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ARTICLE

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Abstract

Decreased marine survival is identified as a component driver of continued declines of Atlantic Salmon *Salmo salar*. However, estimates of marine mortality often incorporate loss incurred during estuary migration that may be mechanistically distinct from factors affecting marine mortality. We examined movements and survival of 941 smolts (141 wild and 800 hatchery-reared fish) released in freshwater during passage through the Penobscot River estuary, Maine, from 2005 to 2013. We related trends in estuary arrival date, movement rate, and survival to fish characteristics, migratory history, and environmental conditions in the estuary. Fish that experienced the warmest thermal history arrived in the estuary 8 d earlier than those experiencing the coolest thermal history during development. Estuary arrival date was 10 d later for fish experiencing high flow than for fish experiencing low flow. Fish released furthest upstream arrived in the estuary 3 d later than those stocked further downstream but moved 0.5 km/h faster through the estuary. Temporally, movement rate and survival in the estuary both peaked in mid-May. Spatially, movement rate and survival both decreased from freshwater to the ocean. Wild smolts arrived in the estuary later than hatchery fish, but we observed no change in movement rate or survival attributable to rearing history. Fish with the highest gill Na^+, K^+-ATPase activity incurred 25% lower mortality through the estuary than fish with the lowest gill Na^+, K^+-ATPase activity. Smolt survival decreased (by up to 40%) with the increasing number of dams passed (ranging from two to nine) during freshwater migration. These results underscore the importance of physiological preparedness on performance and the delayed, indirect effects of dams on survival of Atlantic Salmon smolts during estuary migration, ultimately affecting marine survival estimates.

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The links between the freshwater experience of anadromous fishes and marine survival are poorly understood in general (McCormick et al. 2009). Information about these relationships could have timely implications for the management and conservation of fisheries. Elevated marine mortality in recent years, due in large part to changes in ocean climate (Friedland et al. 2003; Mills et al. 2013; Friedland et al. 2014), is thought to be a driver behind the recovery failure of many endangered populations of Atlantic Salmon *Salmo salar* (Chaput et al. 2005; Chaput 2012; Miller et al. 2012; Mills et al. 2013; Lacroix 2014). However, high mortality during migration through freshwater and estuarine corridors (Thorstad et al. 2012b; Hayes and Kocik 2014) also likely contributes to reduced population sizes (Parrish et al. 1998). Estimates of marine survival also often include estuarine mortality due to the difficulty in separating these processes (Friedland 1998). A better understanding of factors that influence estuary mortality could help to enhance the management of Atlantic Salmon stocks in the face of changing ocean climates (Mills et al. 2013). Despite the importance of estuarine habitats during migration, little is known about Atlantic Salmon smolt behavior and survival in North American estuaries compared with in freshwater and nearshore marine environments (Weitkamp et al. 2014).

The transition of Atlantic Salmon smolts to saltwater is recognized as a period of high mortality in estuaries (Lacroix 2008; Kocik et al. 2009; Dempson et al. 2011) and fjords (Gudjonsson et al. 2005; Svenning et al. 2005; Thorstad et al. 2012b). This period is marked by high predation risk (Hvidsten and Lund 1988; Kocik et al. 2009; Hawkes et al. 2013), physiological stresses (Handeland et al. 1997), and novel environmental conditions (McCormick et al. 1998). In response to these challenges, the process of smolting involves a synchronous suite of changes in physiology, morphology, and behavior that, in concert, enhance the probability of survival following successful saltwater entry (McCormick et al. 1998). Therefore, the seasonal timing of smolt runs is important (McCormick et al. 1998; Thorstad et al. 2012b).

Smolt survival during estuary passage is theoretically maximized by matching migration timing and animal characteristics to predictable annual environmental conditions, along with the presence or absence of predators (Kocik et al. 2009) and sympatric prey buffers (Svenning et al. 2005) during a brief annual period of several weeks, characterizing the "ecological smolt window" (McCormick et al. 1998). To match this ecological window, smolts experience a concurrent period of peak physiological preparedness for saltwater entry, the "physiological smolt window" (McCormick et al. 1998). Gill Na^+, K^+-ATPase (gill NKA; enzyme code 3.6.3.9; IUBMB 1992) activity in Atlantic Salmon is one enzyme measurement that has been found to be a useful indicator of smolt development and preparedness for saltwater entry (Zaugg 1982; McCormick et al.1987, 1989). During smoltification, gill NKA activity peaks during the spring, resulting in a period of increased saltwater tolerance (Duston and Saunders 1990; McCormick 2013). Evidence relating smolt survival in the wild to gill NKA activity is conspicuously absent from this literature, and long-term performance (e.g., growth) is not clearly linked to higher gill NKA activity (Zydlewski and Zydlewski 2012).

The natural timing of estuary arrival, movement rates through estuaries, and ultimately smolt survival during estuary migration are likely affected by the presence of dams in freshwater along smolt migration routes. Estuarine mortality that occurs naturally from causes such as predation and physiological challenges (Blackwell et al. 1997; Handeland et al. 1997; Halfyard et al. 2013) can be exacerbated by anthropogenic influences, such as passage through dams in freshwater. These influences might occur through migratory delay (Keefer et al. 2012), increased predation (Poe et al. 1991; Blackwell and Juanes 1998), physical injuries (Stier and Kynard 1986; Mathur et al. 2000) that can result in physiological impairment (Zydlewski et al. 2010), and reduced survival during estuary passage. However, the presence and magnitude of dam-related estuary mortality (i.e., delayed or indirect effects of dams) during estuary passage by Atlantic Salmon remains uncertain (Stich et al. 2014). Information about dam-related estuary mortality could have important implications for recovery activities involving Atlantic Salmon stocks, including proposals or actions related to dam removals, such as those occurring in the Kennebec and Penobscot rivers in Maine (Day 2006).

The goal of this study was to quantify movement behavior and survival of Atlantic Salmon smolts in the Penobscot River estuary and their potential drivers in the 2005–2013 period. We classified these drivers into three main categories: (1) individual fish characteristics (fork length, mass, condition factor, and rearing history), (2) migratory history (number of dams passed, release distance from ocean, migratory route), and (3) environmental variability (cumulative temperature experienced, discharge, and photoperiod). Our first objective was to relate estuary arrival date and movement rate of smolts to individual fish characteristics, migratory history, and environmental variability from 2005 through 2013. The second objective of this study was to estimate survival of Atlantic Salmon smolts during migration through the estuary using Cormack–Jolly–Seber (CJS) mark–recapture models. These estimates were used to quantify the effects of fish behavior (estuary arrival date and movement rate), individual fish characteristics, migratory history of fish, and environmental variability on survival.

STUDY SITE

The Penobscot River (Figure 1) is the largest watershed within Maine, encompassing approximately 22,000 km^2.
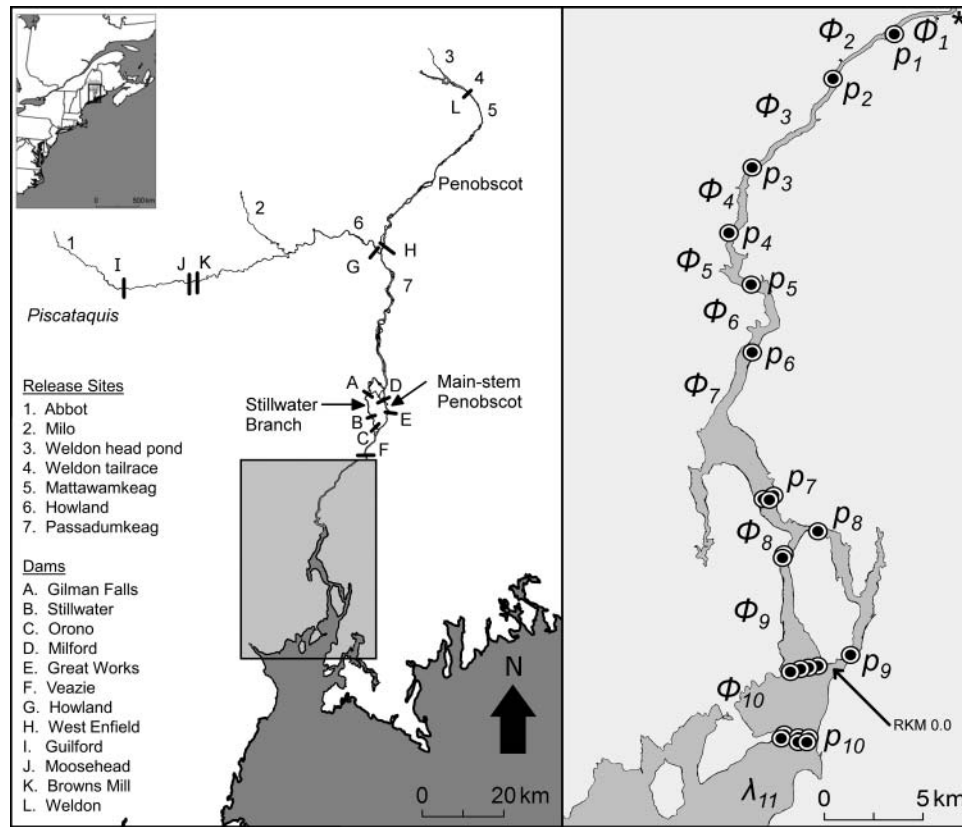
FIGURE 1. Map of the Penobscot River watershed in Maine, showing the locations of tributaries, dams, and release sites in the Penobscot River (left panel). The right panel shows the locations of acoustic receivers used to detect Atlantic Salmon smolts in the estuary. Parameters associated with Cormack–Jolly–Seber survival models are as follows: detection probability at each location following release (p_t), apparent survival within reaches between locations (ϕ_t), and λ_{11} (product of ϕ_{11} in the final reach and p_{11} at the final receiver location). There were 40 receivers in the bay that are not shown. The asterisk indicates the point of virtual release in the estuary for Cormack–Jolly–Seber models.

