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Survival of Atlantic salmon *Salmo salar* smolts through a hydropower complex

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This study evaluated Atlantic salmon *Salmo salar* smolt survival through the lower Penobscot River, Maine, U.S.A., and characterized relative differences in proportional use and survival through the main-stem of the river and an alternative migration route, the Stillwater Branch. The work was conducted prior to removal of two main-stem dams and operational changes in hydropower facilities in the Stillwater Branch. Survival and proportional use of migration routes in the lower Penobscot were estimated from multistate (MS) models based on 6 years of acoustic telemetry data from 1669 smolts and 2 years of radio-telemetry data from 190 fish. A small proportion (0·12, 95% c.i. = 0·06–0·25) of smolts used the Stillwater Branch, and mean survival through the two operational dams in this part of the river was relatively high (1·00 and 0·97). Survival at Milford Dam, the dam that will remain in the main-stem of the Penobscot River, was relatively low (0·91), whereas survival through two dams that were removed was relatively high (0·99 and 0·98). Smolt survival could decrease in the Stillwater Branch with the addition of two new powerhouses while continuing to meet fish passage standards. The effects of removing two dams in the main-stem are expected to be negligible for smolt survival based on high survival observed from 2005 to 2012 at those locations. Survival through Milford Dam was been well below current regulatory standards, and thus improvement of passage at this location offers the best opportunity for improving overall smolt survival in the lower river.

Key words: dams; discharge; downstream passage; migration; Penobscot River; restoration.

INTRODUCTION

Despite extensive efforts to restore Atlantic salmon *Salmo salar* L. 1758, in the U.S.A., total adult returns remain low (NRC, 2004; Saunders *et al.*, 2006). Historically low numbers of *S. salar* led to the federal listing of the species in Downeast Maine, U.S.A., waters in 2000 (USFWS & NOAA, 2000), and the Penobscot and Merrymeeting Bay catchments in 2009 (USFWS & NOAA, 2009). The total number of *S. salar* that returned to U.S.A. waters in 2011 was 4167 fish (USASAC, 2012). The majority of these fish (75%) returned to the Penobscot River in Maine. As the largest returning run of *S. salar* in the U.S.A., the Penobscot River population has been one focus of a major restoration effort in recent years. The Penobscot River Restoration Project (PRRP) was initiated in 1999 by hydropower companies, conservation groups, state

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and federal agencies, the Penobscot Indian Nation and the Penobscot River Restoration Trust (PRRT; Day, 2006). One goal of the PRRP is to balance the restoration of sea-run fisheries (11 species) with hydropower production in the river. Pursuant to this goal, the PRRT purchased the two most seaward dams in the Penobscot for removal (Great Works Dam and Veazie Dam) and a third dam (Howland) for decommissioning and construction of a fish bypass (Day, 2006; Federal Energy Regulatory Commission, 2009).

Dams were cited as the primary cause for the decline of *S. salar* in the Penobscot River (NRC, 2004) and they impede both the upstream migration of adult fish and the downstream migration of smolts (Holbrook *et al.*, 2009; Holbrook *et al.*, 2011). Although all dams alter the physical environment of riverine ecosystems, some have more pronounced effects on fish migration than others (Hall *et al.*, 2010). In general, the most seaward dams in heavily impounded systems present comparatively greater disturbances than do upstream dams in terms of system connectivity, total area affected, species richness or relative abundance of individual species (Vannote *et al.*, 1980; Schlosser, 1982; Herbert & Gelwick, 2003; Hall *et al.*, 2010). Furthermore, dams are known to cause mortality to downstream-migrating salmonids through migratory delay and entrapment (Keefer *et al.*, 2012), increased predation (Poe *et al.*, 1991) and physical injury (Mathur *et al.*, 2000).

With the removal of Great Works Dam (2012) and Veazie Dam (2013; see Fig. 1), Milford Dam is now the lowermost barrier to anadromous fish passage in the Penobscot River (Opperman *et al.*, 2011), and is known to be a site of high *S. salar* smolt mortality (Holbrook *et al.*, 2011). It is thought that the majority of downstream-migrating smolts use the main-stem of the Penobscot as opposed to an alternate migration route around Marsh Island, the Stillwater Branch (Shepard, 1991; Holbrook *et al.*, 2011). Therefore, most of these fish must pass Milford Dam before seawater entry, although precise estimates only exist for 2 years of passage data (Holbrook *et al.*, 2011). These attributes have made Milford Dam a focus for research and assessment regarding anadromous fish passage and survival, as well as for future improvements to upstream and downstream fish passage (Opperman *et al.*, 2011). In addition, two operational dams (Stillwater and Orono Dams) in the Stillwater Branch (Fig. 1) are currently undergoing construction of new facilities that will increase power generation and head-pond height through that route (Day, 2006; Opperman *et al.*, 2011). The requirement for downstream passage of *S. salar* smolts is a survival of 96% at each of these dams (National Marine Fisheries Service, 2012). A baseline of knowledge about fish passage through this complex of dams (the Marsh Island hydropower complex) prior to the implementation of restoration efforts will be necessary for assessment of future improvements of fish passage in the lower river, and for determining the combined effects of dam removal and operational changes on the survival of federally endangered *S. salar* smolts during seaward migration in the lower river.

The goals of this study were (1) to estimate proportional use of migratory routes and the apparent survival rates for *S. salar* smolts through the Marsh Island hydropower complex using a combination of acoustic- and radio-telemetry data and (2) to determine the effects of in-river discharge and fish characteristics [fork length (L_F), mass (M) and rearing origin] on path choice and survival through this section of the river. In order to achieve these goals, the first objective of this study was to estimate proportional use of two migratory routes (Penobscot and Stillwater) by *S. salar* smolts and to estimate path-specific survival using 6 years of acoustic telemetry data. The second objective of

