Transactions of the American Fisheries Society 140:1255–1268, 2011

ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2011.618356

ARTICLE

Survival of Migrating Atlantic Salmon Smolts through the Penobscot River, Maine: a Prerestoration Assessment

Christopher M. Holbrook*[1] and Michael T. Kinnison
School of Biology and Ecology, University of Maine, 5751 Murray Hall, Orono, Maine 04469, USA

Joseph Zydlewski
U.S. Geological Survey, Maine Cooperative Fish and Wildlife Research Unit, 5755 Nutting Hall, University of Maine, Orono, Maine 04469, USA

Abstract
Survival, distribution, and behavior of hatchery (*n* = 493) and naturally reared (*n* = 133) smolts of Atlantic salmon *Salmo salar* migrating through the Penobscot River and estuary in Maine were evaluated with acoustic telemetry in 2005 and 2006. Survival and use of a secondary migration path (the Stillwater Branch) were estimated with a multistate mark–recapture model. Higher rates of mortality per kilometer (range = 0.01–0.22) were observed near release sites and within reaches that contained three particular dams: Howland, West Enfield, and Milford dams. Estimated total survival of tagged hatchery smolts through entire individual reaches containing those dams ranged from 0.52 (SE = 0.18) to 0.94 (SE = 0.09), whereas survival through most of the reaches without dams exceeded 0.95. Of those smolts that survived to the Penobscot River–Stillwater Branch split at Marsh Island, most (≥74%) remained in the main stem around Marsh Island, where they experienced lower survival than fish that used the Stillwater Branch. Movement rates of hatchery-reared smolts were significantly lower through reaches containing dams than through reaches that lacked dams. Smolts arriving at dams during the day experienced longer delays than smolts arriving at night. Planned removal of two dams in this system is expected to enhance the passage of smolts through the main-stem corridor. However, the dams currently scheduled for removal (Great Works and Veazie dams) had less influence on smolt survival than some of the dams that will remain. This case study shows that by examining prerestoration migration dynamics throughout entire river systems rather than just in the vicinity of particular dams, tracking studies can help prioritize restoration efforts or predict the costs and benefits of future hydrosystem changes.

Juveniles of anadromous fishes can face substantial natural and anthropogenic challenges while en route to marine environments. During migration, immediate or delayed mortality may result from predation or direct injury imposed by turbines or other dam-related structures (Ruggles 1980; NMFS 2000). Migratory delays caused by physical or behavioral barriers may further increase predation risk (Nettles and Gloss 1987; Blackwell and Krohn 1997) or may cause poor synchrony of physiological tolerance to salinity (McCormick et al. 1999), possibly increasing estuarine mortality (Budy et al. 2002; Ferguson et al. 2006). Identification and mitigation of such impediments to successful migration are thus important components of programs that seek to maintain or restore anadromous salmonid populations.

Populations of Atlantic salmon *Salmo salar* throughout New England have experienced precipitous declines. Populations in eight Maine rivers were listed as endangered under the U.S. Endangered Species Act in 2000 (NMFS and USFWS 2000). The Endangered Species Act listing was expanded in 2009 to include populations in the Androscoggin, Kennebec, and Penobscot rivers (NMFS and USFWS 2009). Although the causes of decline are numerous, the National Research Council

*Corresponding author: cholbrook@usgs.gov
[1]Present address: U.S. Geological Survey, Great Lakes Science Center, 11188 Ray Road, Millersburg, Michigan 49759, USA.
Received August 15, 2010; accepted March 7, 2011.

(2004) identified dams as one of the potentially most acute impediments to Atlantic salmon restoration in Maine.

The Penobscot River (Figure 1) hosts the largest remnant population of adult Atlantic salmon in the United States (USASAC 2004). Restoration efforts include the release of hatchery-reared fry, parr, and smolts throughout the Penobscot River drainage (Moring et al. 1995). Although most of the adults returning in recent years are hatchery-origin fish that were stocked as smolts (USASAC 2004), the smolt-to-adult return rate has steadily declined since 1970 (Moring et al. 1995; USASAC 2005), indicating increased mortality in the river or at sea.

Earlier studies have suggested that survival of migrating smolts through the main-stem Penobscot River is low (Spicer et al. 1995) and that dams may be responsible for some of these losses (USASAC 2004). An estimated 76% of spawning and rearing habitats for Atlantic salmon in this system are located upstream from at least four hydroelectric dams (Fay et al. 2006). Losses at these dams effectively reduce the realized productivity of upstream rearing habitats and the efficacy of hatchery supplementation. However, only 2 of the 24 hydroelectric dams in the watershed (i.e., West Enfield and Weldon dams) are equipped with downstream passage facilities designed specifically for smolts (see USASAC 2005). Downstream passage at all other dams occurs via spill (i.e., in water passing over the dam) or through turbines or sluiceways, with unknown effectiveness (USASAC 2005).

Information on Atlantic salmon smolt survival through the main stem of the Penobscot River is limited to studies conducted by Shepard (1991a) and Spicer et al. (1995). These two studies presented a wide range of survival estimates (Fay et al. 2006) because of small sample sizes and technological limitations (i.e., few monitoring sites, high tag failure rates, and low or unknown detection probabilities). Thus, the extent of smolt loss and delay at most dams, particularly those in the lower river, has been poorly characterized.

The need for smolt survival data was recently heightened by the Penobscot River Restoration Project, wherein the Penobscot River Restoration Trust acquired three hydroelectric dams in the lower river drainage: two dams for eventual removal (Veazie and Great Works dams; Figure 1) and one dam for decommissioning (Howland Dam). Although these measures are anticipated to ameliorate some of the effects of the hydroelectric dams on Atlantic salmon, plans call for the loss of these facilities to be offset by changes in hydropower generation elsewhere in the system. Additional turbines have already been installed at three dams (Milford, Stillwater, and Orono dams), and reservoir levels have increased at two others (West Enfield and Stillwater dams). Flows may also be altered to use increased hydroelectric generation capacity in an alternate channel of the Penobscot River: the Stillwater Branch. These developments complicate predictions for the passage routes used and the risks faced by migrating Atlantic salmon in various sections of the river.

In the context of the smolt population, the effect of mortality at any single dam on population-level survival depends on the fraction of smolts that are exposed to the dam. Thus, a complete understanding of both survival and distribution among routes is necessary to determine the effects of dam-related mortality on the population. Quantification of migration dynamics (survival and distribution) at the population level (Perry et al. 2010) is necessary to both predict and evaluate the costs and benefits of future hydrosystem changes, including fish passage improvements.

In this study, we used acoustic telemetry to obtain movement histories for hatchery and wild Atlantic salmon smolts through the Penobscot River drainage. Multistate mark–recapture models (Brownie et al. 1993; Skalski et al. 2001) were then used to quantify use of the Stillwater Branch and losses (assumed mortality) for both hatchery and wild smolts through the Penobscot River and estuary (Figure 1). These results characterize and quantify preremoval conditions and may be used to evaluate passage improvements or costs associated with the Penobscot River Restoration Project.

METHODS

Tagging and release of hatchery and wild smolts.—Hatchery-reared Atlantic salmon smolts were obtained from the Green Lake National Fish Hatchery (GLNFH; U.S. Fish and Wildlife Service) and were transported to release sites in a 760-L tank supplied with aerated water (Figure 1). At each release site, each smolt was anesthetized with buffered tricaine methanesulfonate (MS-222, 100 mg/L; buffered to pH 7.0 with $NaHCO_3$), its length and weight were measured, and a nonlethal gill biopsy was collected for measurement of gill Na^+, K^+-ATPase (enzyme code 3.6.3.9; IUBMB 1992) activity (McCormick 1993).

An acoustic transmitter (Model V7-2L in 2005; Model V9-6L in 2006; Vemco, Halifax, Nova Scotia) was surgically implanted into each smolt through a ventral incision, which was subsequently sutured with 5-0 coated Vicryl absorbable sutures (Ethicon, Somerville, New Jersey). Smolts were held in an aerated holding tank for a minimum of 30 min postsurgery. The V7 transmitters were 7 mm in diameter, were 18.5 mm long, weighed 1.6 g in air (0.75 g in water), and had an estimated tag life of 80 d. The V9 transmitters were 9 mm in diameter, were 20 mm in length, weighed 3.3 g in air (2.0 g in water), and had an estimated tag life of 70 d. In 2005, the mass of V7 tags equaled 0.7–4.0% of body mass for hatchery fish and 1.5–5.6% of body mass for wild fish. In 2006, the mass of V9 tags was equivalent to 2.4–6.7% of body mass for hatchery fish and 3.3–7.3% of body mass for wild fish. Each transmitter emitted a unique pattern of acoustic pulses on a random interval ranging from 20 to 60 s.