Atlantic Salmon have been stocked throughout the watershed at egg, fry, parr, and smolt life stages during the last several decades, and limited wild spawning occurs (USASAC 2014). The proportion of the Penobscot River smolt run made up of stocked fish is unknown, but sampling in the Penobscot River bay suggests that more than 90% of the run results from smolt stocking (Sheehan et al. 2011). The majority of the annual adult run (about 83%) is also predominantly composed of hatchery-stocked smolts (USASAC 2012). Hatchery stocking generally occurs less than 160 km above the mouth of the estuary in the Penobscot River and its tributaries (see Figure 1). The peak of the smolt emigration from wild rearing sites occurs between late April and early May most years (USASAC 2014).

The migratory pattern of individual smolts in the Penobscot River depends on rearing history, stocking locations, migratory routing through the lower river, and interannually varying hydropower operations throughout the catchment. All smolts stocked or reared in the upper reaches of the catchment enter the main stem of the Penobscot River at river kilometer (rkm) 100 (measured from the mouth of the estuary; rkm 0 is shown

in the right panel of Figure 1), either by passing Howland Dam (G in Figure 1) from the Piscataquis River or by passing West Enfield Dam (H in Figure 1) from the upper Penobscot River. Upon reaching the lower freshwater portion of the Penobscot River (rkm 60), smolts can use one of two migratory paths around a large island: the main-stem Penobscot River to the east (88% of smolts) or the Stillwater Branch (12% of smolts) to the west (Figure 1). On the eastern side of the island (main-stem Penobscot), smolts passed two dams until the removal of the Great Works Dam (E in Figure 1) in 2012. Concurrently, hydropower production was increased at two dams (Stillwater and Orono) in the Stillwater Branch to the west. The details of changes to operations of the Stillwater (B in Figure 1) and Orono (C in Figure 1) dams are described in Stich et al. (2014). Briefly, hydropower generation was approximately doubled at each of these two dams following the addition of a second powerhouse at each facility in spring 2014. On the western side of the island (Stillwater Branch), smolts passed three dams through which survival was high relative to the dams in the main stem during 2005–2013 prior to changes in hydroelectric generation. This resulted in a cumulative 10%

higher survival for smolts moving through the Stillwater Branch compared with the main-stem route in this area (Holbrook et al. 2011; Stich et al. 2014). Finally, smolts traveling either route would then pass the Veazie Dam, at the head of tide, until 2013, when that dam was removed. Dependent upon stocking location, migratory route through the lower Penobscot River, and year of stocking (because of Great Works Dam removal), smolts stocked in freshwater may have passed two to nine dams before entering the estuary. This study occurred prior to the removal of Veazie Dam (F in Figure 1).

The Penobscot River estuary spans 45 km from the mouth of the estuary to the head of tide, which coincides with the former location of Veazie Dam (F in Figure 1). The upper estuary (from p_1 to p_6 in Figure 1) is tidally influenced but uniformly freshwater (Imhoff and Harvey 1972), while the middle estuary (between p_6 and p_{10} in Figure 1) is characterized by mixing of fresh and salt water (Seiwell 1932; Stich et al., in review), and the lower estuary is physically and chemically stratified (Imhoff and Harvey 1972) with low-salinity (10‰) water occupying only the first 1–2 m of the water column (Haefner 1967).

METHODS

Acoustic receiver array.—An array of stationary VR2 and VR2-W acoustic receivers (Amirix Vemco, Halifax, Nova Scotia) was deployed in the river, estuary, and bay of the Penobscot River prior to the start of the Atlantic Salmon smolt run each year of the study (Figure 1). All receivers monitored continuously on a frequency of 69 kHz using omnidirectional hydrophones and were moored to the bottom of the estuary on cement anchors. Where deemed necessary (wide river sections or reaches containing obstructions such as islands), multiple receivers were deployed in a single location to achieve coverage over the entire width of the channel. Detections at all receivers within a discrete cross section were pooled as a single site for data analysis. A total of 11 acoustic receiver locations within the estuary (and several in the bay) were common to all arrays of the present study (2005–2006, 2009–2013). During all years, fish detections at all (about 40) receivers in the bay (downstream of Fort Point: p_{10} in Figure 1) were pooled as a single, final detection event for all analyses.

Fish measurements, acoustic tagging, and releases.—From 2005 through 2013, 1,824 Atlantic Salmon smolts were acoustically tagged (Table 1) and released throughout the Penobscot River watershed in freshwater (Figure 1). Of these, 941 fish were later relocated during estuary migration and used in this study, including 800 hatchery-reared smolts from the U.S. Fish and Wildlife Service Green Lake National Fish Hatchery and 141 wild-reared smolts. Wild smolts released in the Piscataquis River were captured in rotary screw traps by the Maine Department of Marine Resources, tagged, and released immediately downstream. Wild smolts released in the Penobscot River above rkm 100 were captured by Brookfield Renewable

Power at the Weldon Dam smolt bypass facility and transported using a 250-L tank with air (identical to the tank used to transport hatchery-reared smolts).

The acoustic tagging methods we used are described in detail by Holbrook et al. (2011) and Stich et al. (2014). Identical procedures were used in all years of the present study (2005–2013). Briefly, individual smolts were anaesthetized using a 100-mg/L solution of MS-222 (tricaine methanesulfonate) buffered to pH 7.0 (using 20-mmol $NaHCO_3$), and fork length (mm) and mass (g) were measured. For each smolt, a 1-cm incision was made offset from the ventral line and 1-cm posterior to the pectoral fin girdle. An acoustic tag was inserted intraperitoneal and the incision was closed with two simple, interrupted knots using 4-0 absorbable vicryl sutures (Ethicon, Somerville, New Jersey). Model V7-2 L (Amirix Vemco, Halifax, Nova Scotia) tags were used in 2005, as well as for wild-origin fish tagged in 2011. Expected battery life of V7-2 L tags was 80 d during 2005 and 69 d in 2011. In all other years, we used model V9-6 L acoustic transmitters (Amirix Vemco, Halifax, Nova Scotia) that had an expected battery life of 82 d (except during 2006 when battery life of V9-6 L transmitters was 80 d). Model V7 tags were 7 mm in diameter, 18.5 mm long, and weighed 1.6 g in air (0.75 g in water), while model V9 tags were 9 mm in diameter, were 20 mm long, and weighed 3.3 g in air (2.0 g in water).

Wild and hatchery-reared smolts were released at up to five locations during any single year. The numbers of fish and release sites varied among years (Table 1), and all fish were released on the day of tagging. To determine the potential for direct mortalities due to handling and surgery, samples of 29–120 smolts were dummy-tagged during several years (2005, 2012, and 2013) concurrent with this study and held in an artificial-stream tank for 1–3 weeks (G. B. Zydlewski, unpublished data). No mortality was observed in any of those fish. Previous studies observed elevated mortality immediately following release (up to 50% in wild smolts but generally less than 5% in hatchery-reared fish) associated with the handling, transport, and release of acoustically tagged smolts in the Penobscot River (Holbrook et al. 2011). All smolts used for analyses in the present study were released a minimum of 50 km above the head of tide (rkm 45), so we assumed that residual effects of tagging were minimal during estuary passage. We included all individuals that were ever detected in the estuary or beyond in the ocean, a total of 941 fish, in analyses of estuary arrival date, movement rate, and survival during the present study.

Covariates of estuary arrival date, movement rate, and survival.—We collected data about several hypothesized covariates of estuary arrival date, movement rate, survival, or detection probability of Atlantic Salmon smolts during estuary migration. These covariates were combined to create a priori hypotheses to test effects of potentially important factors on arrival date, movement rate, and survival. Broadly, we categorized these covariates as characteristics of individual fish,

TABLE 1. Release sites, river kilometer of release sites (rkm), rearing history (Origin), and number of fish used in the study (*n*; numbers in parentheses indicate the total number of fish originally released in each group) for Atlantic Salmon smolts acoustically tagged and released throughout the Penobscot River and its estuary in 2005–2013; twp. = township. Summary statistics were calculated with only fish that were used in the current study and include the mean (SD in parentheses) of fork length (FL; mm), gill Na^+, K^+-ATPase (gill NKA) activity (μmol ADP $\cdot$ mg protein$^{-1} \cdot$ h^{-1}), and mass (g).