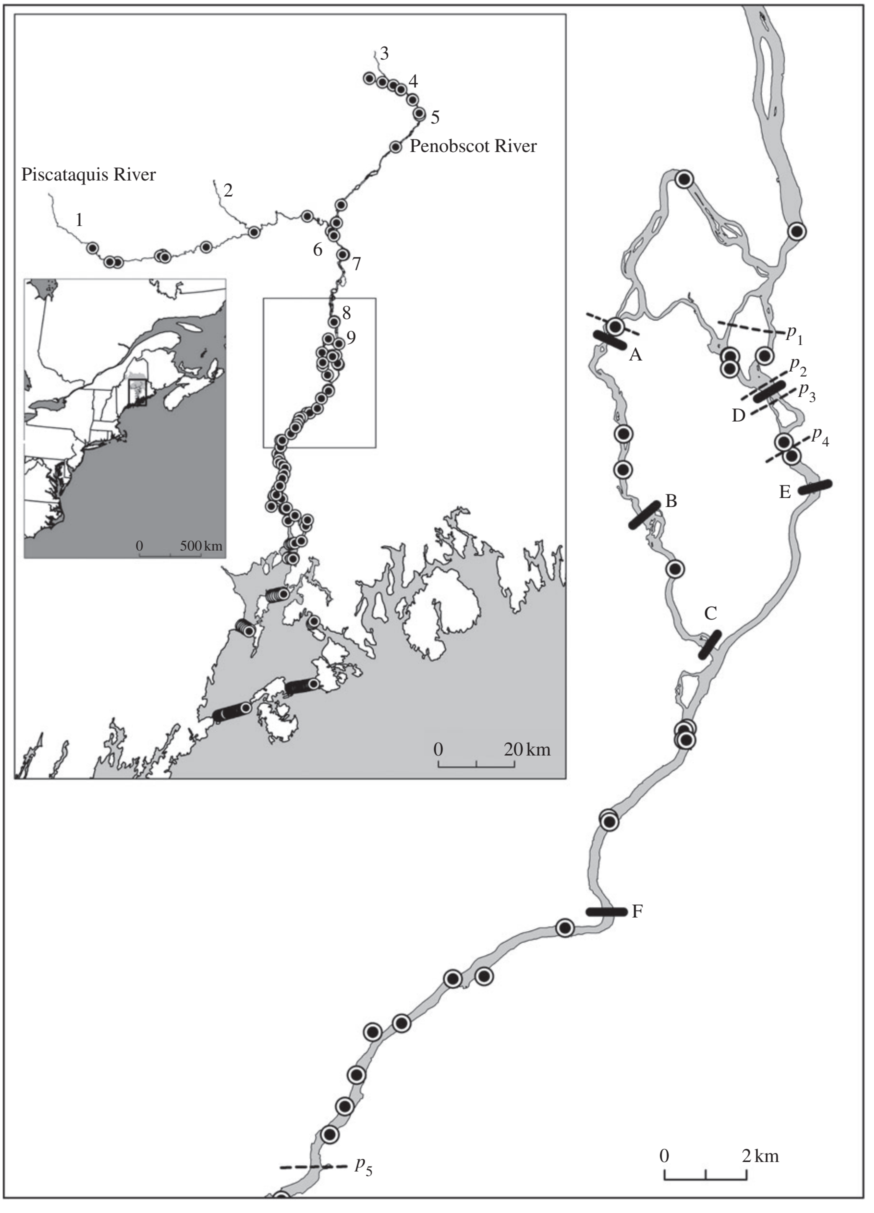


FIG. 1. Map of the Penobscot River catchment showing location in North America in the small inset, coverage of the acoustic telemetry network and release sites for tagged *Salmo salar* smolts (acoustic and radio) in the large inset (1, Abbot; 2, Milo; 3, Weldon head pond; 4, Weldon tailrace; 5, Mattawamkeag; 6, Howland; 7, Passadumkeag; 8, Costigan; 9, Old Town), and locations of dams and coverage of radio receiver network in the large map (A, Gilman Falls; B, Stillwater Dam; C, Orono Dam; D, Milford Dam; E, Great Works Dam; F, Veazie Dam). Release sites for acoustic- and radio-telemetry studies are numbered, and the dams in the lower Penobscot River are represented by solid lines and are lettered. Circles represent locations of acoustic receivers. Dashed lines represent locations of one or more radio receivers used in the radio-telemetry study of passage at Milford Dam, each with multiple antennas. The detection occasions used in radio-telemetry models are indicated by the letter p with subscripts corresponding to detection occasions shown in the radio schematic in Fig. 2.

the study was to estimate path-specific survival through the powerhouse and spillway of Milford Dam using radio-telemetry data from 2010 and 2012. Finally, data from both acoustic- and radio-telemetry are used to characterize variability in selection of migratory route and survival in relation to river discharge. The results of this study will be useful for making decisions about management of downstream fish passage through the complex of dams in the lower Penobscot River and assessing the overall effect of the PRRP on downstream passage of *S. salar* smolts.

MATERIALS AND METHODS

MAIN-STEM DAMS

Milford Dam is located between the City of Old Town and the Town of Milford at river km (rkm) 61 on the main-stem of the Penobscot River in Maine, U.S.A. (Fig. 1). The current site of the hydropower project is also the natural fall line in the Penobscot River (Opperman *et al.*, 2011). Milford Dam is *c*. 6·1 m high, and spans 353 m across the river. The powerhouse at the project, located on the eastern shore of the river, contains six generating turbines, with a maximum authorized generation of *c*. 9 MW. Current fish passage facilities at the site include an eel ladder and a Denil fish way for upstream fish passage, as well as a log sluice between the powerhouse and the spillway for downstream fish passage (Federal Energy Regulatory Commission, 2009). Construction of a new fish elevator for upstream passage is ongoing and is anticipated to be completed in spring 2014. Discharge into the Stillwater Branch is controlled primarily through increases and decreases in head pond level at Milford Dam up to *c*. 430 $m^3 s^{-1}$, at which point the facility can no longer control spill to the main-stem (Federal Energy Regulatory Commission, 2004). Currently, the dam redirects *c*. 30% of total discharge in the lower Penobscot into the Stillwater Branch and under legal agreements involved with the PRRP this can be increased to 40% of total river discharge once new powerhouses in the Stillwater Branch are on-line (Federal Energy Regulatory Commission, 2004).

Great Works Dam (Fig. 1) was removed from the main-stem of the Penobscot River during the summer 2012; just after the final year of this study. The former Great Works project was located at rkm 59, was 6·1 m high and 331 m across (Federal Energy Regulatory Commission, 2009). The powerhouse had 11 horizontal turbines and generating capacity of 7·9 MW. Fish passage facilities at the former Great Works Dam included two Denil fish ways for upstream passage.

Veazie Dam (Fig. 1) was formerly located at rkm 45 in the main-stem of the Penobscot River, and was removed in summer 2013; a year after this study. The project consisted of two powerhouses, one with 15 turbines and another with three turbines, with a maximum generating capacity of 8·4 MW (Federal Energy Regulatory Commission, 2009). The dam was 10 m high and 257 m across, with a slot fish way for upstream passage. Operations at both Great Works and Veazie Dams were subject to periodic shutdowns for regulatory purposes, which had the potential to affect smolt survival during the final 2 years of the study. Although records for turbine shut downs were not publically available to correlate with survival estimates for any of the dams, the PRRT was required to shut down turbines during the smolt migration period 2011–2012 under the conditions of the re-licencing agreement for Great Works and Veazie dams (Federal Energy Regulatory Commission, 2009).

