment Committee 2012).

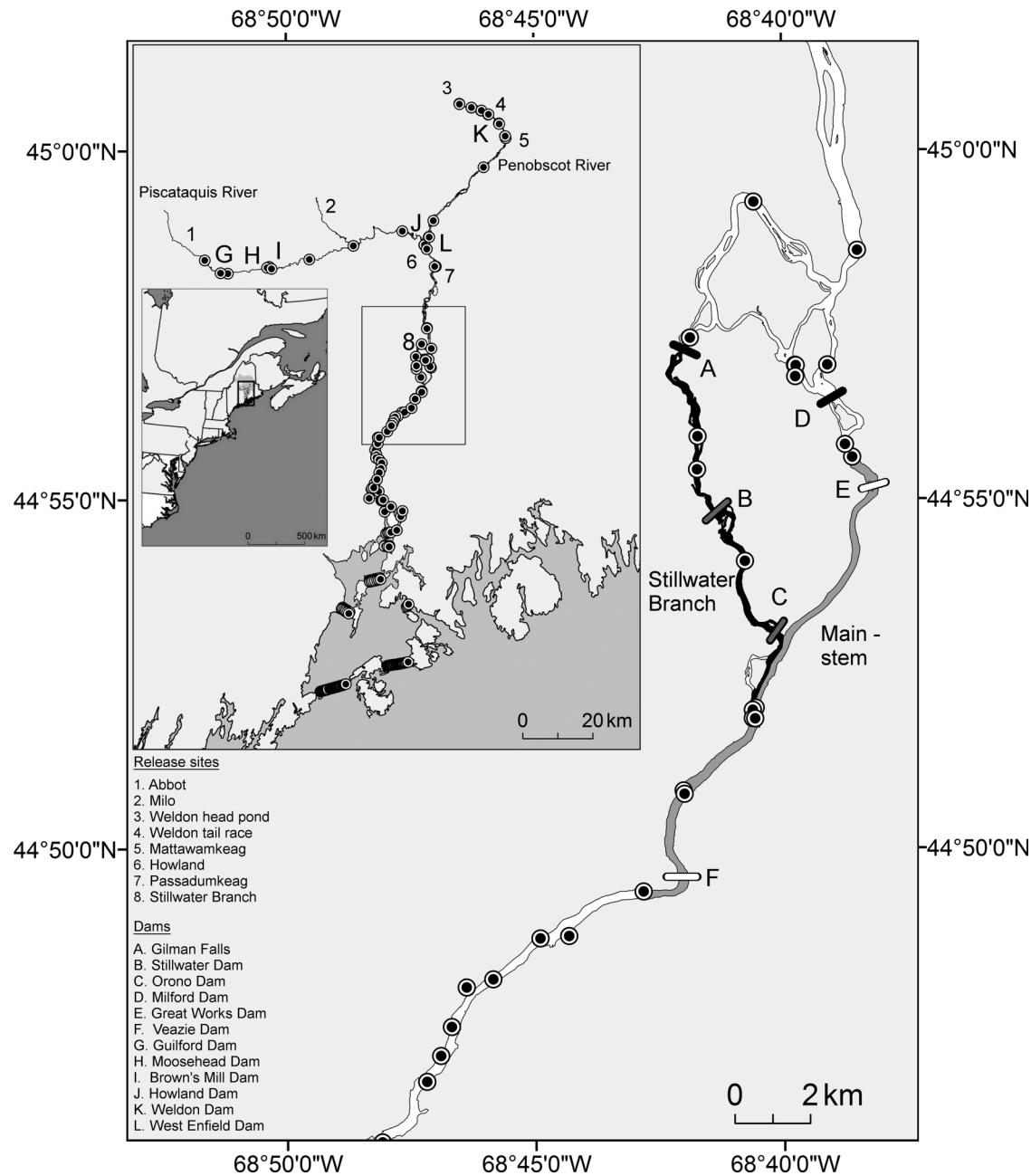
Beginning in 2009, a suite of large-scale conservation activities were initiated as part of a basin-wide restoration project, the Penobscot River Restoration Project (PRRP; Day 2006). The goal of the PRRP was to balance the production of hydropower in the Penobscot River with the revitalization of 11 species of diadromous fishes in the catchment, including Atlantic salmon. The PRRP resulted in major changes to the hydro system (i.e., location and operation of hydropower dams) in the Penobscot River. These changes included (i) the removal of two mainstem dams in the lower river (Great Works (river kilometre (rkm) 58, June 2012) and Veazie (rkm 45, July 2013); Fig. 1) and (ii) decommissioning of a third dam (rkm 99, Howland; Fig. 1) in the mouth of the Piscataquis River (Federal Energy Regulatory Commission 2009).

Other changes in the Penobscot River have resulted from the conditions of The Lower Penobscot River Basin Comprehensive Settlement Accord ("Settlement Accord"; Federal Energy Regulatory Commission 2004) that governed the re-allocation of hydropower throughout the river. The Settlement Accord allowed for increased hydropower generation at six facilities in the river (Federal Energy Regulatory Commission 2004). Generating capacity was increased at Milford Dam at rkm 60 in the main stem (Fig. 1) by raising head pond elevation and increasing the number of turbines in the powerhouse (Federal Energy Regulatory Commission 2009). Concurrently, increased head pond elevation at Stillwater Dam (Federal Energy Regulatory Commission 2005) and the construction of new powerhouses at Stillwater and Orono dams (spring 2013) doubled hydropower generation at each dam (Fig. 1).

### Acoustic receiver array

From 2005 through 2014, a network of stationary acoustic receivers was deployed from the headwaters of the Penobscot River and its primary tributary, the Piscataquis River, downstream to the Gulf of Maine (Fig. 1). The receiver network was deployed collaboratively in all years by 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) National Marine Fisheries Service Northeast Fisheries Science Center. Depending on year of deployment, the network included 100–200 VR2 and (or) VR2-W acoustic receivers (Amirix Vemco Ltd., Halifax, Nova Scotia, Canada) scanning

**Fig. 1.** Map showing the location of the Penobscot River in Maine, USA (small inset), locations of acoustic receivers, release sites and dams, and potential migratory routes in the lower river through the Stillwater Branch or the mainstem Penobscot River around a large island. Head of tide is located immediately downstream of Veazie Dam (F). Dams are shown as black bars across the river; those with grey fill underwent new powerhouse construction, and those with white fill were removed during the course of this study. River reaches shaded in black in the Stillwater Branch and reaches shaded dark grey in the main stem are the reaches used to assess effects of powerhouse construction and dam removal on movement rates of smolts.



continuously at 69 kHz. Receivers in the freshwater reaches and in the Penobscot Estuary were moored near bottom using reinforced cement anchors. In the bay, receivers were suspended approximately 10 m below the surface of the water. Where necessary, multiple receivers were deployed in a transect across the river to provide adequate coverage across wider reaches, and detections of fish at these receivers were pooled as a single location. Detections of fish at receivers downstream of the head of tide at Veazie Dam (Fig. 1, dam label F) were pooled as a single, terminal detection for this study.

#### Acoustic tagging and releases

From 2005 through 2014, a total of 2056 Atlantic salmon smolts was acoustically tagged and released in the Penobscot River (Table 1), of which 1639 (80%) were 18-month-old hatchery smolts from the US Fish and Wildlife Service (USFWS) Green Lake National Fish Hatchery (GLNFH) and 417 (20%) were wild smolts. Fish handling procedures and acoustic tagging methods follow those of Holbrook et al. (2011) and Stich et al. (2014) and were identical in all years (2005–2014). Smolts were anaesthetized using a 100 mg·L<sup>-1</sup> solution of MS-222 (buffered with 20 mmol NaHCO<sub>3</sub>; pH = 7.0), and fork

**Table 1.** Stocking locations with release river kilometre (rkm), number released (*n*), and mean (SD) of fork length ( $L_F$ , mm), mass (g), and gill  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase activity (NKA,  $\mu\text{mol ADP}\cdot\text{mg protein}^{-1}\cdot\text{h}^{-1}$ ), and release date (Date) of acoustically tagged wild (W) and hatchery (H) Atlantic salmon smolts released in Penobscot and Piscataquis rivers, 2005–2014.

Year	Release site	Origin	<i>n</i>	$L_F$	Mass	NKA	Date
2005	Howland (rkm 99)	H	150	189 (11)	75 (15)	6.6 (2.0)	23 Apr. (4)
	Mattawamkeag (rkm 144)	H	40	189 (15)	77 (21)	5.2 (1.5)	14 Apr.
	Milo (rkm 142)	H	85	191 (11)	77 (14)	8.1 (1.9)	24 Apr. (3)
	Weldon (rkm 149)	W	60	180 (18)	53 (17)	9.1 (1.9)	26 May
2006	Milo (rkm 142)	H	72	197 (11)	87 (18)	5.0 (1.2)	24 Apr.
	Weldon (rkm 149)	H	146	199 (15)	87 (19)	4.7 (1.9)	24 Apr.
	Weldon (rkm 149)	W	73	189 (8)	63 (8)	4.2 (0.9)	8 May (13)
2009	Milo (rkm 142)	H	100	180 (8)	62 (9)	3.3 (1.4)	30 Apr.
	Passadumkeag (rkm 92)	H	100	180 (9)	63 (10)	3.0 (0.8)	29 Apr.
2010	Abbot (rkm 187)	W	75	169 (8)	45 (7)	4.7 (1.1)	2 May (1)
	East Branch (rkm 162)	W	74	181 (13)	55 (13)	4.7 (0.9)	7 May (3)
	Milo (rkm 142)	H	100	189 (11)	72 (13)	4.5 (1.0)	24 Apr.
	Passadumkeag (92.3)	H	100	186 (11)	69 (14)	4.6 (1.1)	24 Apr.
2011	Abbot (rkm 187)	W	75	146 (8)	29 (5)	2.6 (1.2)	11 May (1)
	East Branch (rkm 162)	W	60	168 (21)	46 (18)	3.6 (1.5)	24 May (4)
	Milo (rkm 142)	H	100	192 (13)	76 (18)	5.0 (1.5)	25 Apr.
2012	Passadumkeag (rkm 92.3)	H	100	194 (13)	77 (17)	5.4 (1.5)	27 Apr.
	Abbot (rkm 187)	H	72	199 (10)	84 (14)	3.3 (1.3)	20 Apr.
2013	East Branch (rkm 162)	H	85	200 (11)	85 (14)	3.5 (1.6)	20 Apr.
	Abbot (rkm 187)	H	75	185 (11)	70 (13)	2.8 (2.0)	16 Apr.
2014	East Branch (rkm 162)	H	82	185 (9)	71 (11)	2.7 (2.1)	16 Apr.
	Abbot (rkm 187)	H	75	190 (11)	70 (13)	5.1 (1.9)	2 May
	East Branch (rkm 162)	H	82	208 (177)	66 (12)	5.5 (2.8)	2 May
	Stillwater (rkm 62)	H	75	190 (9)	69 (10)	4.9 (2.0)	2 May