Year	Release site	rkm	Origin	FL	Mass	Gill NKA activity	*n*
2005	Howland Dam	99	Hatchery	189 (11)	75 (15)	6.58 (1.95)	90 (150)
	Mattawamkeag twp.	144	Hatchery	185 (12)	69 (15)	6.07 (1.83)	3 (40)
	Milo twp.	142	Hatchery	191 (11)	77 (14)	8.15 (1.94)	44 (85)
	Weldon Dam tailrace	149	Wild	178 (18)	52 (16)	9.08 (1.85)	24 (60)
2006	Milo twp.	142	Hatchery	196 (11)	87 (18)	4.86 (1.24)	38 (72)
	Weldon Dam	149	Hatchery	199 (15)	87 (19)	4.78 (1.85)	53 (146)
	Weldon Dam tailrace	149	Wild	189 (9)	62 (10)	4.12 (1.10)	14 (73)
2009	Milo twp.	142	Hatchery	180 (8)	62 (9)	3.29 (1.38)	73 (100)
	Passadumkeag twp.	92	Hatchery	180 (9)	63 (9)	3.02 (0.82)	77 (100)
2010	Abbot twp.	187	Wild	169 (8)	45 (7)	4.68 (1.10)	19 (75)
	Weldon Dam head pond	162	Wild	180 (14)	55 (13)	4.81 (0.92)	15 (74)
	Milo twp.	142	Hatchery	189 (11)	72 (13)	4.53 (1.04)	63 (100)
	Passadumkeag twp.	92	Hatchery	186 (11)	69 (13)	4.63 (1.13)	77 (100)
2011	Abbot twp.	187	Wild	146 (8)	29 (5)	2.61 (1.17)	55 (75)
	Weldon Dam head pond	162	Wild	163 (19)	42 (16)	3.30 (1.41)	14 (60)
	Milo twp.	142	Hatchery	191 (13)	75 (18)	4.94 (1.47)	55 (100)
	Passadumkeag twp.	92	Hatchery	194 (13)	76 (17)	5.42 (1.49)	74 (100)
2012	Abbot twp.	187	Hatchery	199 (10)	84 (14)	3.35 (1.33)	54 (72)
	Weldon Dam head pond	162	Hatchery	200 (11)	85 (14)	3.48 (1.59)	46 (85)
2013	Abbot twp.	187	Hatchery	185 (11)	70 (13)	2.80 (2.13)	20 (75)
	Weldon Dam head pond	162	Hatchery	185 (9)	71 (11)	2.75 (2.04)	33 (82)
All				187 (16)	71 (19)	4.39 (1.92)	941 (1,824)

characteristics of the migratory history of a fish, and environmental covariates. All continuous covariates were standardized across years and rearing histories prior to each analysis (i.e., timing, movement, and survival analyses) to facilitate ease of interpretation among covariates. Covariate effects were considered statistically significant if the 95% confidence interval of the estimated coefficient for the covariate did not include 0.

Characteristics of individual fish.—Five covariates were used in our models to represent characteristics of individual fish: fork length (mm), Fulton condition factor (K), gill NKA activity, model of acoustic tag that was used (V7 or V9), and rearing history (wild or hatchery). To measure gill NKA activity, a nonlethal gill biopsy (4–6 filaments) was taken from the front, left gill arch of each fish prior to tagging. Individual biopsies were stored at –80°C in 100 μL SEI buffer (250 mM sucrose, 10 mM Na_2-EDTA, 50 mM imidazole) for later analysis of gill NKA activity (expressed as μmol ADP$\cdot$mg protein$^{-1} \cdot$h^{-1}) using the method of McCormick (1993). The concentration of NADH at 25°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 were analyzed in triplicate for gill NKA activity and protein concentration and averaged.

Migratory history of individuals.—We used five covariates to represent the migratory history of each fish: (1) release date, (2) location (in rkm) of release, (3) migratory routing through the lower Penobscot River, (4) number of dams passed during migration (to evaluate dam-related estuary mortality), and (5) median movement rate through the estuary (only in survival models). We used the release date and location of release to represent biological phenomena related to release sites because this allowed us to assess the effects of release locations and fish characteristics at the individual level rather than within artificially structured release groupings. This allowed us to test hypotheses about variation in estuary arrival date, movement rate, and survival over a continuum of release practices rather than within or among groups.

Based on differential survival through the freshwater migration routes in the lower river (Holbrook et al. 2011; Stich et al. 2014), we hypothesized that differential use of the Stillwater Branch or main stem might result in differences in estuary arrival date, movement rates, or dam-related estuary

mortality based on the number of dams in each route. Because of imperfect detection at acoustic receivers in the lower river, the use of the Stillwater Branch by smolts was included as a binary covariate in statistical analyses, and fish with an unknown migratory route were assigned the mean value of the covariate (Stillwater Branch = 1, main stem = 0). This assignment allowed us to use the fish for analysis without biasing estimated effects of migratory route. Statistically, this also results in reduced precision in the estimated regression coefficient (i.e., increases type II error) for this covariate.

Smolts released in the freshwater reaches of the Penobscot River passed two to nine dams from their stocking locations to the head of tide during the years of this study (2005–2013). To test whether or not smolts showed behavioral effects or experienced delayed mortality in the estuary due to the passage of dams (hereafter "dam-related estuary mortality"), we examined the relationship between the number of dams a fish passed and estuary arrival date, movement rate, and survival in the estuary. The number of dams passed by each smolt was conditional on the individual's stocking location and migratory route in the lower river (main stem or Stillwater Branch) because the number of dams differed between routes. The potential number of dams passed also was conditioned by year, as in the summer of 2012, after smolt migration was complete, the main-stem Great Works Dam was removed.

Environmental covariates.—We collected information about environmental covariates for estuary arrival date, movement rate, and survival that included temperature and discharge throughout the catchment, as well as photoperiod at the head of tide. These data were collected because of their previously demonstrated influences on the response variables in this study. In-river temperature data (R. Spencer, Maine Department of Marine Resources, unpublished data; and USGS gauge station 01036390) were used to calculate the accumulated thermal units (ATU) experienced by wild smolts in the watershed from January 1 to the date of tagging. Temperature data from outdoor rearing pools at the Green Lake National Fish Hatchery (A. Firmenich, U.S. Fish and Wildlife Service, unpublished data) were used to calculate ATU for hatchery-reared smolts from January 1 to the date of tagging. Photoperiod was calculated from the latitude at the head of tide in the estuary and the ordinal date using the package "geosphere" in R (R Development Core Team 2014). Discharge data were obtained for the U.S. Geological Survey gauge at the West Enfield Dam (H in Figure 1) for each day during all years from 2005 through 2013 and used to characterize discharge in the main stem of the Penobscot River during the period of smolt migration.

Models of estuary arrival date.—Estuary arrival date was assigned as the first detection in the estuary for each smolt detected below Veazie Dam (rkm 45). We estimated the effects of covariates on estuary arrival date using generalized linear models with a $\log_e$ (Poisson family) link function (Montgomery et al. 2006) in R. We used an information-

theoretic approach to model selection to test hypotheses about the relative influences of fish characteristics, migratory history, and environmental variables on estuary arrival date by comparing a priori combinations of covariates. We thought that it was important to account for release date regardless of what other covariates were included in the timing models; therefore, photoperiod was included in all models of estuary arrival date. Results were plotted with corresponding calendar dates to facilitate interpretation. We note that the entire smolt run occurred prior to the vernal equinox each year such that photoperiod only ever increased with progressively later calendar dates (i.e., no two dates had the same photoperiod). The measure of discharge used in models of estuary arrival date was the mean of discharge experienced from the date of tagging to the estuary arrival date.

We constructed models containing a single variable that we classified as a "fish characteristic" in any given model to reduce the potential for spurious effects, simplify the model set, and facilitate comparison between competing explanations for factors affecting estuary arrival date. We did not consider models that contained dams passed in addition to the rkm of release or use of Stillwater Branch because (1) there was a strong correlation between rkm of release and dams passed and (2) dams passed was conditional on whether fish migrated through the Stillwater Branch or the main stem in the lower river. We evaluated the relative support for candidate models using Akaike information criterion corrected for sample size (AIC$_c$; Burnham and Anderson 2002). Approximation of a variance inflation factor ($\hat{c}$) for the most parameterized model prior to analysis indicated reasonable model fit, so model selection was not adjusted.

Movement rate.—Individual movement rates through the estuary were calculated from consecutive seaward detections of Atlantic Salmon smolts for which detections at more than one receiver location in the estuary were recorded. Movement rate (R) of individual fish (i) through estuary reaches (j) was calculated as kilometers per hour (R_{ij}, km/h) based on the distance between consecutive relocations D_{ij} and the amount of time elapsed between the first detections at consecutive locations (T_{ij}) for each fish using the following equation:

$$R_{ij} = \left(\frac{D_{ij}}{T_{ij}}\right). \quad (1)$$

We used linear mixed-effects models (Zuur et al. 2009) in R (R Development Core Team 2014) to estimate the relative effects of (1) fish characteristics, (2) migratory history, (3) detection location in the estuary, (4) and estuary arrival date on the rate of individual fish movements through the estuary. We included an individual-based random effect on the intercept term in all models to account for repeated, unequal numbers of measurements of movement rate for each fish. Movement rate was constrained to be greater than 0 (i.e.,

predicted movement rate cannot be negative); therefore, we log$_e$ transformed movement rate prior to analysis.

We included estuary location (in rkm), movement timing (photoperiod), and freshwater discharge in all models of movement rate because we had strong a priori expectations that movement rate changed in the estuary during the smolt window and with discharge. The measure of discharge used in movement models was the mean daily discharge on the day during which a movement was initiated. Similarly, photoperiod was calculated on the dates of individual detections. A second-order term was included for photoperiod (photoperiod^2) because we expected that movement rate would peak during the middle of the smolt run. Because we also hypothesized that movement rate would be faster at the head of tide and at the mouth of the estuary than in the primary mixing zone in the middle estuary, we compared models with only a linear term for rkm to models containing a second-order (quadratic) term for receiver rkm. Allowing for these modifications, we followed the same process for a priori model construction and hypothesis testing based on model selection as was used in the analysis of estuary arrival date. Approximation of $\hat{c}$ for the most parameterized model indicated reasonable model fit, so model selection was not adjusted.