STILLWATER BRANCH DAMS

Two operational hydropower dams will remain in the 16·9 km Stillwater Branch after the PRRP. Stillwater Dam (Fig. 1) is located at rkm 60 on the Stillwater Branch, is 6·7 m high and 524 m across (National Marine Fisheries Service, 2012). The original powerhouse contains four horizontal turbines and has a generating capacity of *c*. 2·0 MW. The additional powerhouse being constructed at the Stillwater project will have three vertical turbines and will add 2·2 MW to the total generating capacity of the Stillwater facility, more than doubling the capacity for power generation. Current fish passage facilities at Stillwater Dam include a downstream bypass discharging into the tail race and two eel passage facilities. No further upstream passage will be constructed at Stillwater under the licence amendment for this facility, although a new downstream bypass facility will replace the existing structure (National Marine Fisheries Service, 2012).

Orono Dam is located in the Town of Orono at rkm 55 on the Stillwater Branch, at the confluence of the Stillwater with the main-stem of the Penobscot River (Fig. 1). The dam is 7·6 m high, and is 358 m across, with a powerhouse containing four turbines that have a total generating capacity of 2·3 MW (National Marine Fisheries Service, 2012). The new powerhouse being constructed at Orono Dam will add three vertical turbines that have total generating capacity of 3·7 MW, more than doubling total capacity of the Orono project. Current fish passage facilities at the Orono project include a downstream fish way and an upstream eel-passage facility. The upgrades to the project will include construction of an additional downstream bypass, as well as a fish trap used to catch upstream-migrating fishes for transport to the main-stem Penobscot (National Marine Fisheries Service, 2012).

ACOUSTIC RECEIVER ARRAY

Prior to the start of the *S. salar* smolt run during each year of this study, stationary acoustic receivers (VR2 and VR2-W; Amirix Vemco Ltd; http://vemco.com/) were deployed in the Penobscot River by the University of Maine, in cooperation with U.S. Geological Survey (USGS) Maine Cooperative Fish and Wildlife Research Unit, and the National Oceanic and Atmospheric Administration (NOAA). All receivers contained omnidirectional hydrophones that scanned continuously at 69 kHz. The number and type of receivers deployed in the Penobscot River catchment varied slightly between years. The number of receivers deployed in the catchment increased through time as new units were purchased and as new release sites were added. The acoustic receiver array used in 2005 and 2006 was described in the study of Holbrook *et al.* (2011). Up to 198 acoustic receivers were deployed in a given year, providing detection coverage from the headwaters of the East Branch Penobscot and Piscataquis Rivers through outer Penobscot Bay for years 2009–2012 (Fig. 1). Despite differences in arrays between years, the configuration and proximity of acoustic receivers in and around the Marsh Island hydropower complex were virtually identical through all years of the acoustic telemetry study. Acoustic receivers deployed in the Penobscot River and in the estuary were moored to cement blocks on the river bottom. Acoustic receivers deployed in the Penobscot Bay were moored *c.* 10 m below the surface of the water. Multiple receivers were deployed where the width of the river exceeded the detection range of acoustic receivers or where obstructions (*e.g.* islands) prevented complete coverage with a single deployment, and detections for all receivers at such locations were pooled as single encounter events for survival analyses.

ACOUSTIC TAGGING AND RELEASES

From 2005 to 2012, 1669 *S. salar* smolts, either wild-reared or from the U.S. Fish and Wildlife Service (USFWS) Green Lake National Fish Hatchery, were acoustically tagged and released by the University of Maine and USGS for studies of in-river movements and survival during downstream smolt migration through the Penobscot River (Table I). Acoustic tagging methods were described in detail by Holbrook *et al.* (2011) and identical procedures were used in all years from 2005 to 2012. Smolts were anaesthetized using a 100 mg l^{-1} solution of MS-222, L_F (mm) and M (g) were measured and fish were placed ventral-side up in a v-shaped saddle. A small (1 cm) incision was made offset from the ventral line and *c.* 1 cm posterior to the pelvic-fin girdle. An acoustic tag was inserted intraperitoneally and the incision was closed with two simple, interrupted knots using 4-0 absorbable vicryl sutures (Ethicon; www.ethicon.com). Model V7-2L (Amirix Vemco Ltd) tags were used in 2005, as well as for wild-origin fish tagged in 2011. Expected battery life of V7-2L tags was 80 days for tags used during 2005, and 69 days for tags used during 2011. In all other years, acoustic transmitters used were model V9-6L (Amirix Vemco Ltd) with expected battery life of 82 days (except during 2006 when battery life of V9-6L transmitters was 80 days). Total time for each surgery was <2 min. *Salmo salar* smolts of wild and hatchery origin were released at up to four

TABLE I. Number, origin, tag type, mean ± S.D. fork length (L_F) and release site of *Salmo salar* tagged and released within the Penobscot River drainage each year of study from 2005 to 2012

Year	Release site	Tag type	Origin	Number released	L_F (mm)
2005	Howland	Acoustic	Hatchery	150	189 ± 11
	Mattawamkeag	Acoustic	Hatchery	40	185 ± 12
	Milo	Acoustic	Hatchery	85	191 ± 11
	Weldon tailrace	Acoustic	Wild	60	178 ± 18
2006	Milo	Acoustic	Hatchery	72	196 ± 11
	Weldon tailrace	Acoustic	Hatchery	146	198 ± 15
	Weldon tailrace	Acoustic	Wild	73	190 ± 11
2009	Milo	Acoustic	Hatchery	100	180 ± 8
	Passadumkeag	Acoustic	Hatchery	100	180 ± 9
2010	Abbot	Acoustic	Wild	75	169 ± 8
	Milo	Acoustic	Hatchery	100	189 ± 11
	Passadumkeag	Acoustic	Hatchery	100	186 ± 11
	Weldon head pond	Acoustic	Wild	74	180 ± 13
	Old Town	Radio	Hatchery	58	198 ± 12
2011	Abbot	Acoustic	Wild	75	146 ± 8
	Milo	Acoustic	Hatchery	100	191 ± 13
	Passadumkeag	Acoustic	Hatchery	100	197 ± 32
	Weldon head pond	Acoustic	Wild	60	162 ± 19
2012	Abbot	Acoustic	Hatchery	74	199 ± 11
	Weldon head pond	Acoustic	Hatchery	85	199 ± 11
	Costigan	Radio	Hatchery	130	201 ± 15
Grand total	All		All	1857	–

different sites in a single year, although the numbers of fish and release sites varied between years (Table I).