Groups of 40–76 hatchery-reared smolts (Table 1) were released in April 2005 to coincide (within 1 d) with scheduled GLNFH releases of 15,000–40,000 smolts at three locations (Figure 1): the Pleasant River near the town of Milo (site R_3; in the Piscataquis River drainage), the Penobscot River near the town of Howland (site R_4), and the Mattawamkeag River

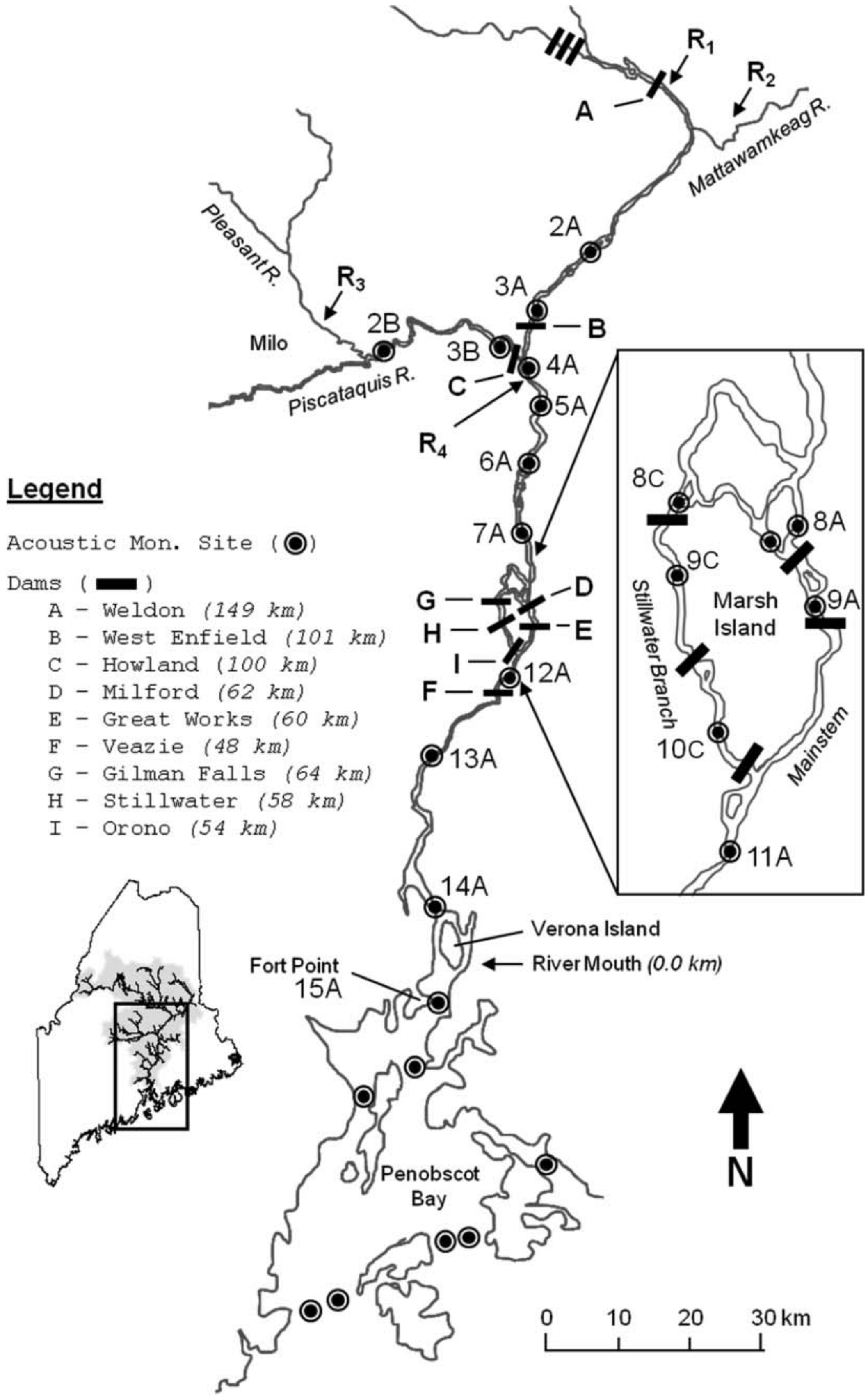

FIGURE 1. Map of the Penobscot River, Maine, indicating locations of dams (bold letters A–I), acoustic monitoring sites (circles; also designated by a number preceding A, B, or C, which represents migration route: A = main-stem Mattawamkeag and Penobscot rivers; B = Pleasant and Piscataquis rivers; C = Stillwater Branch), and release sites (R_1 = Penobscot River below Weldon Dam; R_2 = Mattawamkeag River near Mattawamkeag; R_3 = Pleasant River near Milo; R_4 = Penobscot River near Howland).

TABLE 1. Release date, origin (H = hatchery; W = wild), release site (R_1 = Penobscot River below Weldon Dam; R_2 = Mattawamkeag River near Mattawamkeag; R_3 = Pleasant River near Milo; R_4 = Penobscot River near Howland), number (N) of fish, mean fork length (FL, mm; with range in parentheses), mean weight (W, g; with range in parentheses), and median gill Na^+,K^+-ATPase activity (ATPase; μmol ADP·mg $protein^{-1}·h^{-1}$; with interquartile range in parentheses) for groups of acoustically tagged Atlantic salmon smolts that were released in 2005 and 2006.

Date	Origin	Release site	N	FL	W	ATPase
Apr 14, 2005	H	R_2	40	185 (154–220)	68.7 (41.2–113.7)	6.15 (2.30)
Apr 19, 2005	H	R_4	74	185 (156–212)	69.9 (40.5–112.0)	5.45 (2.54)
Apr 21, 2005	H	R_3	40	190 (159–217)	74.5 (43.6–114.7)	7.25 (2.12)
Apr 27, 2005	H	R_4	76	192 (175–214)	80.4 (57.8–117.6)	7.44 (2.18)
Apr 27, 2005	H	R_3	45	193 (173–214)	79.9 (58.0–114.1)	8.54 (2.00)
May 26, 2005	W	R_1	60	178 (148–227)	52.3 (28.5–107.9)	9.07 (2.72)
Apr 12, 2006	H	R_1	73	190 (166–216)	76.7 (49.0–115.8)	3.68 (2.26)
Apr 24, 2006	H	R_3	72	196 (169–225)	86.6 (53.3–136.4)	4.96 (1.66)
May 8, 2006	H	R_1	73	209 (184–233)	97.3 (64.5–137.2)	5.66 (2.08)
May 8, 2006	W	R_1	73	189 (170–215)	61.9 (45.2–99.1)	4.08 (1.22)

near the town of Mattawamkeag (site R_2). In April 2006, tagged hatchery smolts were released at Milo and at Weldon (in the Penobscot River below Weldon Dam; site R_1) to coincide with GLNFH releases; tagged hatchery smolts were also released at Weldon in May 2006 to coincide with the release of tagged wild smolts.

In both years, wild smolts were collected in the smolt bypass trap at Weldon Dam in May, received surgically implanted acoustic tags, and were released at Weldon (Table 1). We use the term "wild" to refer to any individual that was not stocked as a smolt. The wild smolts used in this study may have been either wild-hatched (from natural, in-river spawning) or hatched in captivity and released as fry. Conversely, the hatchery smolts used in this study were hatched at GLNFH and raised in captivity for 1 year to the smolt stage before release.

Evaluation of tag retention and direct tagging mortality.—By use of the methods described above, dummy tags were implanted in 29 hatchery smolts from GLNFH on May 9, 2005, and the fish were held in a circular tank (1.0-m diameter) for 38 d. Dummy tags were 19–21 mm long, were 7 mm in diameter, and weighed 1.5–1.8 g in air; each dummy tag included an embedded passive integrated transponder tag for individual fish identification. Fork length of dummy-tagged smolts ranged from 165 to 219 mm, and mass ranged from 44.3 to 109.8 g. Tag mass was equivalent to 1.8–3.4% of fish body mass. Fish were fed ad libitum once daily, and tank water temperature ranged from 11°C to 14°C during the trial. Fish were sacrificed on June 16, 2005, and were inspected for tag retention.

The acoustic array.—An array of up to 117 stationary acoustic receivers (Vemco Model VR2) was deployed and maintained in cooperation with the National Marine Fisheries Service (National Oceanic and Atmospheric Administration [NOAA] Fisheries) during April–November 2005 and 2006 in the Penobscot River, estuary, and bay (Figure 1). Receivers contained omnidirectional hydrophones, monitored continuously at 69 kHz, and were deployed to cover the entire width of the system at up to 38 sites/year. In some instances (e.g., at wide river sections or islands), several acoustic receivers were necessary for complete coverage; detections on these receivers were pooled and treated as a single site. Additionally, all receivers in Penobscot Bay (beyond Fort Point) were pooled and treated as a single site. Receivers in the Penobscot River were moored on the river bottom; receivers in the bay were moored at approximately 10 m below the surface. Data were downloaded monthly throughout the period of smolt migration.

Parameter estimation.—Survival (S_{ih}), transition (ψ_{ihk}), and detection (p_{ih}) probabilities were estimated with a separate multistate mark–recapture model (Brownie et al. 1993; White et al. 2006) for each year (Figure 2). Three states (h = A, B, or C) were used to represent three migration routes: state A represented the main stem of the Mattawamkeag and Penobscot rivers; state B represented the Pleasant and Piscataquis rivers; and state C represented the Stillwater Branch. Reach-specific survival probabilities (S_{ih}) estimated the probability of survival between site ih and the next downstream site. Transition probabilities (ψ_{ihk}) estimated the probability of transition from state h at occasion i to state k at occasion $i + 1$ given that the fish survives to site $i + 1$. Transition probabilities were fixed to 0 where transitions were not possible and to 1 where two rivers combined (e.g., where the Piscataquis River and the Stillwater Branch flow into the Penobscot River). After these parameters were fixed, the only estimable transition probability was ψ_{7AC}, which estimated the probability that a fish enters the Stillwater Branch given that it survives to the Penobscot River–Stillwater Branch split. The transition probability ψ_{7AC} also represented the proportion of fish that entered the Stillwater Branch during the study. Detection probabilities (p_{ih}) estimated the probability that a fish is detected at site ih given that it survives to site ih. Since the detection probability could not be estimated for the downstream-most site (aggregated Penobscot Bay receivers), λ was estimated as the joint probability of survival through the last reach and detection on any Penobscot Bay receiver.