Note: Stocking location is shown in Fig. 1. Standard deviation (SD) of release date is in days. For groups of fish that were all tagged on the same date, no SD is given for release date.

length ( $L_F$ , mm) and mass (g) were measured. Condition factor (K) for each fish was calculated as

$$(1) \quad K = \frac{\text{Mass} \times 100\,000}{L_F^3}$$

For each fish, a small (1 cm) incision was made slightly offset from the ventral line and about 1 cm posterior to the pectoral fin girdle. An acoustic tag was inserted intraperitoneally, and the incision was closed with two simple, interrupted knots using 4-0 absorbable vicryl sutures (Ethicon, Somerville, New Jersey, USA). Model V7-2L (Amirix Vemco Ltd., Halifax, Nova Scotia, Canada) tags were used in 2005 and for wild fish in 2011. In all other years, we used model V9-6L or V9-6x tags (Amirix Vemco Ltd., Halifax, Nova Scotia, Canada). Expected battery life of the tags was 80–82 days in all years, with a randomly assigned nominal delay of 20–40 s ( $\pm 50\%$ ). Numbers of fish and release sites varied among years (Table 1). Hatchery smolts were released at up to five locations per year and wild smolts at up to three locations per year (Fig. 1; Table 1).

#### Gill NKA activity

A nonlethal gill biopsy (four to six filaments) was taken from the front, left gill arch of each fish prior to tagging. Individual biopsies were stored at  $-80^\circ\text{C}$  in 100  $\mu\text{L}$  SEI buffer (250  $\text{mmol}\cdot\text{L}^{-1}$  sucrose, 10  $\text{mmol}\cdot\text{L}^{-1}$   $\text{Na}_2\text{-EDTA}$ , 50  $\text{mmol}\cdot\text{L}^{-1}$  imidazole) for later analysis of gill NKA (enzyme code 3.6.3.9; International Union of Biochemistry and Molecular Biology 1992) activity (expressed as  $\mu\text{mol ADP}\cdot\text{mg protein}^{-1}\cdot\text{h}^{-1}$ ) using the method of McCormick (1993). Concentration of NADH at  $25^\circ\text{C}$  and 340 nm was used to measure kinetic rate of ouabain-inhibitable ATP hydrolysis, and protein concentration in gill samples was determined using the bicinchoninic acid method (Smith et al. 1985). Gill samples from each fish were analyzed in triplicate for gill NKA activity and protein concentration, and sample values were averaged for each fish.

#### Environmental data

Mean daily water temperature data for each year were collected from the USGS gage (USGS gage station 01036390) at West Enfield Dam (Fig. 1) where available. We used mean daily water temperature data collected by Maine Department of Marine Resources for years (2005 and 2006) during which gage data were not available (Randy Spencer, Maine Department of Marine Resources, unpublished data). Discharge ( $Q$ ,  $\text{m}^3\cdot\text{s}^{-1}$ ) data used in all analyses were mean daily values collected from the USGS West Enfield gage. Accumulated thermal units (ATU) experienced by wild fish each year were calculated from river temperature data between 1 January and capture date of individual fish. We calculated ATU over the period from 1 January to release date for hatchery smolts using mean daily temperatures ( $^\circ\text{C}$ ) from outdoor rearing pools at GLNFH for each year (A. Firmenich, USFWS, unpublished data). Photoperiod was calculated from ordinal date and latitude for (i) capture location of wild fish or (ii) GLNFH for hatchery fish using the “geosphere” package (Hijmans et al. 2010) in R (R Core Team 2014).

#### Initiation of migratory behavior by hatchery smolts

We assumed that a minimum downstream movement greater than 5 km by hatchery smolts was indicative of the initiation of migratory behavior (hereinafter “initiation”) for this study. Initiation by acoustically tagged smolts was indexed as the total amount of time taken by each tagged smolt to move the first 8–25 km (depending on proximity of receiver locations to release sites) in a downstream direction. This range was used because of variability in the first downstream receiver location that could be used to define initiation for each release site. Given average movement rate, this introduced a potential error of up to 8 h in initiation time based on variability in distance to first location. We accounted for this directly within models of initiation.

#### Models of migration initiation

We used general linear models (Montgomery et al. 2006) to estimate effects of the smolt development (gill NKA activity and

ATU), distance of release from the ocean, and environmental conditions (discharge, photoperiod, and temperature) on migration initiation. The response variable (time to initiation) was  $\log_e$ -transformed prior to analysis because it was right-skewed, and because negative predictions of time were not biologically realistic. All results are presented on the real scale of the variable (hours). We investigated potential support for nonlinear effects of ATU, discharge, photoperiod, and temperature through the inclusion of a second-order term for these covariates in a subset of models (by comparing models with and without quadratic terms). Because the distance used for assigning initiation varied between release sites (see above), we incorporated the distance between release and acoustic receivers as an explanatory variable in all models of initiation.

We considered a covariate to have a statistically significant effect if the 95% confidence interval for the coefficient did not overlap zero. To evaluate the relative support for candidate models we used Akaike's information criterion, corrected for sample size ( $AIC_c$ ; Burnham and Anderson 2002). We assumed models with  $\Delta AIC_c < 2.0$  to have similar support (Burnham and Anderson 2002). The probability that any given model was the best in the candidate set was estimated as the  $AIC_c$  weight ( $w_i$ ). Owing to uncertainty in model selection for initiation, we used model averaging to predict covariate effects on initiation. To assess fit, we also provide the value of the McFadden's pseudo- $R^2$  with model selection statistics (McFadden 1974). Prior to drawing inference on the model set, we conducted standard regression diagnostics (q-q plots, Cook's  $D$ , etc.; Montgomery et al. 2006) to validate model assumptions about normality of residuals.

#### Movement rate

Detections of wild and hatchery smolts at upstream and downstream receivers that delimited reaches were used to calculate movement rates through each of the reaches. Movement rate was expressed as kilometres per hour ( $R_{ij}$ ,  $\text{km} \cdot \text{h}^{-1}$ ) and was calculated as distance traveled in reach  $j$  ( $D_{ij}$ , km) divided by time elapsed between first detections at each location ( $T_{ij}$ ) for each fish ( $i$ ) using

$$(2) \quad R_{ij} = \frac{D_{ij}}{T_{ij}}$$

We recognize that velocity also is commonly expressed as body lengths per second ( $\text{bl} \cdot \text{s}^{-1}$ ) in other systems (see Thorstad et al. 2012). However, because of the scale of movements (generally  $>1$  km), the duration of most movements measured (hours or days), and the fact that we actually were assessing overground velocity (and not swimming speed relative to water), we chose to present the results of this study in terms of  $\text{km} \cdot \text{h}^{-1}$ . Based on potential concerns about the relation of velocity to body length, we ran models using  $\text{bl} \cdot \text{s}^{-1}$  as the response variable and found no differences in the results. We present movement rate in  $\text{km} \cdot \text{h}^{-1}$  for the reasons given above and for simplicity.

#### Models of movement rate

We used linear mixed-effects models (Zuur et al. 2009) in the "lme4" package in R (R Core Team 2014) to estimate effects of covariates on movement rate. We included an individual-based random effect on the intercept in all models to account for repeated and unequal numbers of observations for each fish. Movement rate was a non-negative value and was right skewed. Therefore, we  $\log_e$ -transformed movement rate prior to analysis to achieve normality of residuals. Variables used to represent fish characteristics included rearing history (hatchery or wild), condition factor ( $K$ ), gill NKA activity, release rkm, and release date. Environmental variables included location within the catchment (rkm) for each reach, photoperiod (i.e., day length) on the first date of each movement, discharge, temperature, and reach type

(dam, free-flowing, or head pond). These variables were measured or assigned for each fish in each reach. We only investigated additive combinations of variables to reduce the dimensionality of the questions we asked and minimize the number of models being considered at any given time. Additionally, we only considered a single variable representing fish characteristics in a given model to reduce parameter redundancy. We suspected that movement rate would peak during the year and with cumulative temperature experience (Zydlowski et al. 2005, 2014) and at intermediate temperatures (Karppinen et al. 2014; Zydlowski et al. 2014) and discharges (Sykes et al. 2009). Therefore, based on the results of research in this (Holbrook et al. 2011; Stich et al. 2014, 2015) and other systems, we tested models with linear terms for discharge, temperature, photoperiod, and ATU against similar models that included quadratic effects for these terms.

We assessed model fit using Nakagawa and Schielzeth's  $R^2_{\text{GLMM}}$  for linear mixed-effects models with random intercepts (Nakagawa and Schielzeth 2013). Owing to the downstream movement of individuals, we assessed temporal autocorrelation in the residuals prior to drawing inference and found that temporal autocorrelation was absent at any reasonable lag (1–11). Thus, we did not account for temporal autocorrelation in any way other than through the inclusion of river kilometre in the movement rate models. Otherwise, model selection and regression diagnostics were addressed in the manner used for models of initiation (above). We compared the best model of movement rate with the same model with an extra term for tag mass to body mass ratio post hoc to assess whether tagging affected migration behavior. We found no support for this term in the candidate set ( $\Delta AIC_c > 12$ ).