RADIO RECEIVER ARRAY

A total of 13 data-logging radio receivers (models SRX400 and SRXDL; Lotek Wireless; www.lotek.com) were used to detect radio-tagged *S. salar* smolts during migration through Milford Dam in 2010 and 2012 (Fig. 1). Individually coded radio transmitters spanning three frequencies were used in order to minimize tag collisions while allowing for an acceptable cycling time on radio receivers. At least two frequencies were used in each release group. Radio receivers were set to scan each of the three frequencies for 3 s on each antenna. This resulted in total cycling times that ranged from 9 s in receivers with one antenna to 36 s in receivers with four antennas. The radio receiver array differed slightly between 2010 and 2012 based on smolt release locations. In 2012, smolts were released further upstream than in 2010; therefore, an extra pair of radio receivers was deployed between the release location and Milford Dam in 2012. The location at which the additional pair of receivers was deployed in 2012 corresponded with the release locations that were used in 2010 (Old Town and p_1; Fig. 1). Multiple receivers, each with multiple antennas, were deployed at each detection site immediately above and below Milford dam [a total of five receivers above the dam (p_2 in Figs 1 and 2) and two below (p_3 in Figs 1 and 3)] to ensure that path choice could be determined. Two receivers were deployed just downstream of the Milford tailrace, each with one antenna (p_4 in Figs 1 and 2). Finally, two receivers were deployed at a private residence downstream in the estuary (p_5 in Fig. 1) to allow for estimation of survival in the tailrace of Milford Dam. Receivers were pooled as a single encounter location where multiple receivers or antennas were used to obtain adequate coverage across the width of the river. Because the release site used in 2012 resulted in the possibility of

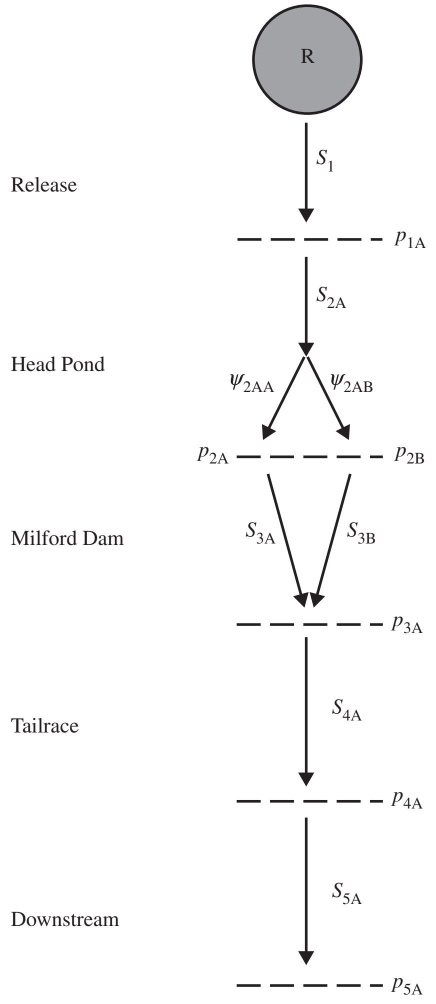


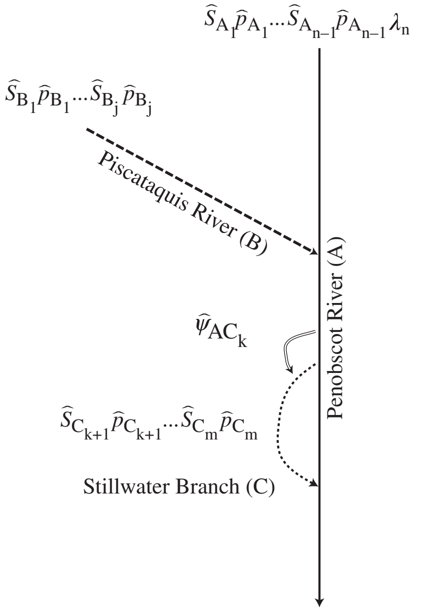
FIG. 2. Schematic representation of multistate survival model used to estimate path choice and path-specific survival of *Salmo salar* smolts through Milford Dam using radio-telemetry data. *R* represents release, $\widehat{p}$ indicates detection probability at each occasion after release, $\widehat{S}$ is survival in each reach and in each state ($\widehat{S}_A$ = main-stem and spillway survival, and = powerhouse survival). Estimates of detection probability ($\widehat{p}_{5A}$) and survival ($\widehat{S}_{5A}$) are confounded during the final interval of the radio-telemetry models, and so λ is the joint probability of survival and detection estimated in the final reach. Ψ, state-transition probabilities for transitions between river and spillway.

fish moving into the Stillwater Branch, and out of the main-stem of the river, a radio receiver was placed below the uppermost dam on the Stillwater Branch (Gilman Falls; Fig. 1) so that these fish ($n = 1$) could be excluded from analysis of passage at Milford Dam.

RADIO TAGGING AND RELEASE

Salmo salar smolts were radio tagged with NTC-3-2 coded nano tags weighing *c*. 0·5 g with 24 cm trailing-whip antenna, 2 s burst rate and 31 day battery life (Lotek Wireless) using a modification of the shielded needle method (Ross & Kleiner, 1982). Fish were anaesthetized

(a)



(b)

		Variable occasions			
Year	Origin	*j*	*k*	*m*	*n*
2005	All	3	7	10	16
2006	All	3	7	10	16
2009	Hatchery	4	8	10	32
2010	Hatchery	5	6	7	25
2010	Wild	9	11	14	31
2011	Hatchery	4	8	10	30
2011	Wild	10	13	17	19
2012	Hatchery	10	13	15	16

FIG. 3. Diagram of the parameters estimated each year in acoustic multistate models of *Salmo salar* smolt survival in the Penobscot River during 2005–2012. (a) The schematic illustrates the three states used to model survival in each year (A = main-stem Penobscot, B = Piscataquis River and C = Stillwater Branch), and includes variables (*j, k, m and n*) that indicate differences in the number of parameters estimated in each year. (b) The table in the diagram contains the value of each variable in each model each year, and can be used to reconstruct annual survival models. As an example, in 2005: survival ($\widehat{S}$) and detection probability ($\widehat{p}$) were estimated for intervals 1–16 (*n*) in state A (main-stem Penobscot), survival and detection probability were estimated for intervals 1–3 (*j*) in state B (Piscataquis), the state-transition probability for movement into the Stillwater ($\widehat{\Psi}_{AC}$) was estimated in interval 7 (*k*), and survival and detection probabilities were estimated in the Stillwater (state C) during intervals 8 ($k+1$) to 10 (*m*).

using a 100 mg l^{-1} solution of MS-222, and L_F (mm) and M (g) were measured prior to surgery (Table I). Smolts were placed ventral-side up in a v-shaped saddle, and a small (0·5 cm) incision was made offset from the ventral line and *c*. 1 cm posterior to the pectoral-fin girdle. Radio tags were tested and the antenna was inserted into a 20 gauge, deflected-tip septum needle. The needle was inserted through the ventral incision and passed from inside the peritoneal cavity through the body wall posterior and dorsal to the pelvic-fin. The needle was removed, leaving only the antenna in the opening through the body wall. The radio tag was gently pushed into the peritoneal cavity and the ventral incision was closed with a single interrupted knot using 4-0 absorbable vicryl sutures (Ethicon). Mean time for radio surgeries was *c*. 1 min.