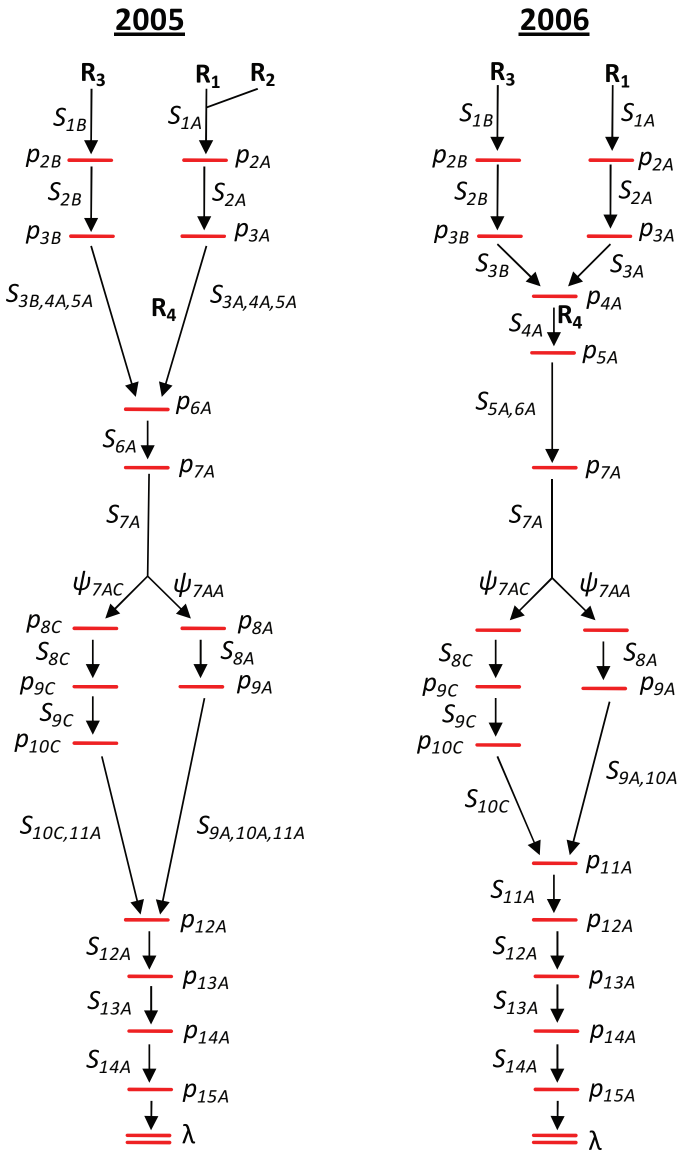

FIGURE 2. Schematic of the mark–recapture model used to estimate survival (S_{ih}), transition (ψ_{ihk}), and detection probabilities (p_{ih}) for Atlantic salmon smolts migrating through the Penobscot River drainage in 2005 and 2006 (R_1–R_4 = release sites; see Figure 1). Horizontal bars represent monitoring stations (λ = joint probability of survival through the last reach and detection on any Penobscot Bay receiver).

Parameters were estimated from complete capture histories in program MARK (White and Burnham 1999). Burnham et al. (1987) and Skalski et al. (2001) present model assumptions and the consequences of violating them; Perry et al. (2010) provide a concise explanation of the encounter histories used in this type of model. The R package RMark (Laake and Rexstad 2009; R Development Core Team 2009) was used to construct models for program MARK. The logit link function was used for all detection and survival parameters. The multinomial logit link function was used for all transition parameters.

In the full model for each year, S_{ih}, ψ_{ihk}, and p_{ih} were estimated separately for hatchery and wild fish at each site in each state. Because some monitoring sites varied between years (Figure 2), capture histories consisted of 12 recapture occasions in 2005 and 14 recapture occasions in 2006. To allow comparison of survival estimates between years, survival through some reaches was expressed as joint survival probabilities through multiple reaches. For example, survival between Orono Dam and Veazie Dam in 2005 is denoted as $S_{10C,11A}$ because no receiver was located at site 11A in that year.

Reach-specific mortality rates.—To compare mortality among reaches of differing lengths, the average rate of mortality (M) within each reach was estimated as

$$M_{ih} = 1 - (S_{ih}^{\frac{1}{L}}), \qquad (1)$$

where L represents the length (in river kilometers [rkm]) of the ith reach in state h. The SE was estimated for all derived parameters by using the delta method (Seber 1982).

Assessment of model fit.—To assess model fit, we estimated the overdispersion parameter ($\hat{C}$) for each full model by using the bootstrap goodness-of-fit and median $\hat{C}$ goodness-of-fit tests in MARK. To estimate the overdispersion parameter with the bootstrap procedure ($\hat{C}_{\text{bootstrap}}$), the observed full-model deviance was divided by the mean deviance among 200 simulated deviances. The median $\hat{C}$ procedure used logistic regression to estimate $\hat{C}_{\text{median}}$. To be conservative, we used the larger of $\hat{C}_{\text{bootstrap}}$ and $\hat{C}_{\text{median}}$ as an estimate of $\hat{C}$. In 2005, $\hat{C}_{\text{bootstrap}}$ was 1.07 and $\hat{C}_{\text{median}}$ was 1.02 ($\widehat{SE}$ =0.011). In 2006, $\hat{C}_{\text{bootstrap}}$ was 1.38 and $\hat{C}_{\text{median}}$ was 1.11 (SE =0.026). Based on these results, variances were not adjusted.

Survival through multiple reaches.—Cumulative survival through multiple reaches was estimated as the product of the survival estimates through each of the component reaches. For direct comparison of survival between the two migration routes around Marsh Island, we calculated the total survival through each route in each year. In 2005, survival through the Stillwater Branch route was estimated as the product of reach-specific survival estimates between the Gilman Falls Dam reservoir and Veazie Dam ($S_{\text{Stillwater}} = S_{8C}S_{9C}S_{10C,11A}$), and survival through the main-stem Penobscot River route was estimated as the product of reach-specific survival estimates between the Milford Dam reservoir and Veazie Dam ($S_{\text{mainstem}} = S_{8A}S_{9A,10A,11A}$). Route-specific reaches were shortened ($S_{\text{Stillwater}} = S_{8C}S_{9C}S_{10C}$; $S_{\text{mainstem}} = S_{8A}S_{9A,10A}$) in 2006 because a receiver was installed at site 11A, about 2 km downstream from the Stillwater Branch–Penobscot River confluence, in that year.

Total survival through the system was calculated as the product of all reach-specific survival estimates weighted by the proportion of fish that used each route. For example, total survival through the 123-km study region (excluding the first reach where fish were released) for fish released at site R_3 in

2005 was calculated as

$$S_{R3} = S_{2B}S_{3B,4A,5A}S_{6A}S_{7A}[(1 - \Psi_{7AC})S_{8A}S_{9A,10A,11A} + \Psi_{7AC}S_{8C}S_{9C}S_{10C,11A}]S_{12A}S_{13A}S_{14A}. \quad (2)$$

Movement rates.—Movement rates were only calculated between individual monitoring sites in 2006 because low detection efficiencies during the 2005 study period meant that sample sizes were inadequate for calculation of site-to-site movement rates. To provide direct comparison among river sections, the movement rate (R_{ij}) for each smolt between any two monitoring sites was calculated as

$$R_{ij} = L_{ij}T_{ij}^{-1}, \quad (3)$$

where L_{ij} is the distance (rkm) between upstream site i and downstream site j, and T_{ij} is the time difference (d) between first detections at sites j and i. Similar detection range at each site was assumed.

Movement rates (R_{ij}) through each reach containing a dam were compared with R_{ij} in a nearby reference reach. Reference reaches selected for West Enfield, Howland, and Milford dams were located immediately upstream from sections containing those dams. A single reference reach was used for Great Works and Veazie dams and was located between the two dams. The movement rate for each fish through each of these reaches was expressed relative to the median rate through the corresponding reference reach at night. A Kruskal–Wallis test was conducted to determine whether relative movement rates differed significantly (1) between smolts arriving during the day (between sunrise and sunset) and those arriving at night or (2) between smolts migrating through river sections with dams and those migrating through sections without dams. When significant differences were detected, a nonparametric multiple comparison test (Zar 1999) was conducted to determine whether differences were associated with arrival time (day versus night), the presence of dams, or both. The significance level for all tests was set at 0.05.

RESULTS

Evaluation of Tag Retention and Direct Tagging Mortality

No mortalities were observed among the 29 tagged Atlantic salmon during the 38-d dummy tagging trial. However, for one fish, the tag was expelled through the body wall at an unknown time during the study.