Survival analysis.—The detections at receiver locations were used to develop individual recapture histories (located = 1, not located = 0) for each fish during estuary passage (Figure 1). We used encounter histories to estimate apparent survival (hereafter "survival"; ϕ) and detection probability (p) of smolts in the estuary using a spatially explicit form of the Cormack–Jolly–Seber (CJS) mark–recapture modeling framework (see Figure 1). While the term survival is used throughout this study for simplicity, estimates reflect only the apparent survival and not the true survival of smolts as information about whether fish were alive or dead was not available. We conducted the survival analysis using maximum-likelihood estimation in MARK (version 7.1; White and Burnham 1999) via the RMark package (Laake 2013) in program R (version 3.1.0, R Development Core Team 2014). All parameters were estimated using the logit link function.

We used 12 encounter occasions (i.e., receiver locations) in the CJS models, which included for a "virtual release," or starting location, at the head of tide (Figure 1). We accounted for differences in reach lengths (i.e., distances between receiver locations) by including reach lengths in the model framework so that survival within reaches could be compared directly as per-kilometer rates and appropriate standard errors could be derived within MARK. As a result, the estuary array provided for estimates of survival through 11 reaches of the Penobscot River estuary, each standardized as a per-kilometer rate within those reaches. However, estimates of survival and detection probability are confounded in the final interval of CJS models and so the joint probability of recapture and survival (λ) was estimated in the 11th and final interval (Penobscot Bay), whereas survival was estimated separately in the first 10 reaches.

We investigated the relationships between survival and (1) fish characteristics, (2) migratory history, and (3) environmental effects by comparing models that represented specific a priori hypotheses. We included five covariates to represent the characteristics of individual fish in CJS models: (1) fork length, (2) K, (3) gill NKA activity, (4) rearing history, and (5) tag type. Based on prior work (Zydlewski, unpublished data) and the difference in signal power between tag models, we expected the smaller (V7; 136 dB) tags to have a lower probability of being detected than the larger (V9; 151 dB) tags. Therefore, tag type was included as a covariate of detection probability (V7 = 0, V9 = 1).

We included five covariates to represent migratory history: (1) photoperiod (to represent timing), (2) median movement rate for each fish during estuary migration, (3) migratory route (Stillwater Branch or main stem) in the lower Penobscot River, (4) release rkm, and (5) number of dams passed. We included year, estuary reach, photoperiod, and discharge in the main stem of the river to explain spatial and temporal variation in survival. Year was included as a categorical variable to account for otherwise unexplained annual variation in survival. Each of the environmental covariates was measured for the first detection of each fish at each location. If fish were not detected, the mean value of the covariate was assigned to avoid bias in estimates and retain sample sizes for remaining covariates. The effects of explanatory variables on survival were considered in an additive framework such that fixed effects were interpreted across years rather than within years to avoid the confounding of year with environmental conditions. Year, estuary interval, and discharge were used to model heterogeneity detection probability. The discharge measurement used in the detection model was the mean discharge experienced by each smolt during migration through the estuary such that all fish had some observation for discharge that was not contingent upon detection.

Goodness of fit and model selection for survival analysis.— We used an information-theoretic approach to model selection in order to compare competing hypotheses about the factors affecting survival and detection probability of acoustically tagged Atlantic Salmon smolts in the Penobscot River estuary. We assessed goodness of fit for our most general model using the median $\hat{c}$ approximation in MARK (White and Burnham 1999) to estimate overdispersion. The result of this test indicated that the most general model was slightly overdispersed ($\hat{c} \approx 1.265$); therefore, we adjusted the model selection and the variances of estimated regression coefficients for overdispersion and we used quasi-Akaike information criterion corrected for small sample size (QAIC$_c$) for model selection (Burnham and Anderson 2002).

Our model-selection approach had two hypothesis-driven phases. First, we identified the best spatial and temporal

model structure for survival (year, reach, and photoperiod) while allowing detection probability to vary according to year, reach, acoustic tag model, and discharge. We compared a priori combinations of survival and detection parameterizations to determine our model for subsequent hypothesis testing. Based on our experience, we did not consider null (i.e., static or constant) models of survival or detection probability. For detection probability we only considered combinations of explanatory variables that included group (year) and reach effects. Due to limitations of sample sizes, we considered only additive group-by-reach effects (i.e., different intercepts for years in each reach but the same slopes) for both survival and detection probability. Our justification for this decision was that if survival or detection probability varied among sites, then it was likely to have either uniformly improved or decreased but would probably vary in magnitude.

After we identified the best spatial and temporal model structure for survival and accounted for factors influencing detection probability, we constructed a second a priori model set, building on this base model, to test hypotheses based on fish characteristics and migratory history. We did not include more than a single covariate representing migratory history of fish in a given model because of known dependencies between some variables (migratory route and dams passed) and colinearity between others (e.g., release rkm and number of dams passed).

RESULTS

Estuary Arrival Date

The best model used to describe estuary arrival date explained 50% of the variation observed during the past decade (McFadden's pseudo $R^2 = 0.50$; Faraway 2005). The mean arrival date in the Penobscot River estuary for Atlantic Salmon smolts released in freshwater was May 9 (SD, 8 d). Smolts released earlier in the year (modeled as photoperiod at release) arrived in the estuary at an earlier date than those fish released later in the season (Table 2). Over the range of release dates used in the past decade (range = April 12–May 29)

arrival date was 24 d earlier on average for the earliest release dates than for the latest release dates.

Smolts released further upstream of the estuary arrived in the estuary at a later date than those fish that were released further downstream. The difference in arrival dates between the furthest upstream and furthest downstream release sites, located approximately 90 km apart (range = rkm 92–rkm 187), was 3 d (Figure 2a), and the effect was not statistically significant at $\alpha = 0.05$ (Table 3) unless discharge was not included in the same model. Observed discharge during the period between release dates and estuary arrival dates in 2005–2013 ranged from a minimum of 175 m³/s to 2,500 m³/s. Fish experiencing the greatest discharge between release date and estuary arrival date arrived in the estuary 10 d later than fish experiencing the least discharge (Figure 2b; Table 3).

Atlantic Salmon smolts that were wild reared (i.e., progeny of wild spawning, egg planting, or fry stocking) arrived in the estuary later than smolts that were reared in the hatchery (Table 3). Mean estuary arrival date for wild-reared fish was May 20 (SD = 7 d), whereas mean estuary arrival date for hatchery-reared smolts was May 7 (6 d), a difference of 2 weeks. The majority of this difference results directly from the later tagging dates of wild-reared smolts (mean = May 13) compared with the release dates of hatchery-reared smolts (mean = April 24).

Fish experiencing a warmer thermal history (higher ATU) prior to tagging and release arrived in the estuary earlier than fish experiencing a lower ATU prior to release when the effect of release date was accounted for (Table 2). This relationship indicated that fish experiencing the greatest ATU (550) arrived 8 d earlier than those fish experiencing the lowest ATU (220) prior to release (Figure 2c). However, ATU covaried with discharge, and discharge was a better predictor of estuary arrival date than ATU because ATU was not included in the best model and was not statistically significant when discharge was included in the same model.

Estuary arrival date was earlier with increasing gill NKA activity, until gill NKA activity reached 6 μmol

TABLE 2. Model-selection statistics for generalized linear models that were used to quantify the relationships between the date of arrival by acoustically tagged Atlantic Salmon smolts in the Penobscot River estuary in 2005–2013 and fish characteristics (rearing history [rearing], gill NKA activity), migratory history (photoperiod at release date [PP], release rkm [release], migratory route through the lower river [SW]), and environmental conditions (accumulated thermal units [ATU], discharge experienced from release to arrival date [discharge]). The number of parameters estimated in each model is k, AIC is the Akaike information criteria for each model, ΔAIC_c is the difference between the AIC_c of each model and the best model in the candidate set, and w is the relative probability that each model is the best in the candidate set. Only models with substantial support ($\Delta AIC_c < 2.0$) are shown.