#### Assessing effects of dams on movement rate

We sought to assess changes in movement rate through the lower Penobscot River following the removal of Great Works and Veazie dams in 2012 and 2013 and the addition of a new powerhouse at both Stillwater and Orono dams in the Stillwater Branch in 2013. Because Milford Dam was located about 2 km upstream of Great Works Dam, and because Veazie Dam formerly was located near the head of tide in the Penobscot River Estuary, we examined changes in movement rates through four reaches between the tail race of Milford Dam and the head of the estuary in the main stem of the Penobscot River (rkm 44–59) to assess effects of dam removal on movement rate. We examined changes in movement rate throughout the Stillwater Branch (rkm 51–63). We tested for shifts in median movement rate through the mainstem Penobscot River in years before (2005–2013) and after the removal of both Great Works and Veazie dams (2014) and before (2005–2013) and after (2014) completion of powerhouse construction at Stillwater and Orono dams using Wilcoxon ranked sums tests (Zar 1999).

## Results

#### Time to initiation of migratory behavior by hatchery smolts

Initiation of migration by hatchery smolts was related to physiological development, environmental conditions at release, and the distance from the ocean at which fish were released (Table 2). Distance to first receiver (distance) appeared to have a negligible effect on initiation (Table 3), but was retained in all models. Hatchery smolts that were better prepared for saltwater entry (measured as gill NKA activity) initiated migratory behavior sooner than fish that had lower gill NKA activity (Fig. 2a; Table 3). Over the range of gill NKA activity observed in hatchery smolts (0.9–16.3  $\mu\text{mol ADP} \cdot \text{mg protein}^{-1} \cdot \text{h}^{-1}$ ), time to initiation of migratory behavior was reduced by about 1 day on average (Fig. 2a).

The ATU experienced by all fish in this study was below theoretical thresholds for loss of smolt characteristics (500 ATU; Handeland et al. 2004) and indicated that most smolts were released before or near the peak of smolting (300–400 ATU). Hatchery smolts with greater ATU initiated migration sooner after

**Table 2.** Model-selection statistics for the ten best models used to quantify variation in the number of days to initiate migration by hatchery Atlantic salmon smolts after release into the Penobscot River, Maine, USA, 2005–2014.

Model	<i>k</i>	AIC <sub>c<sub>i</sub></sub>	ΔAIC <sub>c<sub>i</sub></sub>	w <sub>i</sub>	(R <sup>2</sup> <sub>McF</sub> )
ATU + ATU <sup>2</sup> + NKA + PP + Q + Q <sup>2</sup> + release + <i>T</i>	11	1936.6	0.00	0.28	0.28
ATU + ATU <sup>2</sup> + NKA + PP + Q + Q <sup>2</sup> + release + <i>T</i> + T <sup>2</sup>	12	1936.7	0.12	0.26	0.28
ATU + ATU <sup>2</sup> + L <sub>F</sub> + PP + Q + Q <sup>2</sup> + release + <i>T</i>	11	1938.6	2.00	0.10	0.27
ATU + ATU <sup>2</sup> + NKA + PP + PP <sup>2</sup> + Q + Q <sup>2</sup> + release + <i>T</i>	12	1938.7	2.05	0.10	0.28
ATU + ATU <sup>2</sup> + NKA + PP + PP <sup>2</sup> + Q + Q <sup>2</sup> + release + <i>T</i> + T <sup>2</sup>	13	1938.8	2.17	0.09	0.28
ATU + ATU <sup>2</sup> + L <sub>F</sub> + PP + Q + Q <sup>2</sup> + release + <i>T</i> + T <sup>2</sup>	12	1939.0	2.36	0.09	0.28
ATU + ATU <sup>2</sup> + L <sub>F</sub> + PP + PP <sup>2</sup> + Q + Q <sup>2</sup> + release + <i>T</i>	12	1940.7	4.05	0.04	0.27
ATU + ATU <sup>2</sup> + L <sub>F</sub> + PP + PP <sup>2</sup> + Q + Q <sup>2</sup> + release + <i>T</i> + T <sup>2</sup>	13	1941.0	4.40	0.03	0.28
ATU + NKA + PP + PP <sup>2</sup> + Q + Q <sup>2</sup> + release + <i>T</i> + T <sup>2</sup>	12	1947.1	10.47	0.00	0.27
ATU + L <sub>F</sub> + PP + PP <sup>2</sup> + Q + Q <sup>2</sup> + release + <i>T</i> + T <sup>2</sup>	12	1947.1	10.47	0.00	0.27

Note: Number of parameters estimated in each model is *k*, AIC<sub>c<sub>i</sub></sub> is the Akaike information criterion for each *i*th model, ΔAIC<sub>c<sub>i</sub></sub> is the difference between the AIC<sub>c<sub>i</sub></sub> of each *i*th model and the best model in the set, and w<sub>i</sub> is the relative probability that each *i*th model is the best in the candidate set. Model fit was assessed using McFadden's pseudo-R<sup>2</sup> (R<sup>2</sup><sub>McF</sub>). Explanatory variables are defined as follows: accumulated thermal units (ATU), discharge (Q), distance between release and relocation (Distance), fork length (L<sub>F</sub>), gill NKA activity (NKA), photoperiod (PP), release rkm from ocean (release), and river temperature (T). Distance was included in all models for the candidate set.

**Table 3.** Mean and 95% confidence limits (CL) of standardized, model-averaged regression coefficients from the top ten models of time to initiation of migration by hatchery Atlantic salmon smolts after stocking in the Penobscot River, 2005–2014.

Parameter	Estimate	SE	Lower 95% CL	Upper 95% CL
Intercept	4.750	0.042	4.668	4.832
Distance	-0.065	0.037	-0.137	0.007
ATU	-0.478	0.066	-0.607	-0.348
ATU <sup>2</sup>	-0.151	0.032	-0.214	-0.087
L <sub>F</sub>	0.004	0.023	-0.041	0.048
NKA	-0.037	0.026	-0.088	0.013
PP	0.297	0.070	0.160	0.435
PP <sup>2</sup>	-0.004	0.058	-0.117	0.110
Q	0.070	0.052	-0.031	0.172
Q <sup>2</sup>	-0.199	0.026	-0.250	-0.149
Release	-0.224	0.032	-0.287	-0.161
T	0.236	0.039	0.160	0.312
T <sup>2</sup>	-0.021	0.016	-0.052	0.009

Note: Explanatory variables are defined as follows: accumulated thermal units (ATU), distance between release and relocation (Distance), fork length (L<sub>F</sub>), gill NKA activity (NKA), photoperiod (PP), discharge (Q), release rkm from ocean (Release), and river temperature (T).

stocking than smolts with lower ATU (Fig. 2b; Table 3). Fish with the greatest ATU (439) initiated migration more than 100 h sooner after stocking than those fish with the lowest ATU (234; Fig. 2b). This relationship also was nonlinear, and the reduction in time to initiate migration was most rapid for fish that experienced 300–400 ATU (Fig. 2b).

Initiation of migration took longer at intermediate discharges (~750 m<sup>3</sup>·s<sup>-1</sup>), with reduced time to initiation at very low or very high flows (Fig. 2c; Table 3). Hatchery smolts stocked early in the year initiated migration sooner after release than those fish released later in the year (Fig. 2d; Table 3), resulting in an increase of about 85 h (3.5 days) to time of initiation over the range of release dates (12 April – 8 May) used in this study (Fig. 2d). Similarly, initiation of migration took longer with increasing temperatures (Fig. 2f; Table 3), resulting in a change of about 125 h (5.2 days) across the range of temperatures (3.9–16.1 °C) observed at release date (Fig. 2f).

Finally, hatchery smolts released at a greater distance from the ocean initiated migration sooner after release than did fish released nearer to the ocean (Fig. 2e; Table 3). Over the range of release locations used in this study (63–187 km to ocean), the

mean time for smolts to initiate migration was about 60 h (2.5 days) longer for fish released nearest to the ocean compared with fish released furthest upstream (Fig. 2e).

#### Movement rate of wild and hatchery smolts

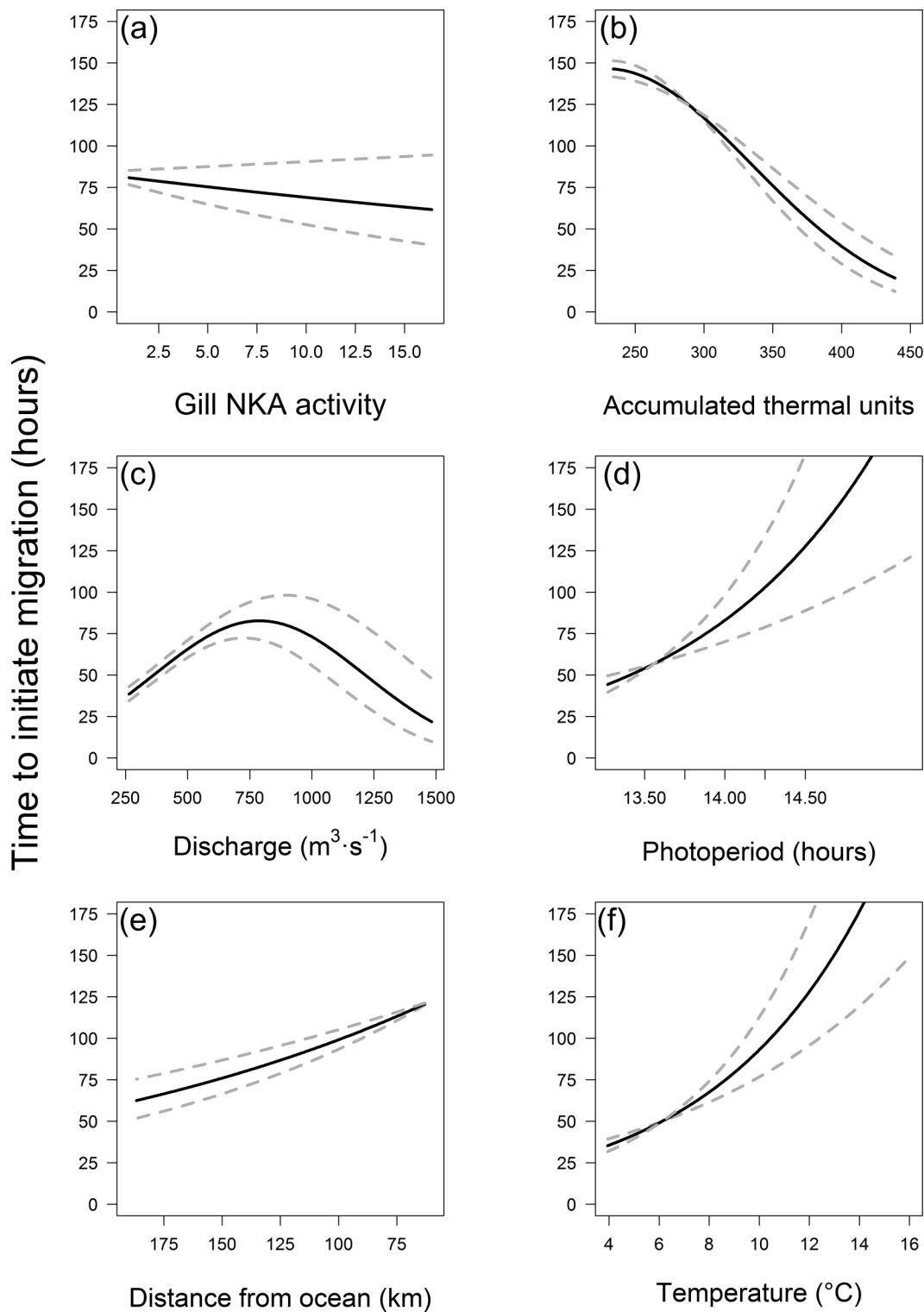
The best predictors of Atlantic salmon smolt movement rate were discharge, release site, photoperiod (day length), physiological development, rearing history, and temperature (Table 4), while the random effect of individual actually explained relatively little variation (Table 4). Mean movement rate of Atlantic salmon smolts during freshwater migration in the Penobscot River was faster through free-flowing reaches of the system (2.1 km·h<sup>-1</sup>) than through reaches that contained dams (1.9 km·h<sup>-1</sup>) or head ponds (1.8 km·h<sup>-1</sup>; Fig. 3; Table 5). Movement rate did not differ among reaches that contained dams compared with reaches that contained head ponds (Fig. 3). In general, wild fish tended to migrate faster than hatchery fish (Table 3).