Survival and Mortality Rates

Survival of Atlantic salmon was generally lower in 2006 than in 2005 (Tables A.1, A.2). For hatchery smolts released at site R_3, the estimated survival to Fort Point ($\hat{S}_{B,hatchery}$) was 0.599 (SE = 0.057) in 2005 and 0.454 (SE = 0.048) in 2006. For hatchery smolts released in the upper Penobscot River system

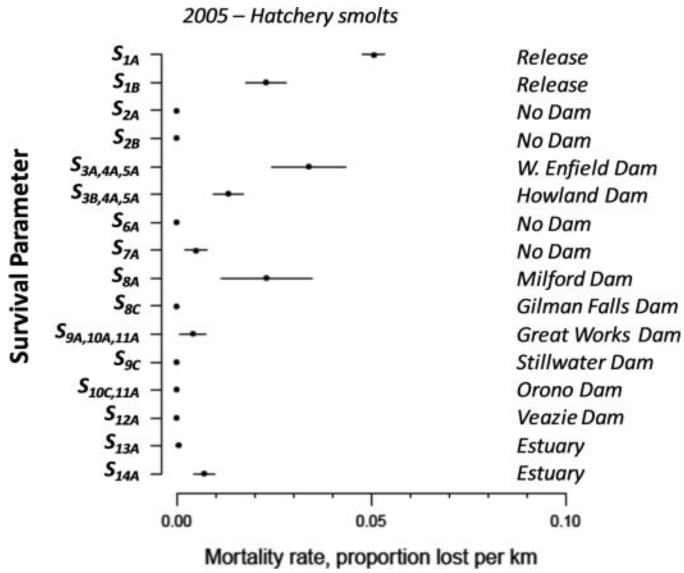

FIGURE 3. Estimated mortality rates (proportion of tagged smolts lost per km; ±SE shown by horizontal bars) through each reach for hatchery Atlantic salmon smolts released in 2005. The *y*-axis denotes the corresponding survival parameter (*S*). Text at right identifies reaches that contained release sites, dams, or estuarine habitat.

(sites R_1 and R_2), estimated survival to Fort Point ($\hat{S}_{A,hatchery}$) was 0.393 (SE = 0.134) in 2005 and 0.530 (SE = 0.043) in 2006. For wild smolts, $\hat{S}_{A,wild}$ was 0.684 (SE =0.082) in 2005 and 0.458 (SE =0.102) in 2006. These estimates do not include survival through the first reach.

Reach-specific survival estimates were lowest near release sites (i.e., S_{1A}, S_{1B}, S_{3A}; Tables A.1, A.2) for both hatchery and wild smolts and through reaches containing West Enfield, Howland, and Milford dams (Figures 3, 4). Among the 16 individual reaches that were monitored in 2005, mortality rates of hatchery smolts exceeded 1% loss per kilometer in only five reaches (Figure 3). These reaches contained the Mattawamkeag and Milo release sites and the West Enfield, Howland, and Milford dams. The mortality rate through all other reaches was less than 1% loss per kilometer.

In 4 of the 18 individual reaches that were monitored during 2006, mortality rates of hatchery smolts exceeded 1% loss per kilometer (Figure 4). These reaches included the Weldon release site and the West Enfield, Howland, and Milford dams. The mortality rate through all other reaches was less than 1% loss per kilometer.

Use of and Survival through the Stillwater Branch

In both years, most smolts used the main-stem Penobscot River as the migration route around Marsh Island (Table 2). Use of the Stillwater Branch was greater in 2005 (for both hatchery and wild smolts) than in 2006 and was greater for wild smolts than for hatchery smolts in both years.

Estimated survival of hatchery smolts from the north end of Marsh Island to Veazie Dam was 1.00 through the Stillwater

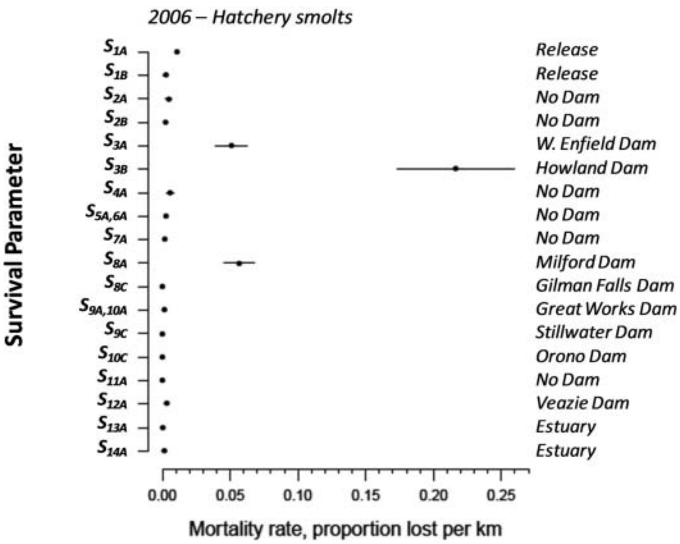

FIGURE 4. Estimated mortality rates (proportion of tagged smolts lost per km; ±SE shown by horizontal bars) through each reach for hatchery Atlantic salmon smolts released in 2006. The *y*-axis denotes the corresponding survival parameter (*S*). Text at right identifies reaches that contained release sites, dams, or estuarine habitat.

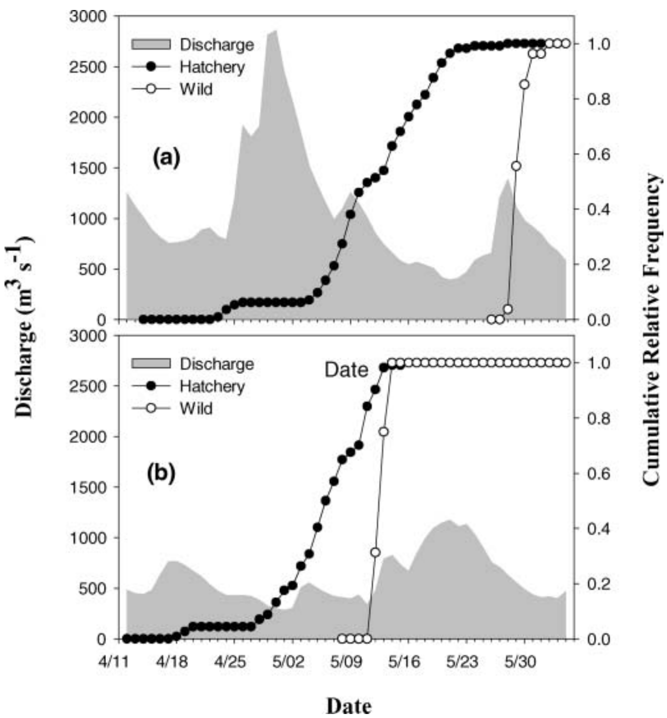

FIGURE 5. Mean daily discharge of the Penobscot River at West Enfield, Maine, and cumulative relative frequency of smolt arrival at Marsh Island for tagged hatchery and wild Atlantic salmon smolts in (**a**) 2005 and (**b**) 2006. Discharge data were obtained from the U.S. Geological Survey (www.waterdata.usgs.gov).

Branch ($S_{\text{Stillwater}}$) and 0.874 ($\widehat{SE} = 0.036$) through the mainstem Penobscot River (S_{mainstem}) in 2005. Estimated route-specific survival for wild smolts was 0.846 ($\widehat{SE} = 0.141$) through the Stillwater Branch and 0.941 ($\widehat{SE} = 0.088$) through the main stem. Note that owing to the small sample size, $S_{\text{Stillwater}}$ and S_{mainstem} are not statistically discernible, as indicated by the large SEs about those estimates. In 2006, a monitoring site was added about 2 km downstream from the Stillwater Branch–Penobscot River confluence (site 11A; Figures 1, 2). All hatchery and wild smolts survived through the Stillwater Branch during 2006. Survival through the main stem was higher for hatchery smolts ($S_{\text{mainstem}} = 0.806$, $\widehat{SE} = 0.038$) than for wild smolts ($S_{\text{mainstem}} = 0.769$, $\widehat{SE} = 0.117$).

Detection Probabilities

Detection probabilities were generally low in 2005 and high in 2006 (Table A.3). Lower detection probabilities in 2005 were primarily due to high discharge in late April and early May. Most of the tagged fish moved at lower flows in 2005 than in 2006 (Figure 5). In 2005, detection probabilities were highest in the estuary because estuarine sites were not as strongly affected by high spring discharge (sites 14A and 15A; Figure 1). Although most fish passed at lower flows in 2005, the equipment was temporarily affected (e.g., turned over, moved, or buried under debris) and the problems were not resolved at some sites until most fish had passed. This partially explains why later-migrating wild fish showed higher detection probabilities at some sites. The V9 tag used in 2006 also had a larger detection range (i.e., stronger signal) than the smaller V7 tag used in 2005.

TABLE 2. Estimated proportion of hatchery (H) and wild (W) Atlantic salmon smolts that used the Stillwater Branch (ψ_{7AC}) versus the main stem of the Penobscot River ($\psi_{7AA} = 1 - \psi_{7AC}$) as a migration path in 2005 and 2006 (CI = confidence interval).