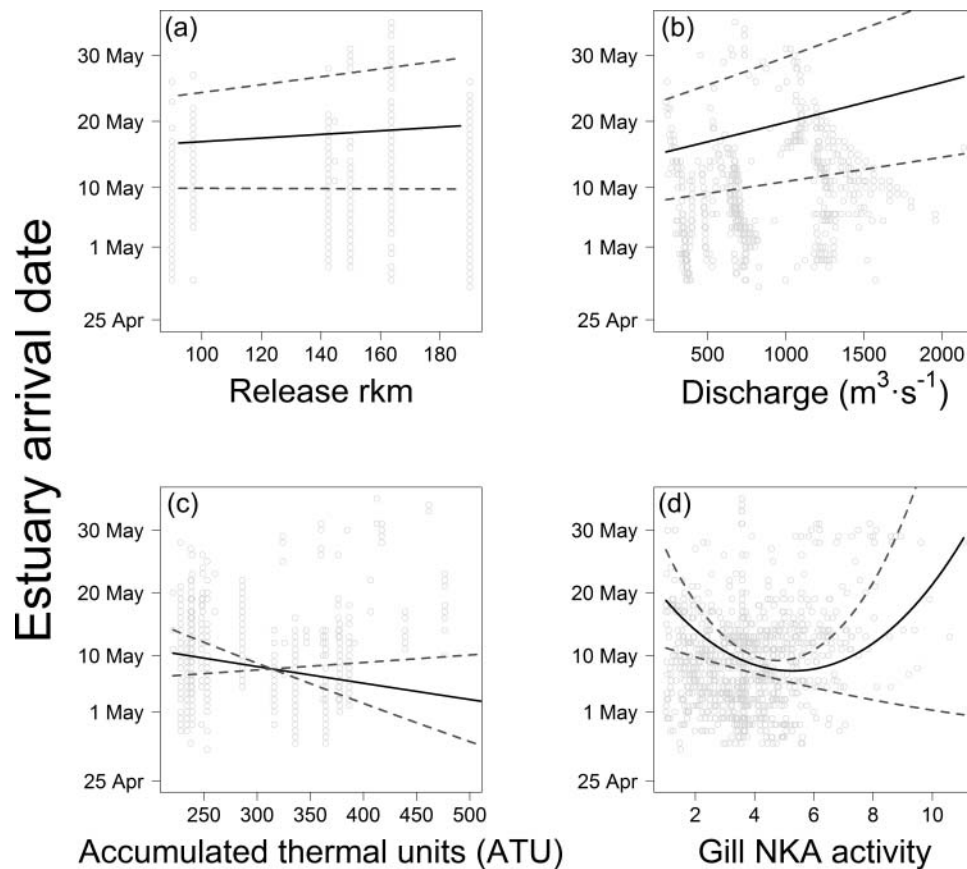| Model	k	AIC_c	ΔAIC_c	w
Discharge + PP + rearing + release	5	6,556.57	0.00	0.16
Discharge + PP + rearing + release + SW	6	6,556.98	0.42	0.13
Discharge + PP + rearing	4	6,558.03	1.47	0.08
ATU + gill NKA activity + PP + release + SW	7	6,558.16	1.59	0.07

FIGURE 2. Predictions from the generalized linear model relating arrival date of acoustically tagged Atlantic Salmon smolts in the Penobscot River estuary in 2005–2013 to (a) release rkm (upstream of estuary), (b) discharge experienced from tagging to estuary arrival date, (c) accumulated thermal units experienced prior to release, and (d) gill NKA activity. The black lines indicate means and the dashed gray lines indicate the 95% CIs.

TABLE 3. Standardized regression coefficients, standard error (SE), and 95% confidence limits (CLs) for the generalized linear model used to model estuary arrival date (as a function of photoperiod at release date [PP], release rkm, rearing history, and discharge). Also shown is the linear mixed-effects model used to model movement rates as a function of location (estuary rkm), discharge, release rkm, and photoperiod for date of movement (PP, PP^2). Covariate effects were significant at $\alpha = 0.05$ if the range of the 95% CLs did not overlap 0.

Model	Parameter	Estimate	SE	Lower 95% CL	Upper 95% CL
Arrival date	Intercept	4.861	0.004	4.854	4.868
	Discharge	0.017	0.003	0.011	0.022
	PP	0.022	0.005	0.013	0.031
	Rearing (wild)	0.040	0.015	0.012	0.069
	Release rkm	0.007	0.004	0.000	0.014
Movement rate	Intercept	0.306	0.019	0.270	0.343
	Discharge	0.034	0.018	0.000	0.069
	Estuary rkm	0.174	0.016	0.144	0.205
	PP	0.057	0.018	0.022	0.092
	PP^2	−0.012	0.011	−0.034	0.009
	Release rkm	0.081	0.016	0.049	0.113

ADP·mg protein^{-1}·h^{-1}, after which estuary arrival date began to increase with gill NKA activity (Figure 2d). As a result, Atlantic Salmon smolts that had very low or very high gill NKA activity arrived in the estuary later than smolts near the mean gill NKA activity. Similar to ATU, gill NKA activity covaried with discharge and was neither included in the best model nor significant when discharge was included in the same model.

Movement Rate

The mean movement rate of smolts through all reaches of the estuary and among all fish was 2.27 km/h (SD = 1.88). The only model of movement rate that received any support was that which included the effects of discharge, date of movement (photoperiod, including quadratic effect), distance released from the ocean, and location at which movement was measured in the estuary. We observed evidence of a quadratic relationship between date of movement and individual movement rate. There was an increased movement rate until the middle of the migration period (early May), after which the movement rate became more variable but appeared to asymptote or even decrease (Figure 3a; Table 3).

The movement rate of smolts decreased in the Penobscot River estuary from the head of tide to the mouth of the estuary (Figure 3b; Table 3) but a second-order term for estuary rkm did not. From the head of tide to the mouth of the estuary, a distance of 50 km, the movement rate of smolts decreased from a mean of 1.8 km/h to 1.1 km/h (Figure 3b).

Smolts released further upstream in the Penobscot River moved faster than tagged smolts released at downstream sites (Figure 3c; Table 3). However, the effect of release rkm on movement rate appeared to be minor in comparison to the effects of arrival date and estuary location: over the range of release rkms used in this study (rkm 92–rkm 187), maximum movement rate increased by less than 0.5 km/h. Movement rate through the estuary increased with increasing discharge (Figure 3d). As with release rkm, the effect of discharge was minimal, resulting in a change of less than 0.3 km/h over the range of discharge observed (217–1,957 m^3/s).

Survival

The survival and detection probability of smolts varied spatially, temporally within years, and among years. In our first phase of hypothesis testing, only the model that allowed
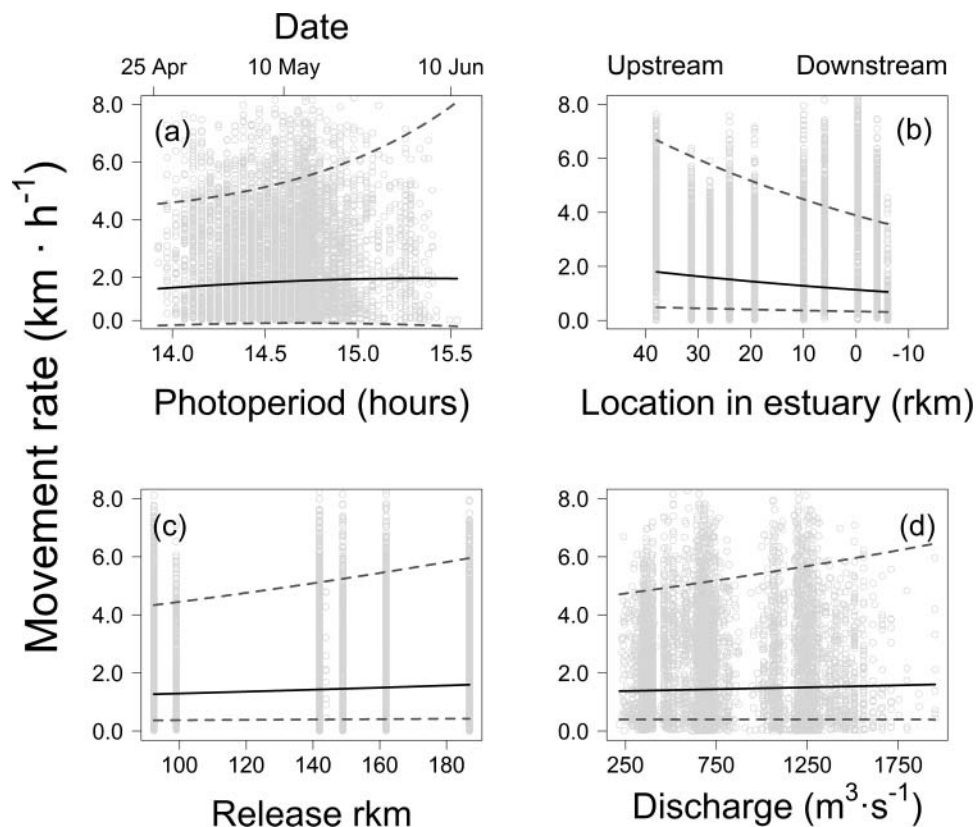