In 2010, 58 *S. salar* smolts from the USFWS Green Lake National Fish Hatchery were radio tagged to assess passage and survival through Milford Dam. An additional 25 fish were tagged with dummy tags of identical dimensions and held in the Green Lake National Fish Hatchery for 3 weeks to assess tag loss and tagging-related mortality. *Salmo salar* smolts were released on 15 May 2010 *c*. 1 km upstream of Milford Dam (Old Town; Table I and Fig. 1). Half of the fish were stocked from the east bank of the river, and half were stocked from the west bank. In 2012, 130 hatchery-reared *S. salar* smolts were released in four groups over the course of 1 week in order to reduce the risk of not detecting smolts at individual receivers in the array. Smolts were released at a public boat launch on the east bank, *c*. 8 km upstream of Milford Dam (Costigan; Fig. 1) during 22 April 2012 to 28 April 2012 (Table I).

MOVEMENT AND SURVIVAL THROUGH MARSH ISLAND HYDROPOWER COMPLEX

MS Cormack–Jolly–Seber mark–recapture survival models were developed and analysed in programme MARK (White & Burnham, 1999) to estimate the proportional use of the Stillwater Branch and main-stem Penobscot River, as well as path-specific survival rates through each route using acoustic telemetry data. The logit-link function was used to model all parameters in acoustic MS models. While the term survival is used throughout this study for simplicity, these estimates reflect only apparent survival and not true survival of *S. salar* smolts as the only data used in these models were recaptures of fish at each receiver location, and information about whether fish were alive or dead was not included. Although only those estimates of survival relevant to the Marsh Island hydropower complex are reported in this study, these estimates are based on MS models that incorporated detections at acoustic receivers through the entire acoustic array. These whole-system survival models were constructed separately for each year due to differences in the acoustic receiver array between years at locations outside of the Marsh Island hydropower complex. Due to differences in migratory histories of hatchery and wild fish resultant from release locations in the Penobscot and Piscataquis Rivers, migratory route and survival were also modelled separately for hatchery and wild fish within years.

Three states were used in the development of acoustic MS survival models in each year: state 1, the main-stem of the Penobscot River (A) from the uppermost interval to Penobscot Bay; state 2, the Piscataquis River (B); state 3, the Stillwater Branch (C) as an alternative migratory route through the Marsh Island hydropower complex (Fig. 3).

The parameters estimated in the acoustic MS survival models varied each year (Fig. 3). Survival ($\widehat{S}$) and detection probability ($\widehat{p}$) were estimated in the main-stem of the Penobscot from release ($\widehat{S}_{\mathrm{A}_1}\widehat{p}_{\mathrm{A}_1}$) through to interval $n-1$ ($\widehat{S}_{\mathrm{A}_{n-1}}\widehat{p}_{\mathrm{A}_{n-1}}$) each year, and the joint probability of detection and survival (λ) was estimated during interval n each year. Survival and detection probability were estimated in the Piscataquis River each year from release ($\widehat{S}_{\mathrm{B}_1}\widehat{p}_{\mathrm{B}_1}$) to interval j ($\widehat{S}_{\mathrm{B}_j}\widehat{p}_{\mathrm{B}_j}$). The probability of moving into the main-stem of the Penobscot River from the Piscataquis River ($\widehat{\Psi}_{\mathrm{BA}_j}$) given survival in state B during interval j was fixed to 1·00 during interval j each year. The proportion of fish that migrated through the Stillwater Branch each year was estimated as the state-transition probability for movement from the Penobscot River into the Stillwater Branch ($\widehat{\Psi}_{\mathrm{AC}_k}$) during interval k and the probability of remaining in the main-stem ($\widehat{\Psi}_{\mathrm{AA}_k}$) was $1-\widehat{\Psi}_{\mathrm{AC}_k}$. Survival and detection probabilities in the Stillwater Branch were estimated each year from interval $k+1$ ($\widehat{S}_{\mathrm{C}_{k+1}}\widehat{p}_{\mathrm{C}_{k+1}}$) through to interval m ($\widehat{S}_{\mathrm{C}_m}\widehat{p}_{\mathrm{C}_m}$), and the state-transition probability for movement from the Stillwater Branch into the main-stem ($\widehat{\Psi}_{\mathrm{CA}_m}$) given survival during interval m was fixed to 1·00. All parameters not shown (Fig. 3) or described above were fixed to zero during model estimation.

PATH-SPECIFIC SURVIVAL THROUGH MILFORD DAM USING RADIO TELEMETRY

MS survival models were developed and analysed in programme MARK (White & Burnham, 1999) to estimate survival and determine proportional passage through two potential paths through Milford Dam by radio-tagged *S. salar* smolts (the spillway or powerhouse). Due to lack of sample sizes required for estimation of a third transition probability, fish passage through a log sluice on the face of the dam was included in the estimation of passage *via* the spillway. The radio MS models used for assessment of smolt passage through Milford Dam consisted of six detection events (Fig. 2). The logit-link function was used to model all parameters in all models. In both years of the radio-telemetry study, a downstream radio receiver station was established such that *S. salar* smolt survival could be estimated through all intervals of interest (Fig. 2). Detections at each receiver location were used to construct individual encounter histories from release to the Penobscot Estuary for all radio-tagged fish. Passage path through Milford Dam (spillway or powerhouse) was discriminated by fine-tuning radio receivers at various locations at the dam and the probability of using the spillway ($\widehat{\Psi}_{\mathrm{2AA}}$) or powerhouse ($\widehat{\Psi}_{\mathrm{2AB}}$) for passage through the dam was estimated (Fig. 2). Each of the two potential passage paths was used as a state in the individual encounter histories, and state-specific survival ($\widehat{S}$) and detection probability ($\widehat{p}$) were estimated for passage through the spillway ($\widehat{S}_{3A}, \widehat{p}_{2A}$) (Fig. 2) and the powerhouse ($\widehat{S}_{3B}, \widehat{p}_{2B}$) (Fig. 2).

In 2010, the release of radio-tagged smolts coincided with draw-down of the Milford head pond for installation of flashboards downstream (this was serendipitous, not a study design detail). Given the timing and degree of the drawdown, in combination with the narrow timeframe of passage by *S. salar* smolts, all of the radio-tagged fish that successfully passed Milford Dam in 2010 did so by way of the powerhouse; therefore, all state-transition probabilities were fixed to zero and are not included in the parameters reported in model results for 2010. *Salmo salar* smolt releases in 2012 occurred during variable discharge conditions; however, water was being spilled over the top of the dam during the majority of the 2012 smolt season. Because discharge conditions and intervals (*i.e.* distance between receivers) used in survival estimation varied between 2010 and 2012, survival was modelled separately for each year of the radio-telemetry study.