Year	Origin	Route	Parameter	Estimate	$\widehat{SE}$	95% CI
2005	H	Stillwater Branch	$\psi_{7AC,\text{hatchery}}$	0.142	0.032	0.090–0.216
	H	Penobscot River	$\psi_{7AA,\text{hatchery}}$	0.858	0.032	0.784–0.910
	W	Stillwater Branch	$\psi_{7AC,\text{wild}}$	0.259	0.084	0.129–0.453
	W	Penobscot River	$\psi_{7AA,\text{wild}}$	0.741	0.084	0.547–0.871
2006	H	Stillwater Branch	$\psi_{7AC,\text{hatchery}}$	0.044	0.019	0.019–0.102
	H	Penobscot River	$\psi_{7AA,\text{hatchery}}$	0.956	0.019	0.898–0.981
	W	Stillwater Branch	$\psi_{7AC,\text{wild}}$	0.188	0.098	0.062–0.447
	W	Penobscot River	$\psi_{7AA,\text{wild}}$	0.812	0.098	0.553–0.938

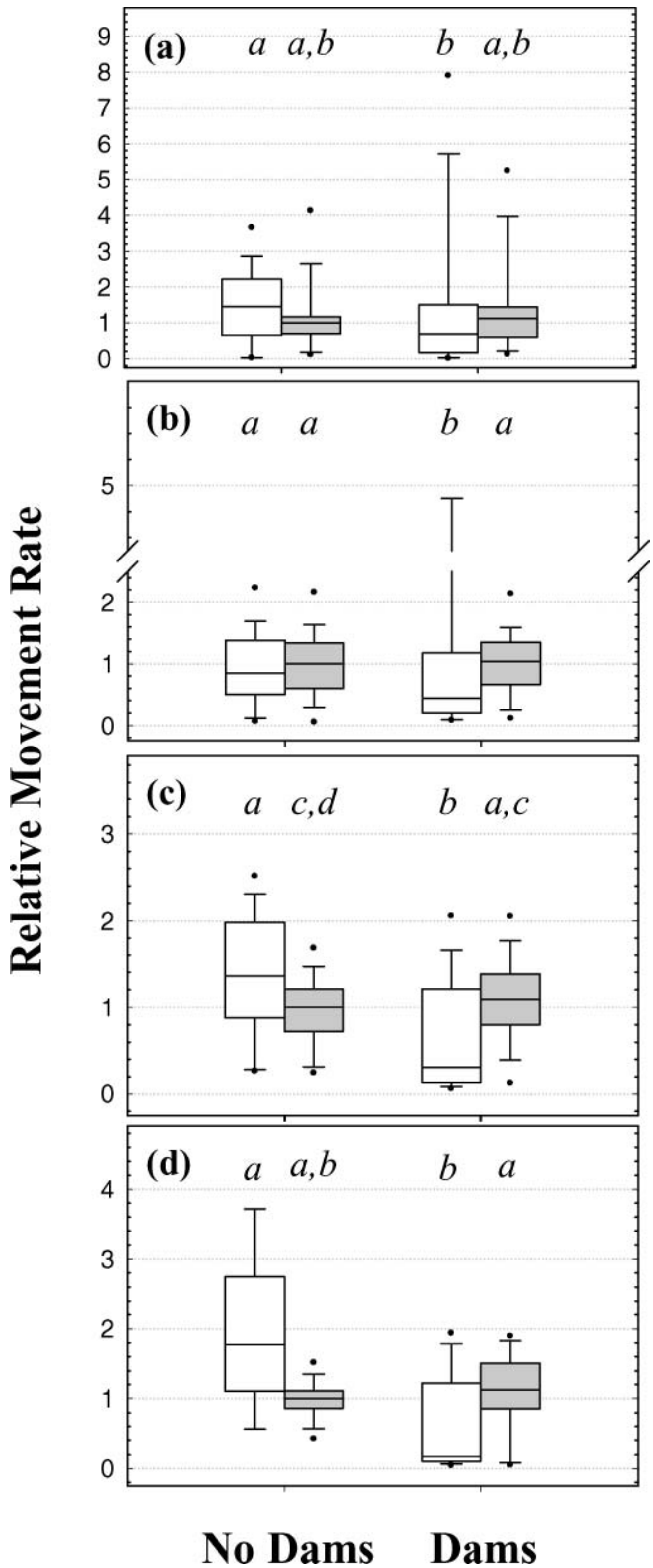

FIGURE 6. Relative movement rates (see Methods) for Atlantic salmon smolts arriving at sections with and without dams during the daytime (unshaded box plots) or nighttime (shaded box plots): **(a)** hatchery smolts released on April 12, **(b)** hatchery smolts released on April 24, **(c)** hatchery smolts released on May 8, and **(d)** wild smolts released on May 8. All groups were released in 2006. Different italicized letters indicate significant differences (nonparametric multiple comparison test: $Q > 2.639$, $P < 0.05$). The lines within the boxes represent the medians, the heights of the boxes the 25th–75th percentiles, the whiskers the 10th and 90th percentiles, and the dots the minimum and maximum values.

Movement Rates and Migration Timing

For all release groups, movement rates were significantly lower through sections containing dams than through sections without dams for fish arriving to the section in the daytime (Figure 6). Conversely, no such differences were observed for fish arriving at night. For sections containing dams, the movement rate of fish arriving in the daytime was significantly lower than the movement rate of those arriving at night for three of the four release groups (Figure 6b–d).

DISCUSSION

Locations of Mortality and Potential Causes

Mortality rates were highest (loss = 1–21% per km) through reaches containing West Enfield, Howland, and Milford dams and in reaches where fish were released (Figures 4, 5). Among years, estimated survivorship ranged from 52% to 91% for the reach that contained West Enfield Dam, from 71% to 79% for the Howland Dam reach, and from 82% to 94% for the Milford Dam reach (Tables A.1, A.2). Although these data do not definitively reveal sources of mortality, the losses are probably attributable to the direct and indirect effects of the dams (e.g., physical injury or predation). Physical injury associated with passage at dams can occur while the fish are entrained in turbines (Cada 2001) or as they move through spill or bypass structures (Ruggles 1980; Coutant and Whitney 2000).

The rate of entrainment mortality depends on two probabilities: the probability that the fish will enter a turbine bay (entrainment) and the probability that the fish will suffer acute mortality as a result of turbine passage, which varies with turbine type and fish size (EPRI 1992; Coutant and Whitney 2000). Previous studies in the early 1990s revealed that turbine entrainment ranged from 38% to 44% at Milford Dam (Shepard 1991a) and from 38% to 92% at West Enfield Dam (Shepard 1991b, 1991c, 1993; BPHA 1993a). In the only empirical study of actual turbine mortality at Penobscot River dams, Bangor-Pacific Hydro Associates (BPHA 1993a) estimated that acute turbine mortality was just 2.3% for fish that were entrained. No other such studies have been conducted in the Penobscot River drainage, but model-based turbine mortality estimates for Weldon, Milford, and Veazie dams range from 5% to 9% per dam (USASAC 2005). These estimates are lower than the mortality rates associated with some dams in 2005 and 2006 during our study, suggesting that indirect effects beyond direct turbine-induced mortality may be important in this system.

Such indirect effects can come from several sources. Injured and disoriented salmon smolts may generally become more vulnerable to predators after passage at dams (Raymond 1979; Rieman et al. 1991; Mesa 1994). Descaling can also impair osmoregulation, possibly leading to estuarine mortality (Zydlewski et al. 2010). Even when mortality at individual dams is low, cumulative losses over several dams can be substantial (Coutant and Whitney 2000). In the case of the Penobscot River system, assessments by NOAA Fisheries demonstrated that many Atlantic salmon smolts captured in the lower river possessed injuries that were consistent with sublethal turbine entrainment (USASAC 2004). Furthermore, fish mortality and injury (e.g., descaling and lacerations) were observed more frequently in the lower Penobscot River than in a smaller river (Narraguagus River) that lacked hydroelectric dams (USASAC 2004).

The installation of downstream fishways and bypass structures offers some hope for ameliorating the potential negative effects of increased hydropower generation (Simmons 2000; Johnson et al. 2005; Scruton et al. 2007). However, existing downstream bypass structures at Penobscot River dams perform poorly, and efforts to improve bypass efficiency have had little success. The collection efficiency of fish passage facilities in the early 1990s ranged from 2% to 22% for West Enfield Dam (Shepard 1991b, 1991c, 1993; BPHA 1993a) and from 17% to 59% for Weldon Dam (GNP 1998, 1999), and modifications to these structures have ultimately failed to improve collection efficiencies (BPHA 1993b; Brown and Bernier 2000). Design of passage facilities is generally challenging due to inherent site-specific hydraulic and operational differences among dams (Roscoe and Hinch 2010), but successful strategies have been developed in other systems by combining fish guidance structures with increased spill (Johnson et al. 2005; Scruton et al. 2008; Williams 2008).

Entrainment rate, bypass efficiency, and proportional spill are often directly related to flow conditions at dams (Coutant and Whitney 2000). Flow conditions are largely determined by river discharge and dam operations. Low river discharge in 2006 (Figure 5) allowed installation of flashboards at West Enfield and Howland dams during the period of smolt emigration (Scott Hall, Pennsylvania Power and Light, Milford, Maine, personal communication). Flashboards reduce spill and increase the proportion of total discharge that flows through the turbines. During this time, all but a short section of Milford Dam contained flashboards (C.M.H., personal observation). Conversely, flashboards were not installed at dams where estimated smolt survival was highest—Veazie and Great Works dams. Thus, we hypothesize that the presence of installed flashboards may compound the effects of low flows by directing a greater proportion of fish through turbines or by causing migratory delay that increases their exposure to predators. The practice of increasing hydroelectric generation should be reconsidered in systems where management of salmon smolt passage is a major concern.

Model Assumptions

A key assumption of mark–recapture survival studies is that tagging and handling do not affect survival. In our study, all hatchery and wild release groups exhibited substantial losses within the first reach after release in both years (Tables A.1, A.2). Similar losses for both hatchery and wild smolts in this study and others (BPHA 1993a; Spicer et al. 1995) suggest that the losses are attributable to indirect effects of prerelease handling (e.g., transport, anesthesia, and surgery). Thus, true survival of untagged fish—at least through the first reach—may be higher than was estimated in this study. Another explanation for perceived losses may be that some fish did not migrate but instead remained in freshwater. However, gill Na^+, K^+-ATPase activities (Table 1) were indicative of active smolts.

Results from the dummy tagging trial revealed that the handling and tagging process did not cause direct mortality, but other factors may have compounded the effects of tagging after release (e.g., predation). Several studies have shown that internal tags can affect the swimming performance and behavior of juvenile salmonids and that effects increase with the tag mass : body mass ratio (Adams et al. 1998; Brown et al. 2010). Although recognition of a single threshold for the tag mass : body mass ratio is probably not realistic (Jepsen et al. 2005), the tag mass : body mass ratio for all fish used in this study was less than the 8% recommended by Lacroix et al. (2004) for Atlantic salmon.