FIGURE 3. Mean (solid line) and 95% CI (dashed lines) predictions from parameters of the generalized linear mixed-effects model used to relate movement rate of acoustically tagged Atlantic Salmon smolts in the Penobscot River estuary in 2005–2013 to (a) photoperiod, (b) location in the estuary (rkm), (c) release distance upstream of the estuary (rkm), and (d) discharge experienced during estuary migration.
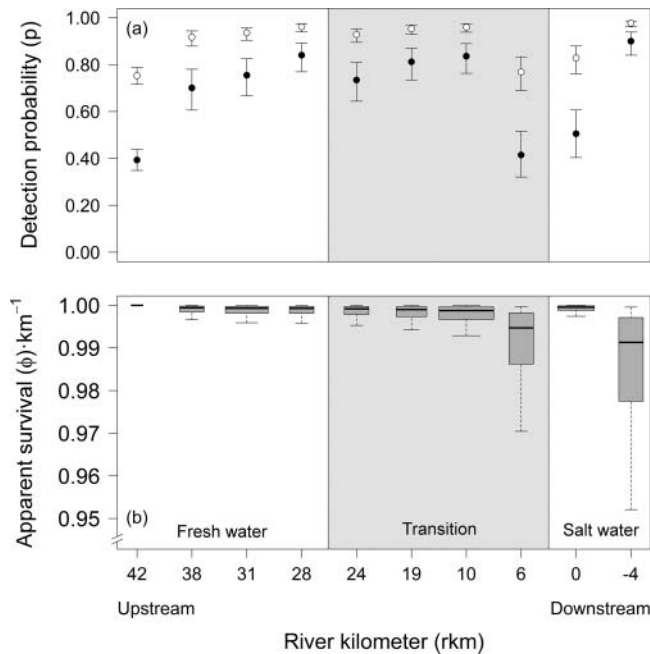
FIGURE 4. Estimates of **(a)** mean (whiskers indicate 95% CI) detection probability for V9 (white) and V7 (black) acoustic tag models in each reach across years 2005–2013 and **(b)** mean apparent survival per kilometer of acoustically tagged Atlantic Salmon smolts in the Penobscot River estuary in 2005–2013, estimated using Cormack–Jolly–Seber models. The solid line in each box in panel (b) indicates median annual survival, box-ends indicate the inner quartile range, and whiskers indicate the 95% CI. The box widths are proportional to the estuary reach lengths to which the estimates apply. From left to right, the three divisions in each panel represent freshwater, the zone of transition from low salinity to high salinity, and salt water within the Penobscot River estuary.

survival to vary among reaches, among years, and with photoperiod (including a quadratic effect) was supported by the data. Survival was highest near the head of tide (>0.99) and the mouth of the estuary and was lowest in the middle estuary (0.98), where tidal influences are strongest (Figure 4). Smolt survival was highest during the middle of the smolt run, peaking in early May, when survival was as much as 70% greater than in the early or late run. Fish arriving in the estuary very early or very late had poor survival (near 0) by comparison to those arriving during the middle of the run (Figure 5a).

As expected, the probability of detecting smolts was higher for fish tagged with large (model V9) acoustic transmitters than for those tagged with smaller (model V7) transmitters (Table 4; Figure 4). The probability of detection also was affected by the discharge experienced by individual smolts during estuary migration (Table 4). Over the range of flows observed (217–1,957 m^3/s), the mean probability of detection was reduced by 0.18 (95% CI = 0.06–0.33) during periods of greatest freshwater discharge compared with periods of lowest discharge. Based on these results, year, estuary reach, and photoperiod all were included in the final parameterization for survival. The final parameterization for the

detection model included year, estuary reach, tag model, and discharge experienced by individual fish during migration. We tested all other hypotheses about effects of fish characteristics and migratory history using the parameterization above as a "base model."

After accounting for these effects, the survival of smolts in the Penobscot River estuary was dependent on physiological development (measured as gill NKA activity), dams passed, and the rate at which fish moved through the estuary (Table 5). We found strong evidence for an optimal timing of estuary passage related to survival (Figure 5a; Table 4). Survival increased until mid-May, after which survival became variable but tended to decrease.

The number of dams passed by individual smolts had a strong, negative effect on fish survival in the estuary (Figure 5b; Table 4). The survival of smolts that passed the greatest number of dams (nine) was reduced by 40% compared with those fish that passed only two dams (the minimum). The model including dams passed outperformed the corresponding model with release rkm by nearly 2 $QAIC_c$, suggesting that the majority of the effect of release location on survival was explained by the number of dams passed during migration and not merely by the distance fish had migrated.

The physiological preparedness of smolts for saltwater entry (measured as gill NKA activity) at tagging was positively related to smolt survival during estuary passage (Figure 5c; Table 4). Atlantic Salmon smolts with the highest gill NKA activity had a 25% greater probability of surviving the estuary migration than those fish with the lowest enzyme activity. The median movement rate of smolts was included in the best model of survival, and survival of smolts decreased slightly with increasing movement rate over the observed range of movement rates; however, the effect of this covariate was not statistically significant (Table 4), and the corresponding model that excluded the effects of movement on survival had virtually identical support in the data.

DISCUSSION

By linking the arrival date, movement rate, physiological preparedness, and survival of smolts over nearly a decade, we were able to improve our understanding of the complex relationships and interactions between behavior and survival during estuary migration. Although a number of other studies have explored the effects of factors influencing estuary arrival date, movement rate, and survival of Atlantic Salmon smolts and postsmolts during early marine migration (see Thorstad et al. 2012b), few (if any) studies have had the opportunity to examine all of these processes together in a single population from distant upriver release sites all the way to the ocean. Furthermore, this study provides an unprecedented link between physiological preparedness (gill NKA activity) and performance in the wild. Similarly, this study is the first to clearly
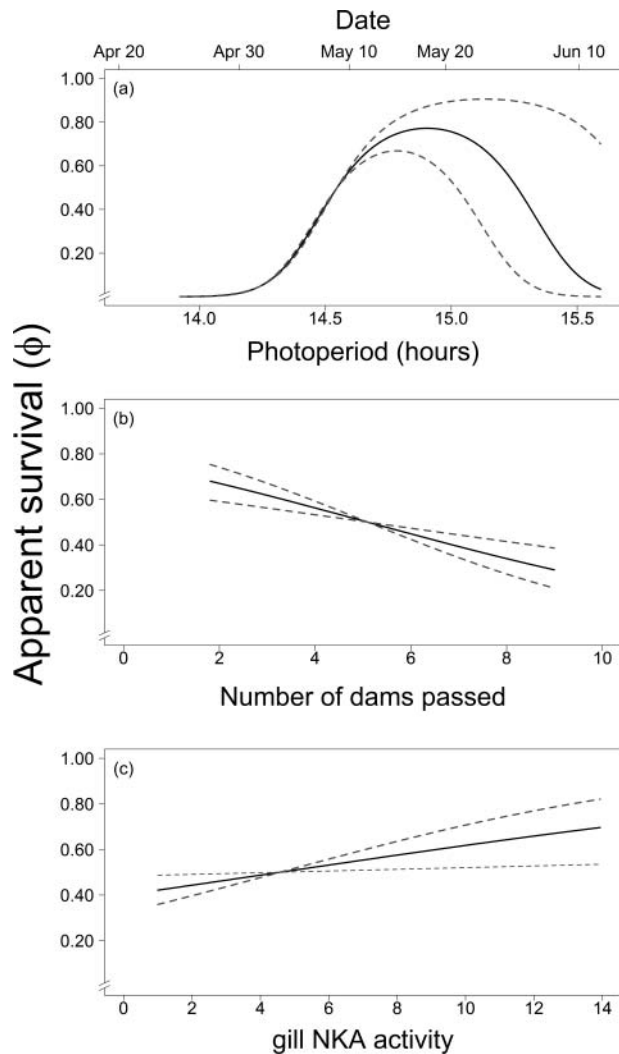
FIGURE 5. Means (solid line) and 95% CIs (dashed lines) of predictions from parameters of the Cormack–Jolly–Seber mark–recapture models used to estimate apparent survival (ϕ) of acoustically tagged Atlantic Salmon smolts through the Penobscot River estuary in 2005–2013. The panels show the effects of **(a)** individual timing, **(b)** number of dams passed by individuals, and **(c)** gill NKA activity of individuals on estimated survival.

relate the estuary survival of Atlantic Salmon directly to the delayed effects of dam passage.

Estuary Arrival Date

Smolt arrival in the Penobscot River estuary was overwhelmingly driven by environmental conditions. We found that estuary arrival date was significantly earlier for smolts subjected to a warmer thermal history (ATU) prior to tagging and for those released in higher freshwater discharges between tagging and arrival date. Migratory behavior in Atlantic Salmon smolts has been shown in multiple laboratory studies to be driven by environmental effects, especially photoperiod

(Zydlewski et al. 2014) and temperature (Zydlewski et al. 2005). Those studies have shown that smolts experiencing cooler temperatures during development initiate migration at a later date. Our field studies are consistent with that laboratory work. Sykes et al. (2009) reported that wild Chinook Salmon *Oncorhynchus tshawytscha* smolts initiated migration later when they experienced cooler temperatures during development and during high discharge. Similarly, global trends in the timing of Atlantic Salmon smolt migrations show that smolts experiencing higher discharge migrate later than those experiencing low discharge (Otero et al. 2014). Thus, our study is consistent with previous studies and the understanding that environmental factors drive the onset of migration in smolts.

The timing of estuary arrival was related to the physiological development of Atlantic Salmon smolts in the Penobscot River. Fish with the lowest or greatest gill NKA activity arrived in the estuary later than fish that had intermediate gill NKA activity at release. This is consistent with behavioral adherence to the physiological smolt window for migration (McCormick et al. 1998). However, the arrival date for smolts with the greatest gill NKA activity was highly variable. This variability at the peak of physiological smolting may be due to the heightened sensitivity to stress that is associated with tagging and handling (Carey and McCormick 1998).

Rates of Movement

The rate of movement in the estuary by smolts was influenced by the release location, date of individual movements, and location within the estuary. Smolts released further upstream in freshwater moved faster through the estuary than did smolts released further downstream. This could result from either increased migratory speed by fish released upstream (Jokikokko and Mäntyniemi 2003) or as a result of station-holding (i.e., staging) behavior by smolts released downstream in the watershed (e.g., Strand et al. 2010). Smolts that arrive in the estuary earliest may delay subsequent migration to synchronize ocean entry with optimal temperatures that favor their ability to avoid predators or access food (Otero et al. 2014). Differences in behavioral priming (Dingle and Drake 2007) or environmental conditions among different regions of the watershed (Whalen et al. 1999; Zydlewski et al. 2005) offer alternative explanations. For example, fish in headwater reaches of the river might experience an increased intensity of exposure to environmental factors that prime migratory behavior compared with fish released downstream in main-stem river reaches due to smaller water volumes that increase exposure to changes in temperature, photoperiod, and discharge.