Discharge (Q) affected movement rate in a complex fashion (Table 5). Movement rate of smolts was slowest at lowest or highest discharges observed (212–1580 m<sup>3</sup>·s<sup>-1</sup>) and fastest at discharges (~750 m<sup>3</sup>·s<sup>-1</sup>) near the middle of this range (Fig. 4). Movement rate of smolts increased with photoperiod until late in the smolt run, at which point the nature of the relationship became highly uncertain owing to low sample sizes (Fig. 4; Table 5). Temperature was inversely related to movement rate, with slower movement rates at higher temperatures. Over the range of temperatures observed (4–16 °C), movement rate decreased from 10 to 2 km·h<sup>-1</sup> (Fig. 4), although the relationship was uncertain at the highest temperatures owing to low sample sizes.

Movement rate increased substantially from the most upstream reaches of the catchment (rkm 180) to the most downstream (rkm 45) freshwater reaches (Table 5). This resulted in an increase in movement rate of about 500% during the course of downstream migration from headwaters to the estuary (Fig. 4). The increase in movement rate was more gradual in the upstream reaches of the river than in downstream reaches, and the most rapid increase in movement rate occurred downstream of rkm 100 (Fig. 4).

Movement rates in the main stem of the Penobscot River increased following the removal of Great Works and Veazie dams when compared with the previous 7 years (Wilcoxon ranked sum test, *W* = 205 124, *P* < 0.001). Median movement rate was 2.8 km·h<sup>-1</sup> through the impacted reaches between Milford Dam and the head of the estuary during years 2005–2013, but doubled during 2014 (5.5 km·h<sup>-1</sup>; Fig. 5a). Movement rate slowed through the Stillwater Branch after the installation of new powerhouses (Wilcoxon ranked sum test, *W* = 14 088, *P* < 0.001). Following installation of new powerhouses on the Stillwater Branch in 2013, median move-

**Fig. 2.** Plots of model-averaged covariate effects on time to initiate migratory behavior (in hours) by hatchery Atlantic salmon smolts stocked throughout the Penobscot River catchment in fresh water, showing effects of (a) gill NKA activity, (b) accumulated thermal units (ATU), (c) discharge at West Enfield Dam, (d) photoperiod on date of release, (e) distance of release upstream of ocean, and (f) water temperature in the Penobscot River at release. Distance from ocean is shown on a reversed scale moving from upstream (left) to downstream (right). Predictions for each covariate were generated by fixing the values of remaining covariates to the mean of the observed value.



ment rate through impacted reaches in 2014 was only  $0.1 \text{ km} \cdot \text{h}^{-1}$ , more than an order of magnitude slower than the long-term median of  $2.2 \text{ km} \cdot \text{h}^{-1}$  during the previous 7 years (Fig. 5b). This result was despite reductions in smolt movement rate during 2013 due

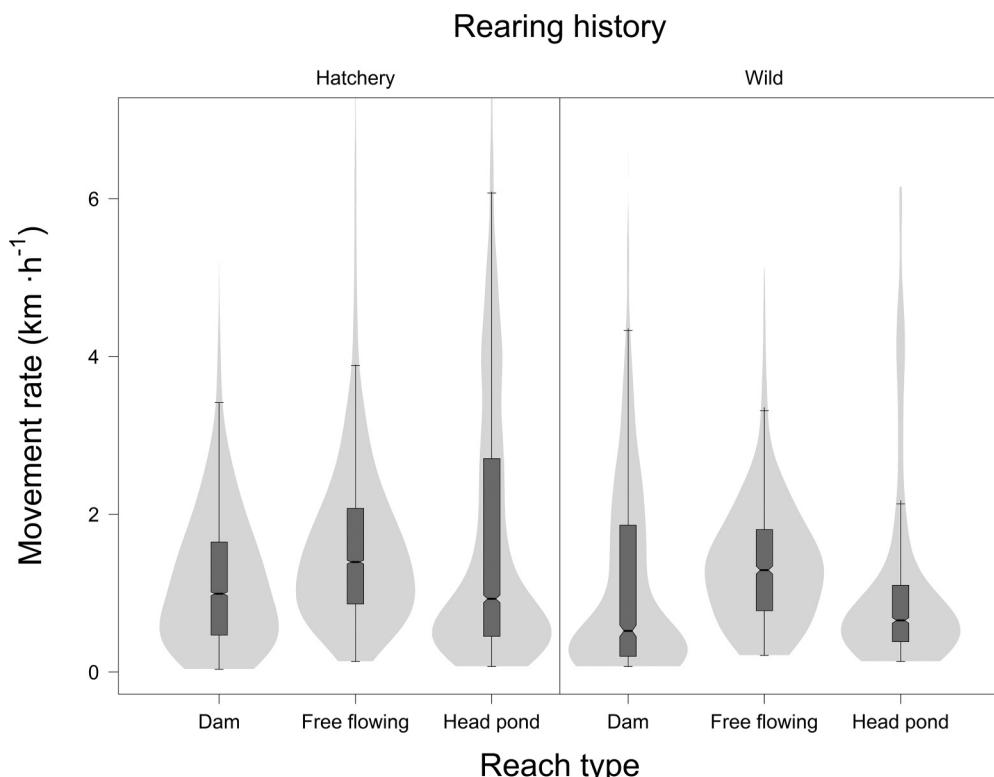
to ongoing powerhouse construction in the Stillwater Branch (Fig. 5b). The appearance of a bimodal distribution through these reaches in 2014 (Fig. 5b) may be related to the concurrent movement of two groups of fish: those stocked several kilometres up-

**Table 4.** Model-selection statistics for the ten best models used to quantify variation in movement rate ( $\text{km} \cdot \text{h}^{-1}$ ) by Atlantic salmon smolts in the Penobscot River, Maine, USA, 2005–2014.

Model	$k$	$\text{AIC}_{\text{ci}}$	$\Delta\text{AIC}_{\text{ci}}$	$w_i$	$(R^2_{\text{GLMM}})$
$\text{PP} + \text{PP}^2 + Q + Q^2 + \text{reach} + \text{rearing} + \text{rkm} + T + T^2$	12	73 613.4	0.00	0.94	0.20
$Q + Q^2 + \text{reach} + \text{rearing} + \text{rkm}$	8	73 619.1	5.72	0.05	0.20
$Q + Q^2 + \text{reach} + \text{rearing} + \text{rkm} + T + T^2$	10	73 624.2	10.80	0.00	0.20
$\text{ATU} + \text{ATU}^2 + Q + Q^2 + \text{reach} + \text{rearing} + \text{rkm}$	10	73 633.7	20.35	0.00	0.20
$\text{ATU} + \text{ATU}^2 + Q + Q^2 + \text{PP} + \text{PP}^2 + \text{reach} + \text{rkm}$	12	73 635.0	21.60	0.00	0.20
$\text{ATU} + \text{ATU}^2 + Q + Q^2 + \text{PP} + \text{PP}^2 + \text{reach} + \text{rkm}$	11	73 656.8	43.46	0.00	0.19
$\text{PP} + \text{PP}^2 + \text{reach} + \text{rearing} + \text{rkm} + T + T^2$	10	73 661.2	47.83	0.00	0.19
$\text{ATU} + \text{ATU}^2 + \text{NKA} + Q + Q^2 + \text{PP} + \text{PP}^2 + \text{reach} + \text{rkm}$	12	73 664.8	51.36	0.00	0.19
$\text{Reach} + \text{rearing} + \text{rkm} + T + T^2$	8	73 668.4	55.05	0.00	0.17
$\text{Reach} + \text{rearing} + \text{rkm}$	6	73 670.2	56.79	0.00	0.17

Note: Number of parameters estimated in each model is  $k$ ,  $\text{AIC}_{\text{ci}}$  is the Akaike information criterion for each  $i$ th model,  $\Delta\text{AIC}_{\text{ci}}$  is the difference between the  $\text{AIC}_{\text{ci}}$  of each  $i$ th model and the best model in the candidate set, and  $w_i$  is the relative probability that each  $i$ th model is the best in the candidate set. Fit was assessed using Nagakawa and Schielzeth's  $R^2$  for linear mixed-effects models ( $R^2_{\text{GLMM}}$ ). Explanatory variables are defined as follows: accumulated thermal units (ATU), discharge ( $Q$ ), distance between release and relocation (Distance), gill NKA activity (NKA), kilometres from ocean (rkm), photoperiod (PP), reach type (dam, free-flowing, or head pond), rearing history (hatchery or wild), and river temperature ( $T$ ).