MODEL FIT AND SELECTION

To assess fit of acoustic and radio-MS survival models, an overdispersion parameter, $\widehat{c}$, was estimated for the saturated models each year using programme U-CARE (Choquet *et al.*, 2009). In all cases, models were structured such that $\widehat{c}$ was <2 and adequate model fit was achieved prior to analysis of competing hypotheses. After assessing the fit of each of the full models, candidate models of *S. salar* smolt survival were chosen, *a priori*, to determine the (hypothesized) relative importance of variability in survival ($\widehat{S}$) and detection probabilities ($\widehat{p}$) among river reaches in models for each year. Probability of using each passage path (spillway or powerhouse) in radio-telemetry models and each migratory route (Stillwater or Penobscot) in acoustic models was estimated as an interval-specific state-transition probability ($\widehat{\Psi}$) in each model.

An information-theoretic approach to model selection, based on corrected Akaike information criterion (AIC_c; Burnham & Anderson, 2002), was used to determine whether survival varied between reaches of the river by comparing models with constant survival between reaches to models with reach-specific survival rates. The relative support for candidate models was evaluated as the difference in AIC_c between the best model and each i^{th} model (Δ_i), and the relative probability of each model being the best was represented using AIC_c weights (w_i; Burnham & Anderson, 2002). Models for which $\Delta_i \leq 2{\cdot}0$ were considered to have similar support to the best model in each candidate model set (Burnham & Anderson, 2002).

EFFECT OF DISCHARGE ON MOVEMENT AND SURVIVAL AROUND MARSH ISLAND

Simple linear regression was used to obtain a characterization of the relationship between discharge and mean survival through the reach of the main-stem Penobscot River containing Milford Dam across all years using survival estimates from both radio and acoustic-telemetry studies. Due to constraints on the possible values of survival (0, 1·0), survival estimates were logit-transformed prior to analysis. It was determined that the variances of individual survival estimates did not influence the results of the regression when the results were compared to a weighted least squares regression. Therefore, for the sake of simplicity, the results of ordinary least squares regression are presented graphically on the real scale of the response variable. Mean daily discharge values ($m^3 s^{-1}$) from the USGS gauge upstream of Milford at West Enfield Dam were used to characterize mean discharge during the window of time when smolts passed through Milford Dam each year.

Generalized linear mixed models (GLMMs; Zuur *et al.*, 2007) were used to assess the relationship between discharge and individual migration route (Stillwater Branch or main-stem Penobscot River), with year as a random effect on the intercept in all models using the lme4 package (Bates *et al.*, 2013) in R 3.0.1. (R Development Core Team; www.r-project.org). Only those fish ($n = 759$) for which passage path was known were used for the analysis, and the results of the GLMM were compared to predictions from MS models to assure that predictions were not biased due to the exclusion of detection probability for fish that were omitted due to unknown passage path. The model used a logit-link function and the response was binary (1 = Stillwater, 0 = main-stem Penobscot). Discharge experienced by individual fish prior to choosing a migratory route was characterized using mean of daily discharges at West Enfield Dam from the time a fish was first located 0·5 km upstream of West Enfield Dam until the time that it was first detected at Milford Dam or in the Stillwater Branch (mean travel time = 4 days for smolts). West Enfield Dam is located *c.* 40 km upstream of the Marsh Island hydropower complex, on the main-stem of the Penobscot, immediately upstream from the mouth of the Piscataquis River (Fig. 1). Although it is recognized that proportional distribution of discharge between the Stillwater Branch and main-stem Penobscot around Marsh Island would have provided an ideal measurement of discharge for this analysis, these data were not available and discharge at West Enfield Dam offered the best available information about discharge in the Marsh Island hydropower complex. The ability of the hydropower company to control the distribution of flows at Milford Dam is lost (due to maximum pond height) at discharges of *c.* 430 $m^3 s^{-1}$. At discharges <430 $m^3 s^{-1}$, operations at Milford Dam maintain proportional flow of *c.* 30% of total river discharge to the Stillwater Branch (Federal Energy Regulatory Commission, 2004). It was, therefore, hypothesized that total discharge through the lower river, as measured at West Enfield Dam, would provide a biologically meaningful predictor of the probability that smolts used the Stillwater Branch that could be indirectly related to hydropower operations in the Marsh Island complex and would also provide comparisons in the future following operational changes. To test the null hypothesis that choice of migratory route was not related to discharge, models of migratory route that did or did not include discharge were compared using AIC_c (Burnham & Anderson, 2002). Fish characteristics (rearing history and L_F) that had the potential to influence choice of migratory route were also investigated using model selection. Approximation of the overdispersion parameter $\hat{c}$ for the most parameterized model in the candidate set indicated that the models were not overdispersed $(\hat{c} \leq 1)$; therefore, model selection was not adjusted.

RESULTS

PATH CHOICE AROUND MARSH ISLAND

In all years and for all release groups, the fully reach-dependent parameterizations for survival and detection probability in MS models based on acoustic telemetry data were the most parsimonious, and therefore model selection for these models are not shown. The mean (95% C.I.) annual probabilities of using the Stillwater Branch ($\hat{\Psi}_{AC_j}$ from acoustic MS survival models) ranged from 0·04 (0·01–0·11) to 0·25 (0·13–0·45), with an overall mean of *c.* 0·12 across years (Fig. 4). Individual-based GLMMs of path choice indicated that of the factors hypothesized to affect proportional use of the Stillwater Branch, discharge at West Enfield Dam was most strongly related to use of the Stillwater Branch by individual smolts; it was the only covariate included in all models that had a meaningful amount of support in the candidate model set, and it was the only covariate included in the best model (Table II). Use of the Stillwater Branch increased with discharge within the observed range of discharges during the smolt window during 2005–2012 (Fig. 5 and Table III). Based on observed flows over the 6 years of this study, the overall mean (95% C.I.) probability of using the Stillwater Branch in any given year, according to the GLMM used to model individual migration route, was 0·12 (0·06–0·25) conditional on flow. This conditional mean is identical to the mean probability of using the Stillwater estimated in MS models.