The smolts decreased their migratory speed throughout the course of estuary emigration. It is likely that reductions in the movement rate during estuary emigration were primarily due to changes in current velocity and tidal influences in the lower

TABLE 4. Standardized regression coefficients (logit) and 95% confidence limits (CLs) for individual covariates included in the top-ranked Cormack–Jolly–Seber mark–recapture model used to estimate apparent survival (ϕ) and detection probability (p) of acoustically tagged Atlantic Salmon smolts during emigration through the Penobscot River estuary in 2005–2013. Tag type was classified as a binary covariate: smaller (V7) tags were assigned to 0 and larger (V9) acoustic tags were assigned to 1. The abbreviations PP and PP^2 indicate photoperiod for the date of movement. Covariate effects were significant at $\alpha = 0.05$ if the range of the 95% CLs did not overlap 0.

Parameter	Covariate	Estimate	SE	Lower 95% CL	Upper 95% CL
ϕ	PP	1.631	0.110	1.414	1.847
	PP^2	−0.545	0.086	−0.713	−0.378
	Gill NKA activity	0.192	0.081	0.032	0.351
	Number of dams passed	−0.376	0.092	−0.557	−0.195
	Movement rate	−0.108	0.064	−0.233	0.018
p	Tag type	0.404	0.033	0.340	0.469
	Discharge	−0.475	0.053	−0.579	−0.371

Penobscot River estuary (Fried et al. 1978; Moore et al. 1995). The reduction in movement rates through estuaries might also result from the reversal of migratory direction during the passage of tidal estuaries and bays (Kocik et al. 2009; Dempson et al. 2011; Halfyard et al. 2013). These behaviors appear to be related to tidal cycles in both estuarine (McCleave 1978; Martin et al. 2009) and coastal systems (Lacroix et al. 2005). This behavior previously has been hypothesized to relate to saltwater acclimation (Gudjonsson et al. 2005; Dempson et al. 2011; Halfyard et al. 2013). However, if it is related to saltwater acclimation, then the behavior may not provide an actual fitness benefit because survival is related to gill NKA activity at the time of release in freshwater, which implies that competence for saltwater entry is developed prior to estuary arrival. This finding is corroborated by results of studies in the northeastern Atlantic Ocean, where smolts acclimated in net-pens within an estuary showed no improvement in survival over fish released directly into the mouth of the river (Thorstad et al. 2012a). Other laboratory experiments have found no period of acclimation occurred for smolts upon reaching salt water (Moore et al. 1995). It is, however, possible that fish use tidal movements to minimize energetic costs, especially because this is the period of migration during which smolts are thought to transition from passive to active migration (Hedger

et al. 2008; Martin et al. 2009). Further investigation of diurnal and tidal factors that influence behavior and survival on localized spatial and temporal scales could provide an improved understanding of those mechanisms and might have implications for strategic stocking of hatchery-reared smolts.

Survival

The estuary arrival date, individual fish characteristics, number of dams passed, and location within the estuary all influenced Atlantic Salmon smolt survival during estuary passage. We found evidence for a strong optimizing effect of estuary arrival date on the survival of Atlantic Salmon smolts through the estuary, emphasizing the importance of timing in determining the success of migrating smolts (McCormick et al. 1998). Although this trend previously was suspected based on narrow windows of estuary passage in many Atlantic Salmon smolt runs (see Thorstad et al. 2012b), this study provides strong, empirically derived evidence linking survival during estuary migration to the variability in timing of individual estuary passage. The shape and spread of the timing–survival relationship in the Penobscot River suggests that normalizing selection may occur on the timing of estuary arrival through a direct link to survival. This relationship

TABLE 5. Model-selection statistics for Cormack–Jolly–Seber mark–recapture models used to estimate survival of acoustically tagged Atlantic Salmon smolts during emigration through the Penobscot River estuary in 2005–2013 and to test hypotheses about fish characteristics and migratory history that influenced survival. Table headings and model-selection statistics are defined as in Table 2, except here we used quasi-Akaike information criterion corrected for small sample size (QAIC$_c$) for model selection. The top 10 candidate models are shown. All candidate models in this set included the covariates representing spatial and temporal variation, ϕ(reach + year + PP + PP^2), in addition to the covariates shown in each model below. Covariates of apparent survival (ϕ) include the gill NKA activity, number of dams passed (dams), median movement rate in the estuary by individual smolts (R), and distance of release from the ocean (release).

Model	k	QAIC$_c$	ΔQAIC$_c$	w
ϕ(dams + gill NKA activity + R) p(reach + year + tag type + discharge)	41	7,194.11	0.00	0.24
ϕ(dams + gill NKA activity) p(reach + year + tag type + discharge)	40	7,194.28	0.17	0.22
ϕ(gill NKA activity + release) p(reach + year + tag type + discharge)	40	7,195.80	1.69	0.10
ϕ(gill NKA activity + R + release) p(reach + year + tag type + discharge)	41	7,195.92	1.81	0.10

likely occurs in response to environmental cues and releasing factors prior to the onset of migration and illustrates the importance of timing for successful estuary passage (McCormick et al. 1987; Hoar 1988). This supposition is supported by the strength of release date in freshwater as a predictor of timing for both wild and hatchery fish and the effect of gill NKA activity on survival in the estuary at a later date.

Estuary arrival date was a stronger predictor of smolt survival than the movement rate of individual smolts. The inclusion of movement rate in the best model of survival was somewhat perplexing, given the lack of significance for the covariate and the unexpected direction of the relationship to survival. An increased movement rate through estuaries is postulated to reduce exposure to predators and environmental stressors, such as pollution (McCormick et al. 1998), but our data suggest that perhaps this may not be the case. Based on the similarity between the best model for survival in the present study and the second-ranked survival model (ΔQAIC $<$ 0.20), it seems that the inclusion of movement rate in the survival models resulted in minimal improvement in model fit and that this variable was included because it covaried with some other important variable of interest, such as the number of dams passed, gill NKA activity, or location within the estuary. Based on the other results of this study, it seems likely that there could be synergistic effects of physiological preparedness and movement rate that result in changes to individual survival, but further investigation of the relationships is needed.

Atlantic Salmon smolt survival in the estuary increased with increasing gill NKA activity at the time of release. This result establishes a critical link between the physiological preparation of smolts in freshwater for osmoregulation in the ocean and survival, which has been long suspected by others (Boeuf 1993; Itokazu et al. 2014). A rich literature exists describing the physiological transformations of diadromous fishes (e.g., Zydlewski and Wilkie 2013), and the study of smolt physiology constitutes a large body of work within that field (McCormick et al. 1998; McCormick 2013). It is well established that gill NKA activity is a useful indicator of osmoregulatory ability (Zaugg and McLain 1972; McCormick et al. 1998, 2009) and migratory readiness in salmonids (Aarestrup et al. 2000). While researchers have demonstrated the performance benefits of smolts up-regulating gill NKA activity in laboratory studies relative to sublethal indicators (McCormick et al. 2009), the present study has provided a direct link between the physiological development of smolts and fitness in a study of actively migrating smolts. Although gill NKA activity is not a strong predictor of long-term growth scope or ocean performance (Zydlewski and Zydlewski 2012), our results underscore the importance of physiological preparedness for successful entrance into the marine environment.

We do not suspect that reduced gill NKA activity led to direct mortality due to inability to osmoregulate in the estuary because mortality is not generally observed in laboratory studies of Atlantic Salmon during the period of smolt migration.

However, proximate causes of mortality, such as predation (Järvi 1990; Handeland et al. 1997; Hawkes et al. 2013) or acidosis due to synergies between osmoregulatory stress and other forms of stress (Järvi 1989; Price and Schreck 2003; Berli et al. 2014), have the potential to dramatically increase when the osmoregulatory capacity of smolts is suboptimal (McCormick et al. 2009). Research targeting the relationships between smolt physiology and the sources of direct mortality (e.g., predation) in estuaries might help to further unravel the links between physiology and the proximate causes of mortality in the wild.

Our data strongly implicate a delayed, negative effect of dam passage on survival in the estuary, reducing estuary survival by 6–7% per dam passed (see Figure 5). We demonstrated that the cumulative number of dams passed (ranging from two to nine dams in this study) was an important predictor of smolt survival. This result is consistent with the work of Schaller et al. (2014), who found that the number of powerhouses passed by out-migrating Chinook Salmon affected marine survival. It is, however, notable that our results are the first to demonstrate this trend in Atlantic Salmon migrations. Furthermore, the *delayed* (indirect) dam-related mortality experienced in the 50-km Penobscot River estuary as a result of passing nine dams was comparable in magnitude with the cumulative, *acute* (direct) mortality incurred by smolts passing those same nine dams during the 150-km freshwater migration (Holbrook et al. 2011, this study). This suggests that studies of survival at dams, which are the basis for dam permitting, may drastically underestimate the effects of those dams.