**Fig. 3.** Changes in movement rate of Atlantic salmon smolts in the Penobscot River with respect to reach type and rearing history (hatchery or wild). Notches in boxes for hatchery (left panel) and wild (right panel) smolts indicate median movement rate within each reach type, box ends indicate inner quartile range, and whiskers are 95% confidence interval. The light gray polygons are violin plots showing density of predicted movement rate for each rearing history in each reach type.



stream in the Stillwater Branch and those using the Stillwater Branch as run-of-river.

## Discussion

A global theme in Atlantic salmon recovery plans is to maximize the number of smolts entering the marine environment (Hansen et al. 2012). To do this requires managers to maximize survival in freshwater rivers and estuaries. For the first time, we now have a comprehensive picture of smolt migration in a single river system, before and after dam removal, including information about factors affecting freshwater survival (Holbrook et al. 2011; Stich et al. 2014), initiation of freshwater migration and rates of movement (this study), and how experiences in fresh water

affect smolt physiology and estuary survival (Stich et al. 2015) in a single river system. Additionally, much of the information (e.g., ATU, discharge, photoperiod, and temperature) used to facilitate annual decision making is available in near real time on the Penobscot River. The integration of these data into decision frameworks for recovery has the potential to inform management in a way that could help maximize the number of smolts leaving the Penobscot River through strategic stocking.

## Initiation

Physiological development and environmental conditions were important predictors of the time to initiate migratory behavior after stocking of hatchery Atlantic salmon smolts. These findings

**Table 5.** Mean and 95% confidence limits (CL) of estimated regression coefficients for the best model of the movement rate of Atlantic salmon smolts in the Penobscot River, Maine, USA, 2005–2014.

Parameter	Estimate	SE	Lower 95% CL	Upper 95% CL
Intercept	-0.580	0.034	-0.646	-0.514
PP	0.168	0.037	0.096	0.241
PP <sup>2</sup>	-0.043	0.015	-0.073	-0.013
Q	0.056	0.031	-0.004	0.116
Q <sup>2</sup>	-0.137	0.016	-0.168	-0.105
Reach (free-flowing)	0.804	0.022	0.761	0.846
Reach (head pond)	0.694	0.023	0.649	0.739
Rearing (wild)	1.064	0.100	0.868	1.260
rkm	-0.884	0.011	-0.906	-0.862
T	-0.269	0.044	-0.356	-0.182
T <sup>2</sup>	0.013	0.013	-0.012	0.039
Random effect	Int = 0.63	Res = 1.27		

**Note:** Explanatory variables are defined as follows: discharge (Q), kilometres from ocean (rkm), photoperiod (PP), reach type (dam, free-flowing, or head pond), rearing history (hatchery or wild), and river temperature (T). The standard deviations of the random effect of individuals on the intercept (Int), as well as of the residuals (Res), are given at the bottom of the table.

could have important implications for strategic stocking of hatchery smolts in the Penobscot River and elsewhere. Other work has shown that smolts stocked as much as 3 weeks apart arrive in estuaries at similar times (McCormick et al. 2014). This suggests a trade-off in the decision by hatchery fish to migrate based on development and (or) environmental cues. It is known that physiological development in Atlantic salmon smolts is entrained by seasonal changes in photoperiod (McCormick et al. 1987) and is regulated by changes in temperature (McCormick et al. 2002). Physiological development of Atlantic salmon smolts previously has been observed to coincide with onset of migratory behavior in laboratory experiments (Zydlowski et al. 2014) and field studies (McCormick et al. 2003, 2013). Influences of local environmental conditions and habitat features also might physically override or inhibit station-holding behavior in smolts rather than incite an active “choice” to migrate. Intensity of exposure to environmental changes (such as in photoperiod, temperature, or discharge) in upper regions of a watershed might be increased relative to those in the lower river because of the local characteristics of the river, such as depth or channel width. The nature of the mechanism controlling differences among reaches of a river could provide an interesting line of inquiry for future work.

We found that the time to initiation of downstream migration decreased when smolts had greater thermal experience (ATU) during hatchery rearing. This result previously has been observed in laboratory studies of Atlantic salmon (Zydlowski et al. 2005, 2014) and in field studies of Chinook salmon (*Oncorhynchus tshawytscha*) (Sykes et al. 2009). It is important to note that the range of ATU experienced by smolts in the present study was below upper thresholds that have been observed to inhibit migratory behavior in Atlantic salmon smolts (Zydlowski et al. 2005, 2014; McCormick 2009). Loss of physiological smolt characteristics occurs at high temperatures (McCormick et al. 1999), and cessation of migratory behavior also occurs at high temperatures (Zydlowski et al. 2014). In the present study, we observed a gradual increase in the amount of time required for initiation of migratory behavior until about 10 °C, after which the amount of time for initiation increased rapidly with temperature. Interestingly, this is approximately the same temperature at which daily counts of migrating smolts also begin to decline in laboratory studies (Zydlowski et al. 2014). Our results suggest that the ATUs experienced by smolts, in

addition to a threshold temperature, may be important for initiation of migratory behavior.

#### Movement rate

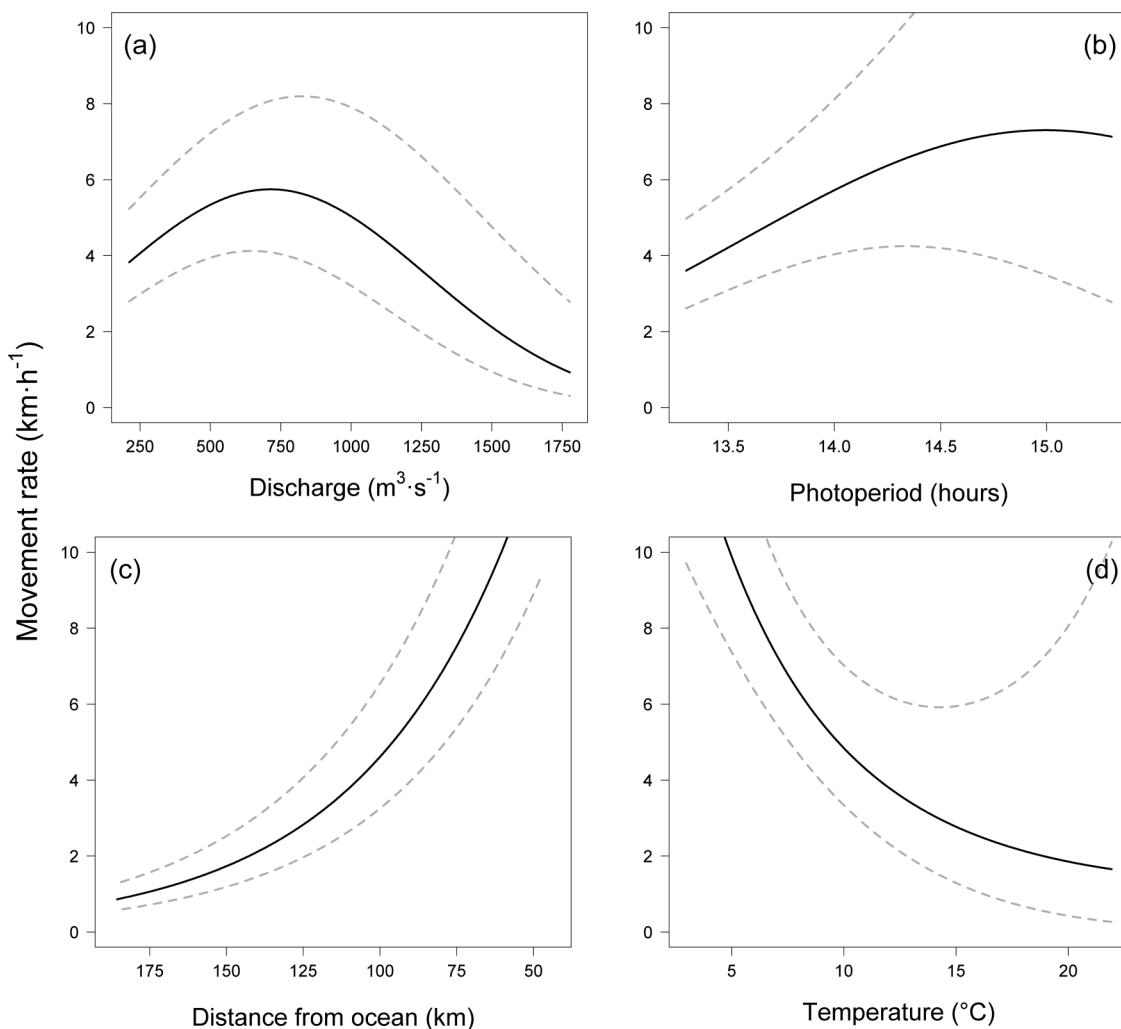
We used two indicators of smolt development to investigate behavior of smolts during the freshwater migration in this study: ATU and gill NKA activity. Previous work has demonstrated that ATU experienced by smolts is a strong predictor of the initiation of migratory behavior in hatchery (Zydlowski et al. 2005) and wild (Sykes et al. 2009) salmon smolts. The freshwater movement rate of smolts was fastest during the seasonal peak of the run (photoperiod of about 14 h; Fig. 4b). Smolts also moved faster at cool temperatures than at warm temperatures (Fig. 4), and this relationship bottomed out after about 12 °C, toward the end of the smolt run. These results indicate that smolts may move faster during the period at which their physiological development is optimal for ocean entry. In fact, loss of smolt characteristics was previously observed toward the end of the Penobscot River run (McCormick et al. 1999).