Another critical assumption in survival studies is that tags are retained throughout the study; this assumption is necessary because lost tags are misinterpreted as fish mortality by mark–recapture models. The single tag that was lost during the dummy tagging trial suggests that tag loss could have negatively biased fish survival to some degree. However, we reason that it is unlikely that such random losses, or even tagging-related injuries, would have resulted in higher mortality at dams than in other reaches. Indeed, reach-specific survivorship increased as fish proceeded downstream through the system, and survival was high in the reaches immediately upstream of West Enfield and Howland dams (Tables A.1, A.2). Thus, we reason that although the tagging and handling process may have negatively biased survival estimates in the first reach, substantial bias was probably limited to the first reach. Taking this into account, we did not include survival through the first reach in our estimates of whole-system survival for any release group.

Movement Rates, Predation, and Estuarine Mortality

Our study indicates that migratory delays of out-migrating smolts at dams most often occur during the day rather than at night (Figure 6; see also BPHA 1993a). Such an outcome may have broad implications for managing smolt passage in the Penobscot River and elsewhere. Delays can increase exposure to predators (Riemann et al. 1991; Blackwell and Krohn 1997; Venditti et al. 2000) or can cause physiological loss of osmoregulatory capacity (McCormick et al. 1999). Daytime migratory delays could increase exposure of smolts to avian predators. Double-crested cormorants *Phalacrocorax auritus*, which mainly feed during daylight hours, have been observed to feed in headponds, under spillways, and in tailraces of dams (Blackwell and Krohn 1997). Although predation by double-crested cormorants may be considered a natural source of mortality, the influence of dams on water velocities and smolt behavior may increase the rate of predation.

Estuarine losses could be due to delayed mortality effects of dams, predation, or physiological impairment. We suspected that during the study period, most smolts would enter seawater between the north tip of Verona Island (∼rkm 7.0) and the marine site at Fort Point (rkm −4.0). Some losses were observed within this reach (Figures 3, 4), but the mortality rate was generally low (<1% loss per km). Thus, delayed mortality was probably not a significant factor, at least for lower river dams.

Use of and Survival through the Stillwater Branch

Our results indicate that most of the smolts passing Marsh Island remained in the Penobscot River instead of migrating through the Stillwater Branch (hatchery smolts: $\psi_{7AC} =$ 0.04–0.14 among years; wild smolts: $\psi_{7AC} = 0.19$–0.26 among years; Table 2). However, compared with the main-stem route, survival through the Stillwater Branch was 13% and 19% higher for hatchery fish in 2005 and 2006, respectively, and was 23% higher for wild fish in 2006. Survival of wild smolts through the Stillwater Branch was lower in 2005 ($S_{\text{Stillwater}} = 0.846$), but there was considerable uncertainty associated with this estimate ($\widehat{\text{SE}} = 0.141$). Lower use of the Stillwater Branch in 2006 by both hatchery and wild smolts may have been due to the lower discharge during migration in that year relative to 2005 (Figure 5).

In this analysis, we sought to quantify the effects of mortality through specific reaches on the larger Penobscot River smolt population. Since survival can differ among available routes, differential use of the Stillwater Branch raises an important consideration for future migration studies and for Atlantic salmon management in this system. Although greater proportional use of the Stillwater Branch may be expected if discharge is increased through the Stillwater Branch hydrosystem, we did not evaluate the relationship between discharge and path choice with these data. A better understanding of the relationship between path choice and hydrodynamics could enhance management of the hydrosystem for both electricity generation and Atlantic salmon protection.

Implications for Restoration

Dam removal projects offer great hope for improving upstream and downstream passage of Atlantic salmon and other diadromous fishes. However, such passage restoration efforts are likely to be most effective when targeted at the dams that cause the greatest impairment of migratory fish survival. Unfortunately, in the Penobscot River system, the two dams scheduled for removal (Veazie and Great Works dams) apparently had the least negative effects on emigrating smolts under the conditions studied in 2005 and 2006. It is possible that Veazie and Great Works dams impose a greater risk to passing smolts under different conditions (e.g., when flashboards are installed), and previous research has shown that these dams negatively affect the upriver migration of adults (Holbrook et al. 2009). Nonetheless, poor survival at Milford and West Enfield dams should be of particular concern to fishery managers given that (1) hydroelectric generation at these dams is planned for the foreseeable future and (2) power generation at the two dams has increased since this study was conducted.

Although survival of Atlantic salmon smolts in the Stillwater Branch was high during both study years, the increased flow and hydroelectric generation capacity in the Stillwater Branch present a mixed set of potential outcomes. Within the Stillwater Branch, only Stillwater Dam was generating electricity during this study. However, starting in 2007, additional turbines were installed at both Stillwater and Orono dams. Additional monitoring is necessary to determine whether concomitant improvements to downstream passage will be needed to minimize the risk of turbine entrainment or migratory delay at the Stillwater Dam and Orono Dam sites. Adequate downstream passage may thus remain an important consideration in the Stillwater Branch and in other parts of the Penobscot River system even after implementation of the Penobscot River Restoration Project. This case study shows that by examining prerestoration migration dynamics throughout entire river systems rather than just in the vicinity of particular dams, tracking studies can help prioritize restoration efforts or predict costs and benefits of future hydrosystem changes.

ACKNOWLEDGMENTS

We thank John Kocik and Tim Sheehan (NOAA Fisheries), James McCleave, Michael Bailey (University of Maine), Nick Johnson (U.S. Geological Survey), and two anonymous reviewers for providing valuable feedback on the manuscript. Financial support was generously provided by the University of Maine, the West Enfield Fund, the Maine Agricultural and Forest Experiment Station, and the Maine Cooperative Fisheries and Wildlife Research Unit. We are grateful to the U.S. Fish and Wildlife Service for providing Atlantic salmon and to the Penobscot Nation for access to their land. We also acknowledge S. Hall (Pennsylvania Power and Light); R. Saunders, G. Goulette, P. Music, and E. Hastings (NOAA Fisheries); C. Fay (Penobscot Nation); J. Trial, R. Dill, and M. Simpson (Maine Atlantic Salmon Commission); and L. Holbrook, C. Gardner, S. Fernandes, and many students from the University of Maine for their assistance and insights. Mention of trade names or commercial products does not imply endorsement by the U.S. Government. This paper is contribution number 3228 of the Maine Agricultural and Forest Experiment Station.

REFERENCES

Adams, N. S., D. W. Rondorf, S. D. Evans, J. E. Kelly, and R. W. Perry. 1998. Effects of surgically and gastrically implanted radio transmitters on swimming performance and predator avoidance of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 55:781–787.

Blackwell, B. F., and W. B. Krohn. 1997. Spring foraging distribution and habitat selection by double-crested cormorants on the Penobscot River, Maine, USA. Colonial Waterbirds 20:66–76.

BPHA (Bangor-Pacific Hydro Associates). 1993a. 1992 evaluation of downstream fish passage facilities at the West Enfield hydroelectric project. Report prepared by the Bangor-Pacific Hydro Associates for the U.S. Federal Energy Regulatory Commission, Report Number 2600-027, Washington, D.C.

BPHA (Bangor-Pacific Hydro Associates). 1993b. 1993 evaluation of downstream fish passage facilities at the West Enfield hydroelectric project. Report prepared by the Bangor-Pacific Hydro Associates for the U.S. Federal Energy Regulatory Commission, Report Number 2600-029, Washington, D.C.

Brown, R., and K. Bernier. 2000. The use of an aquatic guidance strobe lighting system to enhance the safe bypass of Atlantic salmon smolts. Pages 149–154 *in* M. Odeh, editor. Advances in fish passage technology: engineering design and biological evaluation. American Fisheries Society, Bethesda, Maryland.

Brown, R. S., R. A. Harnish, K. M. Carter, J. W. Boyd, K. A. Deters, and M. B. Eppard. 2010. An evaluation of the maximum tag burden for implantation of acoustic transmitters in juvenile Chinook salmon. North American Journal of Fisheries Management 30:499–505.

Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. Biometrics 49:1173–1187.

Budy, P., G. P. Thiede, N. Bouwes, C. E. Petrosky, and H. Schaller. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. North American Journal of Fisheries Management 22:35–51.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society, Monograph 5, Bethesda, Maryland.

Cada, F. 2001. The development of advances hydroelectric turbines to improve fish passage survival. Fisheries 26(9):14–23.

Coutant, C. C., and R. R. Whitney. 2000. Fish behavior in relation to passage through hydropower turbines: a review. Transactions of the American Fisheries Society 129:351–380.

EPRI (Electrical Power Research Institute). 1992. Fish entrainment and turbine mortality review and guidelines. Stone and Webster Engineering, Boston.

Fay, C., M. Barton, S. Craig, A. Hecht, J. Pruden, R. Saunders, T. Sheehan, and J. Trial. 2006. Status review for anadromous Atlantic salmon (*Salmo salar*) in the United States. Report prepared for the National Marine Fisheries Service, Silver Spring, Maryland, and U.S. Fish and Wildlife Service, Arlington, Virginia.

Ferguson, J. W., R. F. Absolon, T. J. Carlson, and B. P. Sandford. 2006. Evidence of delayed mortality on juvenile pacific salmon passing through turbines at Columbia River dams. Transactions of the American Fisheries Society 135:139–150.

GNP (Great Northern Paper). 1998. Report on the effectiveness of the permanent downstream passage system for Atlantic salmon at Weldon Dam. Great Northern Paper, Millinocket, Maine.