Smolts experience injuries, such as descaling, when passing dams in the Penobscot River (Music et al. 2011). Such injuries can severely impair osmoregulatory ability, and impairment can persist for several days after injury (Zydlewski et al. 2010). All fish entering the Penobscot River estuary passed at least one dam prior to estuary arrival. Many fish passed several dams just 24–48 h prior to estuary arrival. Our results suggest that this experience reduced the survival of smolts during estuary passage. Reduction in osmoregulatory ability during estuary passage has previously been linked to a decreased ability to avoid predators (Handeland et al. 1997; Price and Schreck 2003), which could increase mortality in estuaries. Spatial patterns in survival through the Penobscot River estuary indicate that one possible mechanism of reduced survival in the estuary is the interaction between multiple factors (such as dam-related injury, gill NKA activity, and predators) because the greatest reduction in survival occurred upon reaching the saltwater reaches of the estuary, where osmoregulatory perturbance would have the greatest effect.

Conservation and Management Implications

Atlantic salmon smolts may be particularly susceptible to chronic and acute anthropogenic impacts. Climate change, based on our data, has the potential to squeeze Penobscot

River Atlantic Salmon against the ecological and physiological limits to adaptability. Earlier seasonal warming could result in mismatches between physiological and ecological smolt windows based on run timing (McCormick et al. 1997; Todd et al. 2012; Otero et al. 2014). Although changes in physiological smolt development and the timing of initiation of migratory behavior could shift run times initially (McCormick et al. 1997), these changes are also both entrained by circannual rhythms in photoperiod (Zydlewski et al. 2014), so there may be limits to how early physiological and behavioral smolting can occur (Otero et al. 2014). The resilience of many North American stocks to strong selection pressures imposed by these shifts is unknown (Mills et al. 2013; Friedland et al. 2014; Hayes and Kocik 2014).

Successful and expedient passage through estuaries may become increasingly important based on relations between temperature, physiology, and survival (Figure 6). Migratory delay through dams (Keefer et al. 2012) and physical injuries incurred during dam passage (Music et al. 2011) have the potential to further promote the loss of smolt characteristics (McCormick et al. 1999; Marschall et al. 2011) and impair osmoregulatory ability directly (Zydlewski et al. 2010). Recent modeling suggests the possibility that dams affect smolt migrations through migratory delay and potential mismatch in the timing of estuary arrival (McCormick et al. 2009; Marschall et al. 2011).

In the Penobscot River, indirect dam-related estuary mortality is nearly as great as the cumulative direct mortality incurred as a result of dam passage in freshwater (Holbrook et al. 2011; Stich et al. 2014). Indirect, dam-related estuary mortality resultant from passage of a single dam during migration also has the potential to be greater than the acute mortality incurred during passage of multiple hydropower projects in the lower Penobscot River (Holbrook et al. 2011; Stich et al. 2014). This clearly highlights the importance of considering dam-related estuary mortality within regulatory frameworks used to assess the effects of hydropower projects on fish passage.

The removal of Great Works and Veazie dams will likely increase smolt survival in the Penobscot River estuary by reducing dam-related mortality in the estuary (Figure 5), even though these dams resulted in little acute mortality during freshwater smolt migration (Holbrook et al. 2011; Stich et al. 2014). Indeed, the indirect, dam-related estuary mortality resulting from each of these structures (about 6%; Figure 5) was greater than the direct mortality incurred during passage (0–1%; Holbrook et al. 2011; Stich et al. 2014). Because both of these dams were less than a 12-h travel to the estuary, we hypothesize that their effects also may have been greater than dams located further upstream (see Zydlewski et al. 2010), but this remains to be tested. Prior to the removal of Veazie and Great Works dams, 88% of Atlantic Salmon smolts passed both dams (Stich et al. 2014) and 100% of smolts passed Veazie Dam during our study (2005–2013).

As such, we expect that estuary survival will increase as a result of the removal of Veazie Dam alone (6%; Figure 5). Additional increased survival is expected for 88% of the emigrating smolts due to Great Works Dam removal (6%; Figure 5). With the removal of these two dams, 20 km of lotic habitat was restored in the lower main stem of the Penobscot River below the now lowermost dam (Milford Dam). This resulted in the opportunity to stock hatchery-reared smolts in the main stem below any dams during the 2014 smolt run.

Smolts incur relatively high rates (about 10%/km) of acute mortality at main-stem dams compared with the background mortality in the Penobscot River (about 1%/km), resulting in a total loss of 40–60% of fish prior to arrival in the estuary (Holbrook et al. 2011; Stich et al. 2014). Fish passing the most dams (nine) during the present study experienced 40% increased dam-related estuary mortality compared with fish passing the fewest dams (two). Smolts stocked in 2014 passed no dams, eliminating dam-related mortality in the estuary (Figure 6). However, stocking nearer to the estuary may require closer attention to the physiological development of smolts (Figure 6) and environmental conditions (Figure 6). Similarly, there are potential ramifications for adult homing that result from stocking further downstream (Gorsky et al. 2009).

The number of smolts exiting the Penobscot River estuary is expected to increase (by 12%) based on reductions in dam-related estuary mortality following the removal of the two lowermost dams. Through improvements in estuary survival by stocking below dams and monitoring smolt gill NKA activity, we expect that the proportion of fish exiting the estuary each year could approximately double in a best-case scenario. Based on a lack of differential survival in marine habitats after leaving Penobscot Bay (Sheehan et al. 2011), and the fact that patterns in marine mortality are similar among North American stocks (Friedland et al. 2003; Mills et al. 2013), this gain would likely translate directly to increases in returning adults.
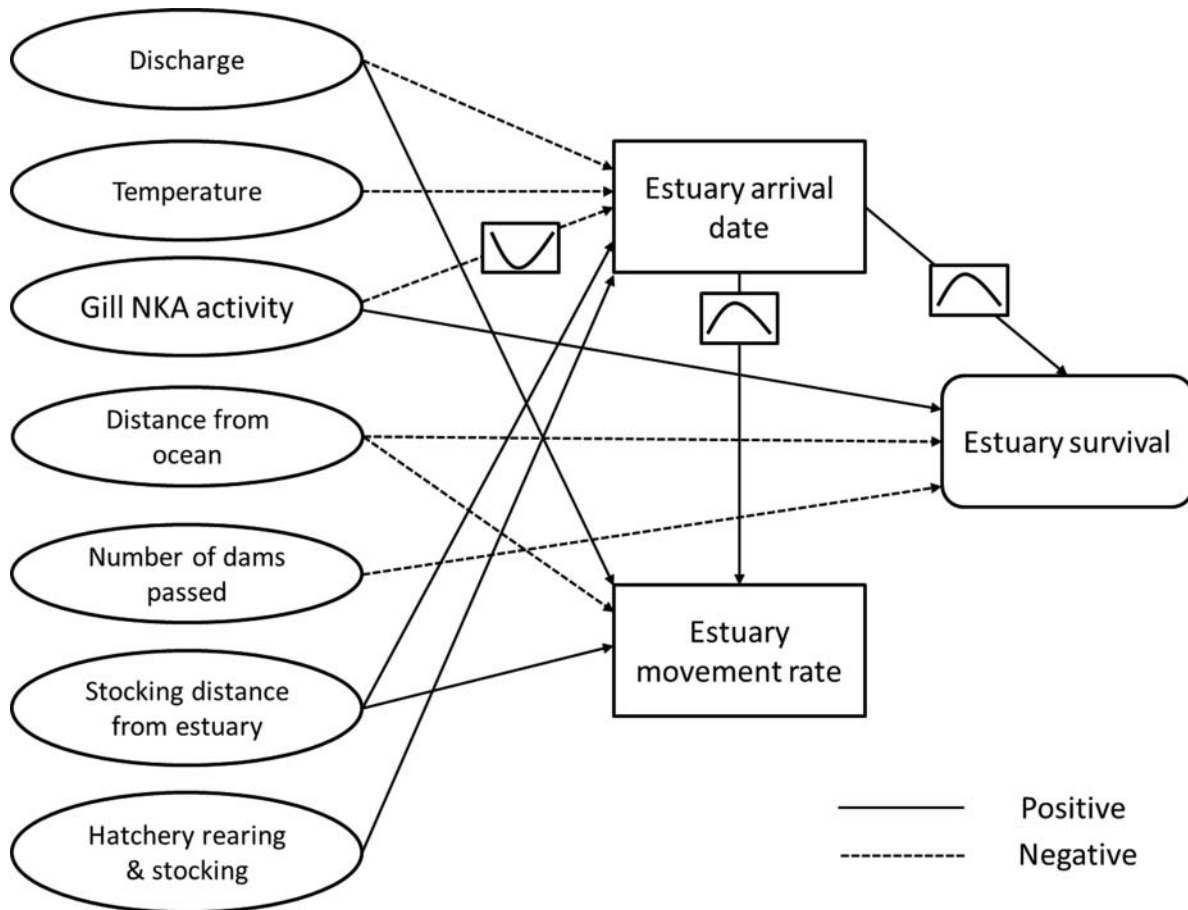
FIGURE 6. Diagram synthesizing the major findings about the factors affecting aspects of estuary migration of Atlantic Salmon smolts during the present study. The dotted lines indicate negative relationships, whereas solid lines indicate positive influences. The assumed causality of relationships is indicated by the direction of the arrows. Nonlinear (quadratic) relationships are indicated by the parabolas in boxes on top of the arrows that describe the relationships.

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