When variability in environmental conditions was accounted for, we found that movement rate of smolts was slower in reaches of the Penobscot River that contained head ponds or dams associated with hydropower projects than it was through free-flowing reaches of the river. Reduced movement rates previously have been observed through dams for Atlantic salmon (Holbrook et al. 2011; Norrgård et al. 2013) and for Pacific salmon (*Oncorhynchus* spp.) (Ransom et al. 2008). This delay has the potential to result in loss of physiological smolt characteristics (McCormick et al. 1999; Handeland et al. 2004) and increased estuary mortality (Stich et al. 2015) as a result of mismatches (sensu Cushing 1969) between physiological development and timing of arrival in the estuary caused by dam passage (Marschall et al. 2011). Given that the effects of dams on movement rates were more pronounced in wild smolts than in hatchery smolts, estuary mortality resultant from delays at dams could be greater in wild smolts than in hatchery smolts.

We documented a 96% increase in movement rate after the removal of two dams compared with median movement rates in the same reaches during 7 years prior to dam removal (Fig. 5). We also found that movement rate decreased markedly through a migration route in the lower river (the Stillwater Branch) following the addition of a second powerhouse at each of the dams located therein (Fig. 5). Although movement rates through impacted reaches have only been collected for a single year after dam removal and hydropower re-allocation, the results are, at minimum, deserving of attention. The methods used in this study provide both a framework for analysis and a baseline of information for future assessments.

Our results demonstrate that the removal of mainstem dams could improve smolt survival during estuary passage by reducing delay at these facilities, thus decreasing potential for predation (Blackwell and Juanes 1998) and temperature-related loss of physiological smolt characteristics such as elevated gill NKA activity (McCormick et al. 1999). Counter to this potential positive change in the main stem is the decrease in movement rates through the Stillwater Branch that could potentially result in increased estuary mortality following construction of new powerhouses. This may be particularly relevant given that survival of smolts in the Penobscot River Estuary also was recently related to gill NKA activity and number of dams passed in fresh water (Stich et al. 2015). Additionally, previous work has shown that more fish use the main stem as a migratory route compared with the Stillwater Branch (Holbrook et al. 2011; Stich et al. 2014), so a net increase in movement rate through the lower river is expected for smolts following changes to the hydro-system. These results highlight the importance of considering effects beyond acute mortality when assessing the effects of mainstem dam removal on anadromous fish migrations.

**Fig. 4.** Plots of relationships between freshwater movement rate of migrating Atlantic salmon smolts and (a) discharge at West Enfield Dam ( $\text{m}^3 \cdot \text{s}^{-1}$ ), (b) photoperiod (hours), (c) distance from the ocean (km), and (d) water temperature ( $^{\circ}\text{C}$ ) in the Penobscot River. Distance from ocean is shown on a reversed scale moving from upstream (left) to downstream (right). Mean predicted movement rate ( $\text{km} \cdot \text{h}^{-1}$ ) from each covariate is shown by the solid black line and 95% confidence interval is indicated by the dashed gray lines. Predictions for each covariate were generated by fixing the values of remaining covariates to the mean of the observed value.



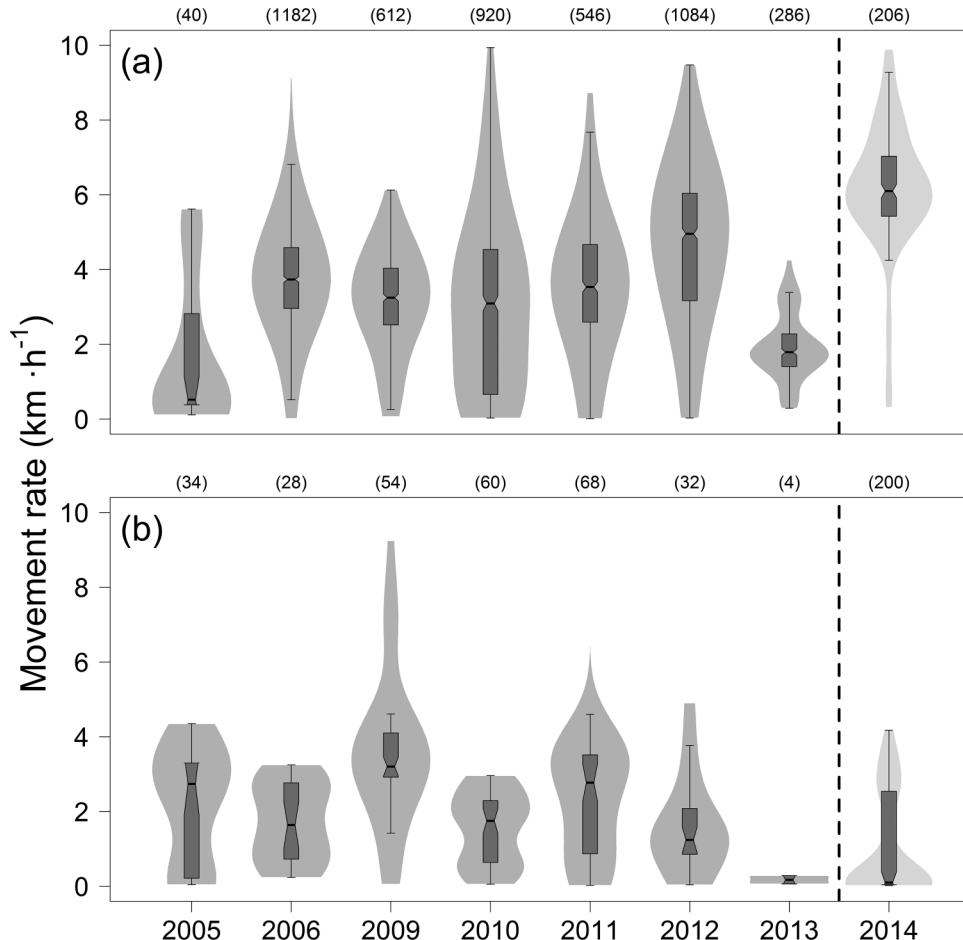
### Implications for conservation hatcheries

The results of this study have important implications for two decisions that are made annually at conservation hatcheries charged with Atlantic salmon smolt stocking: (i) when to stock fish each spring and (ii) where to stock those fish. Inherent in these decisions is the need to minimize residency time in fresh water and the associated risk of increased predator exposure and mismatch between physiological development and timing of estuary arrival. In the Penobscot River, there seems to be some compensatory interplay between the time to initiate migration by stocked smolts and movement rate throughout the system. For example, fish that are stocked close to the ocean take longer to initiate migration than smolts stocked further upstream, but fish also move faster close to the ocean than further upstream. Similar trade-offs in behavioral tactics were observed with respect to discharge (late initiation but fast movement at intermediate discharges) and photoperiod (late initiation but fast movement rate at advanced photoperiods). There is potential that interactions among these environmental factors could lead to stabilization in the timing of estuary entrance, and normalizing selection on timing of estuary arrival has been observed in the Penobscot previously (Stich et al. 2015). Annual decision making about when and

where to stock fish could be greatly facilitated by incorporating knowledge about factors that influence how soon fish begin to migrate and how fast they move.

Information about temperature could be used to balance time to initiate migratory behavior with movement rate based on when fish are stocked. Measures of smolt development and environmental conditions were important predictors of when hatchery-stocked smolts initiated migration (Fig. 2). Given the strong relationships between time to initiation of migration and (i) ATU and (ii) temperature, hatcheries potentially could use both ATU and river temperature as annual indicators for when to stock smolts. Our results demonstrated that hatchery stocking of smolts in the Penobscot River has occurred in advance of the number of accumulated thermal units (about 500 ATU) that can connote loss of smolt characteristics and thus is predicted to increase the number of hatchery smolts that actually migrate to the ocean. Knowledge of smolt development could be used to inform stocking of hatchery smolts as well based on the relationship between physiological development and initiation. However, the relation of initiation to both ATU and river temperature provides a simpler, less expensive planning tool, and these factors were quantitatively better predictors of initiation than gill NKA activi-

**Fig. 5.** Movement rates of Atlantic salmon smolts during each year of this study through (a) the river reach between Milford Dam and Penobscot River Estuary, Maine, and (b) the reach from the upstream end of the Stillwater Branch and the first receiver downstream of the confluence of the Stillwater Branch with the mainstem Penobscot River. The vertical line represents the time after which both Veazie and Great Works dams were removed and new powerhouses had been installed at Stillwater and Orono dams. Box ends represent the inner quartile range, whiskers represent 95% confidence interval, and the notches in the boxes represent median movement rate. The shadows behind boxes are violin plots showing density of observations, and sample size is given above each plot. The slow movement through the Stillwater Branch in 2013 coincided with drawdown for construction, but was used in the 2005–2013 movement rates for Wilcoxon tests.



ity. Although developmental indices were not related to movement rate, temperature was (Fig. 4). Daily temperature data also are already collected throughout the catchment and at salmon hatcheries, so integration of information about temperature would require little investment beyond the status quo.

Daily discharge in the Penobscot River can be used as another source of information about when to stock hatchery smolts based on its relation to initiation of migration and movement rate. It took fish longer to initiate migration under intermediate flows (Fig. 4), but once migrating, this was when fish moved most rapidly (Fig. 2). Similar to temperature data, information about discharge in the Penobscot River also is collected several times a day in various locations.

We found two important results that could be used to inform decisions about where to stock smolts: (i) stocking location and (ii) locations of dams and head ponds. Stocking location has the potential to influence movement rate during migration as well as initiation of migratory behavior. Hatchery smolts moved much faster through the lower river than through reaches further upstream (Fig. 4). Conversely, fish released in the upper watershed initiated migration sooner after stocking than fish released nearer to the ocean (Fig. 2). As with the influences of temperature and discharge, these results suggest an opportunity to balance

stocking location based on differential effects on initiation and movement rate.