SURVIVAL AROUND MARSH ISLAND

Estimated survival of *S. salar* smolts (from acoustic MS models) varied between reaches and between states during passage through the Marsh Island hydropower

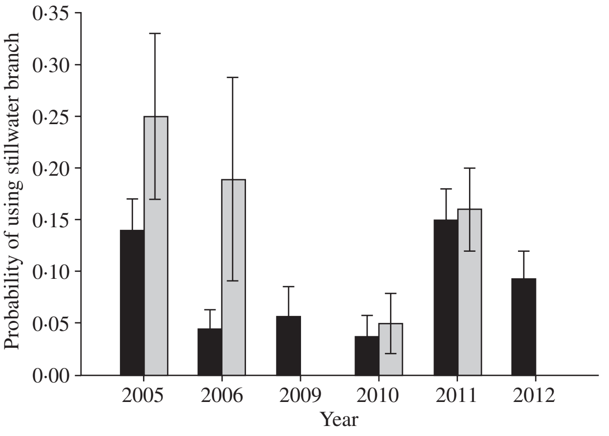


FIG. 4. Annual estimates of the mean ± S.E. probability of *Salmo salar* smolt migration through the Stillwater Branch estimated using acoustic multistate models of smolt movement and survival in the Penobscot River during 6 years from 2005 to 2012 for wild (□) and hatchery (■) smolts.

complex (Fig. 6). Survival through the project generally was higher for smolts that migrated through the Stillwater Branch than for smolts that migrated through the main-stem of the Penobscot River. Acoustic telemetry estimates of mean (95% C.I.) *S. salar* smolt survival through the 1 km reach of the main-stem Penobscot containing Milford Dam ranged from 0·75 (0·51–0·89) to 1·00 (1·00–1·00) during 2005–2012. In contrast, survival km^{-1} through any of the free-flowing (undammed) reaches in the Penobscot River was ≥99% in all years. Survival at the main-stem dams, Veazie (0·99 ± 0·00) and Great Works Dams (0·98 ± 0·02) that were removed was higher than at Milford Dam (0·91 ± 0·02) in all 6 years of this study. Similarly, mean

TABLE II. Model selection statistics for generalized linear mixed models (GLMMs) used to characterize relationships between the probability of *Salmo salar* smolts using the Stillwater Branch for migration and several factors of interest, including rearing history (Origin: hatchery or wild), fork length (L_F) and discharge measured at West Enfield Dam (Discharge). All models included a random effect of year on the intercept, which accounts for one of the estimated parameters in each model. Symbols in table are defined as number of parameters (k), corrected Akaike information criterion (AIC_c), the difference in AIC_c between the best model and the i^{th} model (Δ_i), and the relative probability that the i^{th} model is the best model in the candidate set (w_i)

Model	k	AIC_c	Δ_i	w_i
Discharge	3	567·442	0·000	0·287
Discharge + L_F	4	567·454	0·012	0·286
Discharge + origin	4	567·507	0·065	0·278
Discharge + L_F + origin	5	568·972	1·530	0·134
Origin	3	574·948	7·506	0·007
L_F	3	575·585	8·143	0·005
L_F + origin	4	576·309	8·867	0·003

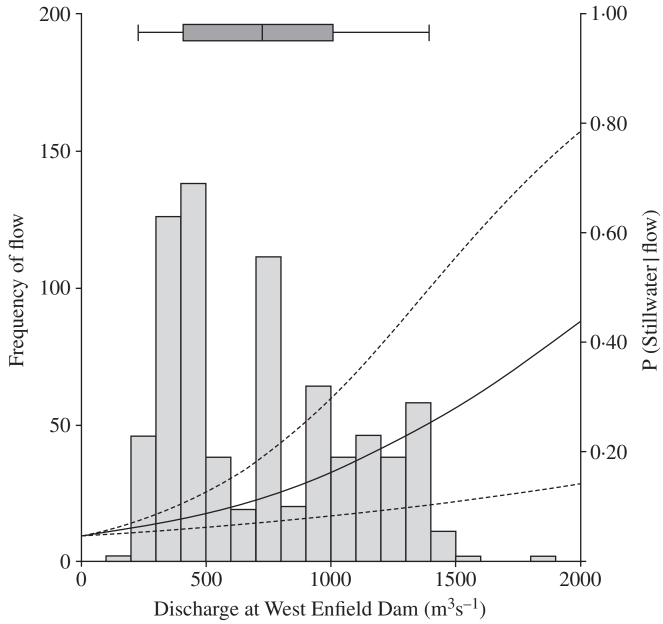


FIG. 5. Frequency of observed mean daily discharge values (▢) from 2005 to 2012 *Salmo salar* smolt runs compared to predicted proportional use of the Stillwater Branch (——) and asymmetric 95% prediction intervals (- - -). The horizontal box plot at the top of the plot indicates median value of observed discharge, the box ends represent the inner quartile for values of observed discharge and the whiskers represent the 95% C.L. of observed discharge values during smolt runs 2005–2012.

survival across years at the two dams in the Stillwater Branch was high at Stillwater (0·97 ± 0·02) and Orono Dams (1·00 ± 0·00).

MOVEMENT AND SURVIVAL THROUGH MILFORD DAM

The most parsimonious models for the 2010 and 2012 radio-telemetry models differed between years and model selection for MS radio-telemetry models are presented with the results (Table IV). No loss of tags or tagging-related mortality was observed in fish that were dummy tagged as part of the 2010 radio-telemetry study.

In 2010, a drawdown of the Milford head pond coincided with the radio-telemetry study such that any smolt passing through Milford Dam must have done so *via* the

TABLE III. Parameter estimates for the model of p(Stillwater Branch) that included all covariates [p(Stillwater Branch), Discharge], showing direction of relations between p(Stillwater Branch) and discharge. Symbols are defined as the logit-scale parameter estimates (β_j), S.E., critical value of the test statistic (z) and the P-value for the test

Parameter	β_j	S.E.	z	P
Intercept	−3·0131295	0·3656585	−8·240	<0·001
Discharge	0·0013813	0·0003941	3·505	<0·001