GNP (Great Northern Paper). 1999. Report on the effectiveness of the permanent downstream passage system for Atlantic salmon at Weldon Dam. Great Northern Paper, Millinocket, Maine.

Holbrook, C. M., J. Zydlewski, D. Gorsky, S. L. Shepard, and M. T. Kinnison. 2009. Movements of prespawn adult Atlantic salmon near hydroelectric dams in the Lower Penobscot River, Maine. North American Journal of Fisheries Management 29:495–505.

IUBMB (International Union of Biochemistry and Molecular Biology). 1992. Enzyme nomenclature 1992. Academic Press, San Diego, California.

Jepsen, N., C. Schreck, S. Clements, and E. B. Thorstad. 2005. A brief discussion of the 2% tag/body mass rule of thumb. Pages 255–259 *in* M. T. Lembo and G. Marmullaed, editors. Aquatic telemetry: advances and applications. Food and Agriculture Organization of the United Nations, Rome.

Johnson, G. E., S. A. Anglea, N. S. Adams, and T. O. Wik. 2005. Evaluation of a prototype surface flow bypass for juvenile salmon and steelhead at the powerhouse of Lower Granite Dam, Snake River, Washington, 1996–2000. North American Journal of Fisheries Management 25:138–151.

Laake, J., and E. Rexstad. 2009. RMark: an alternative approach to building linear models in MARK. Appendix C *in* E. Cooch and G. White, editors. Program MARK: a gentle introduction, 8th edition. Available: http://www.phidot.org/software/mark/docs/book/.

Lacroix, G. L., D. Knox, and P. McCurdy. 2004. Effects of implanted dummy acoustic transmitters on juvenile Atlantic salmon. Transactions of the American Fisheries Society 133:211–220.

McCormick, S. D. 1993. Methods for non-lethal gill biopsy and measurement of Na^+,K^+-ATPase activity. Canadian Journal of Fisheries and Aquatic Sciences 50:656–658.

McCormick, S. D., R. A. Cunjack, B. Dempson, M. O'Dea, and J. B. Carey. 1999. Temperature-related loss of smolt characteristics in Atlantic salmon (*Salmo salar*) in the wild. Canadian Journal of Fisheries and Aquatic Sciences 56:1649–1658.

Mesa, M. G. 1994. Effects of multiple acute stressors on predator avoidance ability and physiology of juvenile Chinook salmon. Transactions of the American Fisheries Society 123:786–793.

Moring, J. R., J. Marancik, and F. Griffiths. 1995. Changes in stocking strategies for Atlantic salmon restoration and rehabilitation in Maine, 1871–1993. Pages 38–46 *in* H. L. Schramm and R. G. Piper, editors. Uses and effects of cultured fishes in aquatic ecosystems. American Fisheries Society, Symposium 15, Bethesda, Maryland.

Nettles, D. C., and S. P. Gloss. 1987. Migration of landlocked Atlantic salmon smolts and effectiveness of a fish bypass structure at a small-scale hydroelectric facility. North American Journal of Fisheries Management 7:562–568.

NMFS (National Marine Fisheries Service) and USFWS (U.S. Fish and Wildlife Service). 2009. Determination of endangered status for the Gulf of Maine distinct population segment of Atlantic salmon. Federal Register 74:117(19 June 2009):29343–29387.

NMFS (National Marine Fisheries Service) and USFWS (U.S. Fish and Wildlife Service). 2000. Final endangered status for a distinct population segment of anadromous Atlantic salmon (*Salmo salar*). Federal Register 65:223(17 November 2000):69459–69483.

NMFS (National Marine Fisheries Service). 2000. Salmon travel time and survival related to flow in the Columbia River Basin. NMFS, Seattle.

NRC (National Research Council). 2004. Atlantic salmon in Maine. National Academy Press. Washington, D.C.

Perry, R. W., J. R. Skalski, P. L. Brandes, P. T. Sandstrom, A. P. Klimley, A. Ammann, and B. MacFarlane. 2010. Estimating survival and migration route probabilities of juvenile Chinook salmon in the Sacramento-San Joaquin River delta. North American Journal of Fisheries Management 30:142–156.

R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Raymond, H. L. 1979. Effects of dams and impoundments on the migration rate of juvenile Chinook salmon and steelhead trout from the Snake River, 1966–1975. Transactions of the American Fisheries Society 108:509–529.

Rieman, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poe. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day reservoir, Columbia River. Transactions of the American Fisheries Society 120:448–458.

Roscoe, D. W., and S. G. Hinch. 2010. Effectiveness monitoring of fish passage facilities: historical trends, geographic patterns and future directions. Fish and Fisheries 11:12–23.

Ruggles, C. P. 1980. A review of the downstream migration of Atlantic salmon. Canadian Technical Report of Fisheries and Aquatic Sciences 952.

Scruton, D. A., C. J. Pennell, C. E. Bourgeois, and R. F. Goosney. 2007. Assessment of a retrofitted downstream fish bypass system for wild Atlantic salmon (*Salmo salar*) smolts and kelts at a hydroelectric facility on the Exploits River, Newfoundland, Canada. Hydrobiologia 582:155–169.

Scruton, D. A., C. J. Pennell, C. E. Bourgeois, R. F. Goosney, L. King, R. K. Booth, W. Eddy, T. R. Porter, L. M. N. Ollerhead, and K. D. Clarke. 2008. Hydroelectricity and fish: a synopsis of comprehensive studies of upstream and downstream passage of anadromous wild Atlantic salmon, *Salmo salar*, on the Exploits River, Canada. Hydrobiologia 609:225–239.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters, 2nd edition. Charles Griffin, London.
Shepard, S. L. 1991a. Report on radio telemetry investigations of Atlantic salmon smolt migration in the Penobscot River. Bangor Hydro-Electric, Bangor, Maine.
Shepard, S. L. 1991b. Evaluation of upstream and downstream fish passage facilities at the West Enfield hydroelectric project. Report prepared by Bangor Hydro-Electric for the U.S. Federal Energy Regulatory Commission, Report Number 2600-010, Washington, D.C.
Shepard, S. L. 1991c. Evaluation of upstream and downstream fish passage facilities at the West Enfield hydroelectric project. Report prepared by the Bangor Hydro-Electric for the U.S. Federal Energy Regulatory Commission, Report Number 2600-010, Washington, D.C.
Shepard, S. L. 1993. Survival and timing of Atlantic salmon smolts passing the West Enfield hydroelectric project. Report prepared by the Bangor Hydro-Electric to the US Federal Energy Regulatory Commission, Washington, D.C.
Simmons, R. A. 2000. Effectiveness of a fish bypass with an angled bar rack at passing Atlantic salmon and steelhead trout smolts at the lower Saranac hydroelectric project. Pages 95–102 *in* M. Odeh, editor. 2000. Advances in fish passage technology: engineering design and biological evaluation. American Fisheries Society, Bethesda, Maryland.
Skalski, J. R., J. Lady, R. Townsend, A. Giorgi, J. R. Stevenson, C. M. Peven, and R. D. McDonald. 2001. Estimating in-river survival of migrating salmonid smolts using radiotelemetry. Canadian Journal of Fisheries and Aquatic Sciences 58:1987–1997.
Spicer, A. V., J. R. Moring, and J. G. Trial. 1995. Downstream migratory behavior of hatchery-reared, radio-tagged Atlantic salmon (*Salmo salar*) smolts in the Penobscot River, Maine, USA. Fisheries Research 23:255–266.
USASAC (U.S. Atlantic Salmon Assessment Committee). 2004. Annual report of the U.S. Atlantic salmon assessment committee, Report 16-2003 activities. USASAC, Annual Report 2004/16, Woods Hole, Massachusetts.
USASAC (U.S. Atlantic Salmon Assessment Committee). 2005. Annual report of the U.S. Atlantic salmon assessment committee, Report 17–2004 activities. USASAC, Annual Report 2005/17, Woods Hole, Massachusetts.
Venditti, D. A., D. W. Rondorf, and J. M. Kraut. 2000. Migratory behavior, and forebay delay of radio-tagged juvenile fall Chinook salmon in a lower Snake River impoundment. North American Journal of Fisheries Management 20:41–52.
White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(Supplement):120–138.
White, G. C., W. L. Kendall, and R. J. Barker. 2006. Multistate survival models and their extensions in program MARK. Journal of Wildlife Management 70:1521–1529.
Williams, J. G. 2008. Mitigating the effects of high-head dams on the Columbia River, USA: experience from the trenches. Hydrobiologia 609:241–251.
Zar, J. H. 1999. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.
Zydlewski, J., G. Zydlewski, and R. G. Danner. 2010. Descaling injury impairs the osmoregulatory ability of Atlantic salmon smolts entering seawater. Transactions of the American Fisheries Society 138:129–136.

Appendix: Reach-Specific Survival and Detection Probabilities

TABLE A.1. Reach-specific survival probability estimates ($\widehat{S_{ih}}$) with standard errors ($\widehat{\text{SE}}$s) and profile likelihood 95% confidence intervals (CIs) for tagged hatchery and wild Atlantic salmon smolts in 2005 (L = length of each reach, km). Release sites (see Table 1 for code definitions) or dams are indicated where applicable.