Stocking location also is related to the number of dams fish pass as well as which dams fish pass in the Penobscot River. Our results clearly demonstrated that movement rate was reduced through reaches containing dams or head ponds associated with dams (Fig. 3). We showed that changes to the hydro system have the potential to influence movement rate during migration (Fig. 5). These results underscore the importance of considering the locations of dams and head ponds with respect to stocking location. It is important to note that passage of multiple dams will compound effects on movement rate if only in an additive sense, although multiplicative effects have been observed (Norrgård et al. 2013). This is important given that dams also are known sites of elevated mortality of Atlantic salmon smolts (Holbrook et al. 2011; Norrgård et al. 2013; Stich et al. 2014), and these structures can have spatially removed effects on migration (Marschall et al. 2011) and even result in delayed mortality during estuary passage (Stich et al. 2015). Following the removal of Veazie Dam in 2013, about 20 km of lotic habitat was reclaimed in the lower Penobscot River between the now lowermost dam (Milford) and the estuary. This resulted in the stocking of all smolts in the tail race of Milford Dam in an effort to minimize in-river and estuary mortality in-

curred through dam passage in the Penobscot River in 2014. There are clear trade-offs between homing or straying rates and smolt-to-spawn survival that warrant consideration in such a stocking strategy. Research suggests that incidence of straying increases when smolts are released nearer to the ocean, but losses to straying do not generally offset gains in survival until stocking occurs at the coast (Gunnerød et al. 1988). Similarly, although release within the Penobscot River affects homing to natal streams, the number of fish reaching the lower river (at which point most returning adults currently are trucked to hatcheries) was unaffected by stocking location in previous research (Gorsky et al. 2009). Thus, stocking below dams in the Penobscot River likely will increase the number of adults that return for spawning.

## Acknowledgements

Financial support for this research was provided by the National Fish and Wildlife Foundation, the American Recovery and Reinvestment Act (ARRA), and NOAA Open Rivers Initiative through the Penobscot River Restoration Trust and NOAA National Marine Fisheries Service (NMFS). Additional funding was provided by Brookfield Renewable Power (Great Lakes Hydro America), Maine Department of Marine Resources, The Nature Conservancy, University of Maine, and US Geological Survey, Maine Cooperative Fish and Wildlife Research Unit. We acknowledge substantial contributions to this work by M. Bailey, C. Gardner, C. Holbrook, and A. O’Malley (Department of Wildlife, Fisheries, and Conservation Biology). We thank M. Altenritter, P. Dionne, S. Fernandes, and C. Johnston (School of Marine Sciences, University of Maine), as well as G. Goulette and J. Hawkes (NMFS) for their efforts in maintaining the acoustic receiver array in the Penobscot Estuary. We thank G. Zydlewski (School of Marine Sciences, University of Maine) and M. Bailey for thoughtful reviews during previous versions of this manuscript. The USFWS, GLNFH provided juvenile Atlantic salmon and was instrumental in facilitating the marking and stocking of smolts for this research. This work was done in coordination and cooperation with NOAA Fisheries Northeast Fisheries Science Center and Maine Department of Marine Resources. Mention of trade names or commercial products does not imply endorsement by the US Government. This work was conducted under the auspices of University of Maine Institutional Animal Care and Use Committee (IACUC) protocols 2008-07-01 and A2011-06-06.

## References

- Blackwell, B.F., and Juanes, F. 1998. Predation on Atlantic Salmon smolts by striped bass after dam passage. *N. Am. J. Fish. Manage.* **18**(4): 936–939. doi: [10.1577/1548-8675\(1998\)018<0936:POASSB>2.0.CO;2](https://doi.org/10.1577/1548-8675.018-0936.POASSB>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. *Colon. Waterbirds*, **20**(1): 77–86. doi: [10.2307/1521766](https://doi.org/10.2307/1521766).
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach, second edition. Springer, New York, New York.
- Cushing, D.H. 1969. The regularity of the spawning season of some fishes. *ICES J. Mar. Sci.* **33**(1): 81–92. doi: [10.1093/icesjms/33.1.81](https://doi.org/10.1093/icesjms/33.1.81).
- Day, L.R. 2006. Restoring native fisheries to Maine’s largest watershed: the Penobscot River Restoration Project. *J. Contemp. Water Res. Educ.* **134**(1): 29–33. doi: [10.1111/j.1936-704X.2006.mpj134001006.x](https://doi.org/10.1111/j.1936-704X.2006.mpj134001006.x).
- Federal Energy Regulatory Commission. 2004. Submittal of the Lower Penobscot River Basin comprehensive settlement accord with explanatory statement for FERC project numbers 2403, 2534, 2666, 2710, 2712, 2721, and 10981 [online]. United States Department of Energy, Washington, D.C. Available from <http://elibrary.ferc.gov/idmws/common/OpenNat.asp?fileID=10188480> [accessed 13 August 2014].
- Federal Energy Regulatory Commission. 2005. Order modifying and approving amendment of license for FERC project number 2712-055 [online]. United States Department of Energy, Washington, D.C. Available from <http://elibrary.ferc.gov/idmws/common/opennat.asp?fileID=10499146> [accessed 13 August 2014].
- Federal Energy Regulatory Commission. 2009. Draft environmental assessment, application for surrender of license for FERC project numbers 2403-056, 2312-019 and 2721-20 [online]. United States Department of Energy, Washington, D.C. Available from <http://elibrary.ferc.gov/idmws/common/OpenNat.asp?fileID=10188480> [accessed 13 August 2014].
- Gunnerød, T.B., Hvidsten, N.A., and Heggberget, T.G. 1988. Open sea releases of Atlantic salmon smolts, *Salmo salar*, in Central Norway, 1971–83. *Can. J. Fish. Aquat. Sci.* **45**(8): 1340–1345. doi: [10.1139/f88-157](https://doi.org/10.1139/f88-157).
- Handeland, S.O., Wilkinson, E., Sveinsbø, B., McCormick, S.D., and Stefansson, S.O. 2004. Temperature influence on the development and loss of seawater tolerance in two fast-growing strains of Atlantic salmon. *Aquaculture*, **233**(1–4): 513–529. doi: [10.1016/j.aquaculture.2003.08.028](https://doi.org/10.1016/j.aquaculture.2003.08.028).
- Hansen, L.P., Hutchinson, P., Reddin, D.G., and Windsor, M.L. 2012. Salmon at sea: scientific advances and their implications for management: an introduction. *ICES J. Mar. Sci.* **69**(9): 1533–1537. doi: [10.1093/icesjms/fss146](https://doi.org/10.1093/icesjms/fss146).
- Haugland, M., Holst, J.N., Holm, M., and Hansen, L.P. 2006. Feeding of Atlantic salmon (*Salmo salar* L.) post-smolts in the Northeast Atlantic. *ICES J. Mar. Sci.* **63**(8): 1488–1500. doi: [10.1016/j.icesjms.2006.06.004](https://doi.org/10.1016/j.icesjms.2006.06.004).
- 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](https://doi.org/10.1656/045.020.0101).
- Hijmans, R.J., Williams, E., and Vennes, C. 2010. Package ‘geosphere’ (manual) [online]. Available from <http://cran.r-project.org/web/packages/geosphere/geosphere.pdf>.
- 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](https://doi.org/10.1080/00028487.2011.618356).
- International Union of Biochemistry and Molecular Biology. 1992. Enzyme nomenclature 1992. Academic Press, San Diego, Calif.
- 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](https://doi.org/10.1111/eff.12097).
- Kocik, J., Hawkes, J., Sheehan, T., Music, P., and Beland, K. 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 Symposium 69. Edited by A. Haro, K.L. Smith, R.A. Rulifson, C.M. Moffitt, R.J. Klauda, M.J. Dadswell, R.A. Cunjak, J.E. Cooper, K.L. Beal, and T.S. Avery. American Fisheries Society, American Fisheries Society, Bethesda, Md. pp. 293–310.
- Marschall, E.A., Mather, M.E., Parrish, D.L., Allison, G.W., and McMenemey, J.R. 2011. Migration delays caused by anthropogenic barriers: modeling dams, temperature, and success of migrating salmon smolts. *Ecol. Appl.* **21**(8): 3014–3031. doi: [10.1890/10-0593.1](https://doi.org/10.1890/10-0593.1).
- Mathur, D., Heisey, P.G., Skalski, J.R., and Kenney, D.R. 2000. Salmonid smolt survival relative to turbine efficiency and entrainment depth in hydroelectric power generation. *J. Am. Water Resour. As.* **36**(4): 737–747. doi: [10.1111/j.1752-1688.2000.tb04302.x](https://doi.org/10.1111/j.1752-1688.2000.tb04302.x).
- McCormick, S.D. 1993. Methods for nonlethal gill biopsy and measurement of  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase activity. *Can. J. Fish. Aquat. Sci.* **50**(3): 656–658. doi: [10.1139/f93-075](https://doi.org/10.1139/f93-075).
- McCormick, S.D. 2013. Smolt physiology and endocrinology. In *Fish physiology: euryhaline fishes*. Vol. 32. Edited by S.D. McCormick, A.P. Farrell, and C.J. Brauner. Academic Press, San Diego, Calif. pp. 199–251.
- McCormick, S.D., Saunders, R.L., Henderson, E.B., and Harmon, P.R. 1987. Photoperiod control of parr-smolt transformation in Atlantic salmon (*Salmo salar*): changes in salinity tolerance, gill  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase activity and thyroid hormones. *Can. J. Fish. Aquat. Sci.* **44**(8): 1462–1468. doi: [10.1139/f87-175](https://doi.org/10.1139/f87-175).
- McCormick, S.D., Hansen, L.P., Quinn, T.P., and Saunders, R.L. 1998. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* **55**(S1): 77–92. doi: [10.1139/d98-011](https://doi.org/10.1139/d98-011).
- McCormick, S.D., Cunjak, R.A., Dempson, B., O’Dea, M.F., and Carey, J.B. 1999. Temperature-related loss of smolt characteristics in Atlantic salmon (*Salmo salar*) in the wild. *Can. J. Fish. Aquat. Sci.* **56**(9): 1649–1658. doi: [10.1139/f99-099](https://doi.org/10.1139/f99-099).
- McCormick, S.D., Shrimpton, J.M., Moriyama, S., and Björnsson, B.T. 2002. Effects of an advanced temperature cycle on smolt development and endocrinology indicate that temperature is not a zeitgeber for smolting in Atlantic

- salmon [online]. *J. Exp. Biol.* **205**(22): 3533–3560. Available from <http://jeb.biologists.org/content/205/22/3553.full.pdf+html> [accessed 13 October 2014].
- McCormick, S.D., O'Dea, M.F., Moekel, A.M., and Björnsson, B.T. 2003. Endocrine and physiological changes in Atlantic salmon smolts following hatchery release. *Aquaculture*, **222**(1–4): 45–57. doi:10.1016/S0044-8486(03)00101-7.
- McCormick, S.D., Lerner, D.T., Monette, M.Y., Nieves-Puigdoller, K., Kelly, J.T., and Björnsson, B.T. 2009. Taking it with you when you go: how perturbations to the freshwater environment, including temperature, dams, and contaminants, affect marine survival of salmon. In *American Fisheries Society Symposium*. Edited by A. Haro, K.L. Smith, R.A. Rulifson, C.M. Moffit, R.J. Klauda, M.J. Dadswell, R.A. Cunjak, J.E. Cooper, K.L. Beal, and T.S. Avery. American Fisheries Society, Bethesda, Md. pp. 195–214. Available from <http://citeserx.ist.psu.edu/viewdoc/download?doi=10.1.1.419.4147&rep=rep1&type=pdf> [accessed 18 June 2014].
- McCormick, S.D., Sheehan, T.F., Björnsson, B.T., Lipsky, C., Kocik, J.F., Regish, A.M., and O'Dea, M.F. 2013. Physiological and endocrine changes in Atlantic salmon smolts during hatchery rearing, downstream migration, and ocean entry. *Can. J. Fish. Aquat. Sci.* **70**(1): 105–118. doi:10.1139/cjfas-2012-0151.
- McCormick, S.D., Haro, A., Lerner, D.T., O'Dea, M.F., and Regish, A.M. 2014. Migratory patterns of hatchery and stream-reared Atlantic salmon *Salmo salar* smolts in the Connecticut River, U.S.A. *J. Fish Biol.* **85**(4): 1005–1022. doi:10.1111/jfb.12532. PMID:25263185.
- McFadden, D. 1974. Conditional logit analysis of qualitative choice behavior. In *Frontiers in econometrics*. Edited by P. Zarembka. Academic Press, San Diego, Calif. pp. 105–142.
- Montgomery, D.C., Peck, E.A., and Vining, G.G. 2006. Introduction to linear regression analysis. 4th ed. John Wiley and Sons Inc., Hoboken, New Jersey.
- Music, P.A., Hawkes, J.B., and Cooperman, M.S. 2010. Magnitude and causes of smolt mortality in rotary screw traps: an Atlantic salmon case study. *N. Am. J. Fish. Manage.* **30**(3): 713–722. doi:10.1577/M09-181.1.
- Nakagawa, S., and Schielzeth, H. 2013. A general and simple method for obtaining  $R^2$  from generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**(2):133–142. doi:10.1111/j.2041-210x.2012.00261.x.
- Norrgård, J.R., Greenberg, L.A., Piccolo, J.J., Schmitz, M., and Bergman, E. 2013. Multiplicative loss of landlocked Atlantic salmon *Salmo salar* L. smolts during downstream migration through multiple dams. *River Res. Appl.* **29**(10): 1306–1317. doi:10.1002/rra.2616.
- Otero, J., L'Abée-Lund, J.H., Castro-Santos, T., Leonardsson, K., Storvik, G.O., Jonsson, B., Dempson, B., Russell, I.C., Jensen, A.J., Bagliniere, J., Dionne, M., Armstrong, J.D., Romakkaniemi, A., Letcher, B.H., Kocik, J.F., Erkinaro, J., Pooke, R., Rogan, G., Lundqvist, H., Maclean, J.C., Jokikokko, E., Arnekleiv, J.V., Kennedy, R.J., Niemelä, E., Caballero, P., Music, P.A., Antonsson, T., Gudjonsson, S., Veselov, A.E., Lamberg, A., Groom, S., Taylor, B.H., Taberner, M., Dillane, M., Arnason, F., Horton, G., Hvistend, N.A., Jonsson, I.R., Jonsson, N., McKelvey, S., Næsje, T.F., Øystein, S., Smith, G.S., Sægrov, H., Stenseth, N.C., and Vøllestad, L.A. 2014. Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (*Salmo salar*). *Glob. Chang. Biol.* **20**(1): 61–75. doi:10.1111/gcb.12363. PMID:23966281.
- Petrosky, C.E., and Schaller, H.A. 2010. Influence of river conditions during seaward migration and ocean conditions on survival rates of Snake River Chinook salmon and steelhead. *Ecol. Freshw. Fish*, **19**(4): 520–536. doi:10.1111/j.1600-0633.2010.00425.x.
- Poe, T.P., Hansel, H.C., Vigg, S., Palmer, D.E., and Prendergast, L.A. 1991. Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day Reservoir, Columbia River. *Trans. Am. Fish. Soc.* **120**(4): 405–420. doi:10.1577/1548-8659(1991)120<405:POPOFO>2.3.CO;2.
- R Core Team. 2014. R: a language and environment for statistical computing, Version 3.1.0. R Foundation for Statistical Computing, Vienna, Austria.
- Ransom, B.H., Steig, T.W., Timko, M.A., and Nealson, P.A. 2008. Basin-wide monitoring of salmon smolts at US dams [online]. *Int. J. Hydropower Dams*, **15**(3): 43–49. Available from [http://htisonar.com/publications/Basin-wide\\_monitoring\\_US\\_dams.pdf](http://htisonar.com/publications/Basin-wide_monitoring_US_dams.pdf) [accessed 16 October 2014].
- Russell, I.C., Aprahamian, M.W., Barry, J., Davidson, I.C., Fiske, P., Ibbotson, A.T., Kennedy, R.J., Maclean, J.C., Moore, A., Otero, J., Potter, T., and Todd, C.D.
2012. The influence of the freshwater environment and the biological characteristics of Atlantic salmon smolts on their subsequent marine survival. *ICES J. Mar. Sci.* **69**(9): 1563–1573. doi:10.1093/icesjms/fsr208.
- Sheehan, T.F., Renkawitz, M.D., and Brown, R.W. 2011. Surface trawl survey for U.S. origin Atlantic salmon *Salmo salar*. *J. Fish Biol.* **79**(2): 374–398. doi:10.1111/j.1095-8649.2011.03025.x.
- Smith, P.K., Krohn, R.I., Hermanson, G.T., Mallia, A.K., Gartner, F.H., Provenzano, M.D., Fujimoto, E.K., Goede, N.M., Olson, B.J., and Klenk, D.C. 1985. Measurement of protein using bicinchoninic acid. *Anal. Biochem.* **150**(1): 76–85. doi:10.1016/0003-2697(85)90442-7. PMID:3843705.
- Stich, D.S., Bailey, M.M., and Zytlewski, J.D. 2014. Survival of Atlantic salmon *Salmo salar* smolts through a hydropower complex in the lower Penobscot River, Maine U.S.A. *J. Fish Biol.* **85**(4): 1074–1096. doi:10.1111/jfb.12483. PMID:25130320.
- Stich, D.S., Kocik, J.F., Zytlewski, G.B., and Zytlewski, J.Z. 2015. Linking behavior, physiology, and survival of Atlantic salmon smolts during estuary migration. *Mar. Coast. Fish. Dyn. Manage. Ecosyst. Sci.* **7**(1): 68–86. doi:10.1080/19425120.2015.1007185.
- Stier, D.J., and Kynard, B. 1986. Use of Radio telemetry to determine the mortality of Atlantic salmon smolts passed through a 17-MW Kaplan turbine at a low-head hydroelectric dam. *Trans. Am. Fish. Soc.* **115**(5): 771–775. doi:10.1577/1548-8659(1986)115<771:UORTTD>2.0.CO;2.
- Svenning, M.A., Borgstrøm, R., Dehli, T.O., Moen, G., Barrett, R.T., Pedersen, T., and Väder, W. 2005. The impact of marine fish predation on Atlantic salmon smolts (*Salmo salar*) in the Tana estuary, North Norway, in the presence of an alternative prey, Lesser Sandeel (*Ammodytes marinus*). *Fish. Res.* **76**(3): 466–474. doi:10.1016/j.fishres.2005.06.015.
- Sykes, G.E., Johnson, C.J., and Shrimpton, J.M. 2009. Temperature and flow effects on migration timing of Chinook salmon smolts. *Trans. Am. Fish. Soc.* **138**(6): 1252–1265. doi:10.1577/T08-180.1.
- Thorstad, E.B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A.H., and Finstad, B. 2012. 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.
- United States Atlantic Salmon Assessment Committee. 2012. Annual report of the U.S. Atlantic Salmon Assessment Committee [online]. USASAC Report 24, United States Atlantic Salmon Assessment Committee, Old Lyme, Connecticut. Available from <http://www.nfsc.noaa.gov/USASAC/Reports/> [accessed 13 August 2014].
- United States Atlantic Salmon Assessment Committee. 2014. Annual report of the U.S. Atlantic Salmon Assessment Committee [online]. USASAC Report 26, United States Atlantic Salmon Assessment Committee, Old Lyme, Connecticut. Available from <http://www.nfsc.noaa.gov/USASAC/Reports/> [accessed 13 August 2014].
- Whalen, K.G., Parrish, D.L., and McCormick, S.D. 1999. Migration timing of Atlantic Salmon smolts relative to environmental and physiological factors. *Trans. Am. Fish. Soc.* **128**(2): 289–301. doi:10.1577/1548-8659(1999)128<289:MTOASS>2.0.CO;2.
- Zar, J.H. 1999. Biostatistical analysis. Prentice Hall, Upper Saddle River, New Jersey.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., and Smith, G.M. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.
- Zytlewski, G.B., Haro, A., and McCormick, S.D. 2005. Evidence for cumulative temperature as an initiating and terminating factor in downstream migratory behavior of Atlantic salmon (*Salmo salar*) smolts. *Can. J. Fish. Aquat. Sci.* **62**(1): 68–78. doi:10.1139/f04-179.
- Zytlewski, G.B., Stich, D.S., and McCormick, S.D. 2014. Photoperiod control of downstream movements of Atlantic salmon *Salmo salar* smolts. *J. Fish Biol.* **85**(4): 1023–1041. doi:10.1111/jfb.12509. PMID:25263186.
- Zytlewski, J., and Wilkie, M. 2013. Freshwater-seawater transitions in juvenile euryhaline fish. In *Euryhaline fishes. Fish physiology*, Vol. 32. Edited by S.D. McCormick, A.P. Farrell, and C.J. Brauner. Academic Press, San Diego, Calif. pp. 253–326.