Parameter	Dam or release site	$\widehat{S_{ih}}$	$\widehat{\text{SE}}$	95% CI	L
$S_{1A,\text{hatchery}}$	R_2	0.246	0.074	0.129–0.417	26.98
$S_{1B,\text{hatchery}}$	R_3	0.774	0.057	0.644–0.867	11.02
$S_{2A,\text{hatchery}}$		1.000			14.41
$S_{2B,\text{hatchery}}$		1.000			30.00
$S_{3A,4A,5A,\text{hatchery}}$	West Enfield Dam	0.520	0.175	0.215–0.811	18.89
$S_{3B,4A,5A,\text{hatchery}}$	Howland Dam	0.792	0.064	0.641–0.890	17.39
$S_{3B,4A,5A,\text{hatchery}}$	R_4	0.661	0.040	0.578–0.734	14.55
$S_{6A,\text{hatchery}}$		1.000			10.04
$S_{7A,\text{hatchery}}$		0.953	0.028	0.854–0.986	9.72
$S_{8A,\text{hatchery}}$	Milford Dam	0.916	0.043	0.785–0.971	3.73
$S_{8C,\text{hatchery}}$	Gilman Falls Dam	1.000			2.51
$S_{9A,10A,11A,\text{hatchery}}$	Great Works Dam	0.954	0.037	0.801–0.991	11.01
$S_{9C,\text{hatchery}}$	Stillwater Dam	1.000			4.66
$S_{10C,11A,\text{hatchery}}$	Orono Dam	1.000			7.82
$S_{12A,\text{hatchery}}$	Veazie Dam	1.000			9.98
$S_{13A,\text{hatchery}}$		0.984	0.017	0.879–0.998	27.95
$S_{14A,\text{hatchery}}$		0.905	0.038	0.802–0.957	14.08
$S_{1A,\text{wild}}$	R_1	0.536	0.065	0.409–0.658	32.07
$S_{2A,\text{wild}}$		0.985	0.039	0.299–0.999	14.41
$S_{3A,4A,5A,\text{wild}}$	West Enfield Dam	0.905	0.068	0.670–0.978	18.89
$S_{6A,\text{wild}}$		1.000			10.04
$S_{7A,\text{wild}}$		0.954	0.058	0.611–0.996	9.72
$S_{8A,\text{wild}}$	Milford Dam	0.941	0.088	0.422–0.997	3.73
$S_{8C,\text{wild}}$	Gilman Falls Dam	1.000			2.51
$S_{9A,10A,11A,\text{wild}}$	Great Works Dam	1.000			11.01
$S_{9C,\text{wild}}$	Stillwater Dam	0.846	0.141	0.396–0.979	4.66
$S_{10C,11A,\text{wild}}$	Orono Dam	1.000			7.82
$S_{12A,\text{wild}}$	Veazie Dam	1.000			9.98
$S_{13A,\text{wild}}$		0.878	0.080	0.625–0.969	27.95
$S_{14A,\text{wild}}$		1.000			14.08

TABLE A.2. Reach-specific survival probability estimates ($\widehat{S_{ih}}$) with standard errors ($\widehat{SEs}$) and profile likelihood 95% confidence intervals (CIs) for tagged hatchery and wild Atlantic salmon smolts in 2006 (L = length of each reach, km). Release sites (see Table 1 for code definitions) or dams are indicated where applicable.

Parameter	Dam or release site	$\widehat{S_{ih}}$	$\widehat{SE}$	95% CI	L
$S_{1A,\text{hatchery}}$	R_1	0.705	0.038	0.627–0.774	32.2
$S_{1B,\text{hatchery}}$	R_3	0.972	0.019	0.896–0.993	10.7
$S_{2A,\text{hatchery}}$		0.940	0.028	0.856–0.976	13.3
$S_{2B,\text{hatchery}}$		0.929	0.031	0.840–0.970	30.2
$S_{3A,\text{hatchery}}$	West Enfield Dam	0.820	0.042	0.723, 0.888	3.8
$S_{3B,\text{hatchery}}$	Howland Dam	0.711	0.057	0.589–0.809	1.4
$S_{4A,\text{hatchery}}$		0.965	0.018	0.907–0.987	6.3
$S_{5A,6A,\text{hatchery}}$		0.949	0.020	0.891–0.977	20.2
$S_{7A,\text{hatchery}}$		0.983	0.012	0.922–0.998	9.4
$S_{8A,\text{hatchery}}$	Milford Dam	0.815	0.037	0.730–0.878	3.5
$S_{8C,\text{hatchery}}$	Gilman Falls Dam	1.000			2.0
$S_{9A,10A,\text{hatchery}}$	Great Works Dam	0.988	0.012	0.922–0.998	8.1
$S_{9C,\text{hatchery}}$	Stillwater Dam	1.000			5.2
$S_{10C,\text{hatchery}}$	Orono Dam	1.000			4.3
$S_{11A,\text{hatchery}}$		1.000			3.3
$S_{12A,\text{hatchery}}$	Veazie Dam	0.967	0.019	0.904–0.989	9.7
$S_{13A,\text{hatchery}}$		0.990	0.011	0.919–0.999	28.0
$S_{14A,\text{hatchery}}$		0.980	0.022	0.843–0.998	14.1
$S_{1A,\text{wild}}$		0.329	0.055	0.231–0.444	32.2
$S_{2A,\text{wild}}$		0.958	0.041	0.756–0.994	13.3
$S_{3A,\text{wild}}$	West Enfield Dam	0.870	0.070	0.665–0.957	3.8
$S_{4A,\text{wild}}$		0.950	0.049	0.718–0.993	6.3
$S_{5A,6A,\text{wild}}$		0.842	0.084	0.608–0.948	20.2
$S_{7A,\text{wild}}$		1.000			9.4
$S_{8A,\text{wild}}$	Milford Dam	0.846	0.100	0.549–0.961	3.5
$S_{8C,\text{wild}}$	Gilman Falls Dam	1.000			2.0
$S_{9A,10A,\text{wild}}$	Great Works Dam	0.909	0.087	0.561–0.987	8.1
$S_{10C,\text{wild}}$	Orono Dam	1.000			4.3
$S_{11A,\text{wild}}$		1.000			3.3
$S_{12A,\text{wild}}$	Veazie Dam	1.000			9.7
$S_{13A,\text{wild}}$		0.923	0.074	0.609–0.989	28.0
$S_{14A,\text{wild}}$		0.917	0.080	0.587–0.988	14.1

TABLE A.3. Detection probability estimates ($\widehat{p_{ih}}$; with standard errors [$\widehat{\text{SEs}}$] in parentheses) for tagged hatchery and wild Atlantic salmon smolts that passed fixed acoustic monitoring sites in 2005 and 2006 (λ = the joint probability of survival through the last reach and detection on any Penobscot Bay receiver).

Parameter	2005 $\widehat{p_{ih}}$ ($\widehat{\text{SE}}$)	2006 $\widehat{p_{ih}}$ ($\widehat{\text{SE}}$)
$p_{2A,\text{hatchery}}$	0.407 (0.165)	1.000
$p_{2A,\text{wild}}$	0.871 (0.060)	1.000
$p_{2B,\text{hatchery}}$	0.562 (0.066)	1.000
$p_{3A,\text{hatchery}}$	0.713 (0.167)	0.899 (0.034)
$p_{3A,\text{wild}}$	0.821 (0.072)	1.000
$p_{3B,\text{hatchery}}$	0.258 (0.055)	1.000
$p_{4A,\text{hatchery}}$		0.876 (0.030)
$p_{4A,\text{wild}}$		1.000
$p_{5A,\text{hatchery}}$		0.974 (0.015)
$p_{5A,\text{wild}}$		1.000
$p_{6A,\text{hatchery}}$	0.243 (0.035)	
$p_{6A,\text{wild}}$	0.105 (0.057)	
$p_{7A,\text{hatchery}}$	0.646 (0.039)	1.000
$p_{7A,\text{wild}}$	0.558 (0.095)	1.000
$p_{8A,\text{hatchery}}$	0.670 (0.045)	1.000
$p_{8A,\text{wild}}$	0.889 (0.074)	1.000
$p_{8C,\text{hatchery}}$	0.583 (0.112)	1.000
$p_{8C,\text{wild}}$	0.705 (0.175)	1.000
$p_{9A,\text{hatchery}}$	0.323 (0.044)	0.977 (0.016)
$p_{9A,\text{wild}}$	0.105 (0.071)	1.000

(*Continued on next page*)

TABLE A.3. Continued.

Parameter	2005 $\widehat{p_{ih}}$ ($\widehat{\text{SE}}$)	2006 $\widehat{p_{ih}}$ ($\widehat{\text{SE}}$)
$p_{9C,\text{hatchery}}$	0.777 (0.098)	1.000
$p_{9C,\text{wild}}$	0.705 (0.175)	1.000
$p_{10C,\text{hatchery}}$	0.777 (0.098)	1.000
$p_{10C,\text{wild}}$	1.000	1.000
$p_{11A,\text{hatchery}}$		0.924 (0.028)
$p_{11A,\text{wild}}$		1.000
$p_{12A,\text{hatchery}}$	0.444 (0.043)	1.000
$p_{12A,\text{wild}}$	0.399 (0.100)	1.000
$p_{13A,\text{hatchery}}$	0.557 (0.043)	1.000
$p_{13A,\text{wild}}$	0.160 (0.074)	1.000
$p_{14A,\text{hatchery}}$	0.911 (0.027)	0.976 (0.016)
$p_{14A,\text{wild}}$	0.955 (0.044)	1.000
$p_{15A,\text{hatchery}}$	0.846 (0.041)	0.950 (0.028)
$p_{15A,\text{wild}}$	1.000	1.000
$\lambda_{\text{hatchery}}$	0.660 (0.047)	0.695 (0.051)
λ_{wild}	0.409 (0.105)	0.818 (0.116)