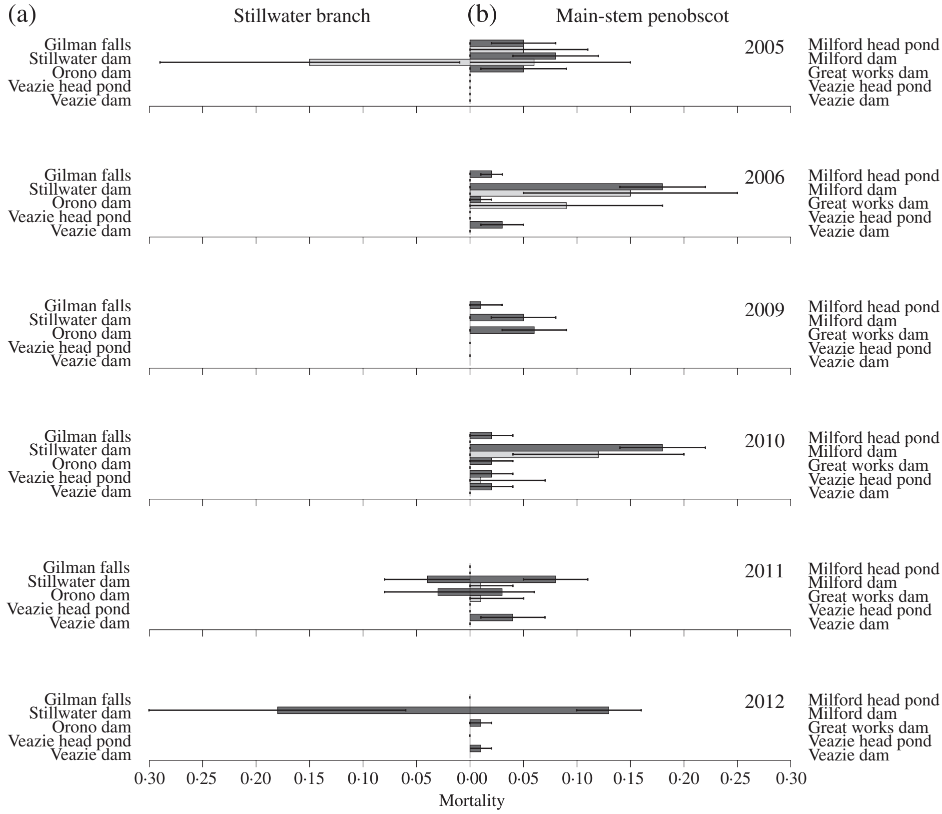


FIG. 6. Reach-specific mortality (calculated as 1 − apparent survival in each reach) of acoustically tagged *Salmo salar* smolts of wild (□) and hatchery (■) origin through the (a) Stillwater Branch and (b) main-stem Penobscot River during passage of the Marsh Island hydropower complex in each year of study from upstream (top of each plot) to downstream (bottom of each plot). Names of the reaches in each migration route are shown to side of plots, and correspond to intervals containing dams in the acoustic array shown in Fig. 1. Mortality during the final two reaches (Veazie Head Pond and Veazie Dam) occurred downstream of the confluence of Stillwater Branch and Penobscot River, and therefore was experienced by all fish, regardless of migration route.

powerhouse. Therefore, estimates of path choice and survival through the spillway were not carried out in 2010, although model selection suggested that survival did vary between reaches of the study area (Table IV). The mean (95% C.I.) survival of *S. salar* smolts through the Milford powerhouse was 0·90 (0·79–0·95) in 2010 according to models based on radio-telemetry locations. In 2012, discharges allowed for estimation of path-specific survival through Milford Dam using MS models based on radio-telemetry locations. The 2012 radio-telemetry study indicated that estimated mean survival of *S. salar* smolts did not differ between the powerhouse (0·88, 95% C.I.: 0·42–0·99) and the spillway (0·88, 95% C.I.: 0·76–0·94; Fig. 7). This finding was corroborated by the fact that the model using state-specific survival rates did not receive a meaningful amount of support in the candidate model set of 2012 radio-telemetry models of smolt survival through Milford Dam (Table IV). The wide confidence intervals for individual estimates of survival through the powerhouse

Table IV. Model selection statistics for the 2010 and 2012 radio-telemetry models of *Salmo salar* smolt survival through Milford Dam. Parameters estimated in the multistate (MS) mark–recapture survival models were survival ($\hat{S}$), detection probability ($\hat{p}$) and state-transition probabilities ($\hat{\Psi}$) for transitions between river and spillway (state A) and the powerhouse (state B) at Milford Dam. Symbols in the table heading are defined as in Table II. Reported number of parameters does not include parameters fixed for maximum likelihood estimation (*e.g.* $\Psi_{3BA} = 0{\cdot}00$ for MS models used in 2012). The (.) next to survival or detection parameters indicates that survival or detection was held constant in the corresponding model

Year	Model	k	AIC$_c$	Δ_i	w_i
2010	$S_{(reach)}p_{(.)}$	6	152·187	0·000	0·854
	$S_{(reach)}p_{(reach)}$	10	155·913	3·725	0·133
	$S_{(.)}p_{(reach)}$	6	160·574	8·386	0·013
	$S_{(.)}p_{(.)}$	2	267·000	114·813	0·000
2012	$S_{(reach)}p_{(state \times reach)}\Psi_{AB(reach)}\Psi_{BA(reach)}$	11	615·538	0·000	0·935
	$S_{(.)}p_{(state \times reach)}\Psi_{AB(reach)}\Psi_{BA(reach)}$	10	621·094	5·557	0·058
	$S_{(reach)}p_{(reach)}\Psi_{AB(reach)}\Psi_{BA(reach)}$	9	626·331	10·793	0·004
	$S_{(state \times reach)}p_{(state \times reach)}\Psi_{AB(reach)}\Psi_{BA(reach)}$	10	628·413	12·876	0·002
	$S_{(state \times reach)}p_{(reach)}\Psi_{AB(reach)}\Psi_{BA(reach)}$	11	630·504	14·967	0·001
	$S_{(.)}p_{(reach)}\Psi_{AB(reach)}\Psi_{BA(reach)}$	7	630·887	15·350	0·000
	$S_{(reach)}p_{(.)}\Psi_{AB(reach)}\Psi_{BA(reach)}$	7	682·472	66·934	0·000
	$S_{(state \times reach)}p_{(.)}\Psi_{AB(reach)}\Psi_{BA(reach)}$	10	688·694	73·156	0·000
	$S_{(.)}p_{(.)}\Psi_{AB(reach)}\Psi_{BA(reach)}$	3	737·870	122·332	0·000

suggest that precisions of the powerhouse survival estimate may have been low owing to the small probability of smolts using that movement path (0·09, 95% C.I.: 0·05–0·16) in 2012.

Discharge experienced by smolts in each year was found to explain a relatively large amount of variation in estimated smolt survival through Milford Dam ($r^2 = 0{\cdot}44$), and discharge had a significant, positive influence on smolt survival (simple linear regression, d.f. = 15, $F_{1,15} = 11{\cdot}89$, $P < 0{\cdot}01$; Fig. 8).

DISCUSSION

Passage through the Marsh Island hydropower complex represents a critical transition during downstream migration of the federally endangered *S. salar* population in the Penobscot River. This hydropower complex represents the final set of physical barriers to downstream migration in the Penobscot River. To reach the free-flowing portion of the river (and eventually the estuary), all of the out-migrating smolts in this system must pass either through Milford Dam on the east side of Marsh Island by using the main-stem Penobscot River or through the west side using the Stillwater Branch and passing through two other operational dams (Stillwater Dam and Orono Dam). This study provides a baseline of information about fish passage through the Marsh Island hydropower project before anticipated changes to discharge around the island, installation of new powerhouses at Stillwater and Orono Dams and installation of new downstream passage facilities at each of those facilities.

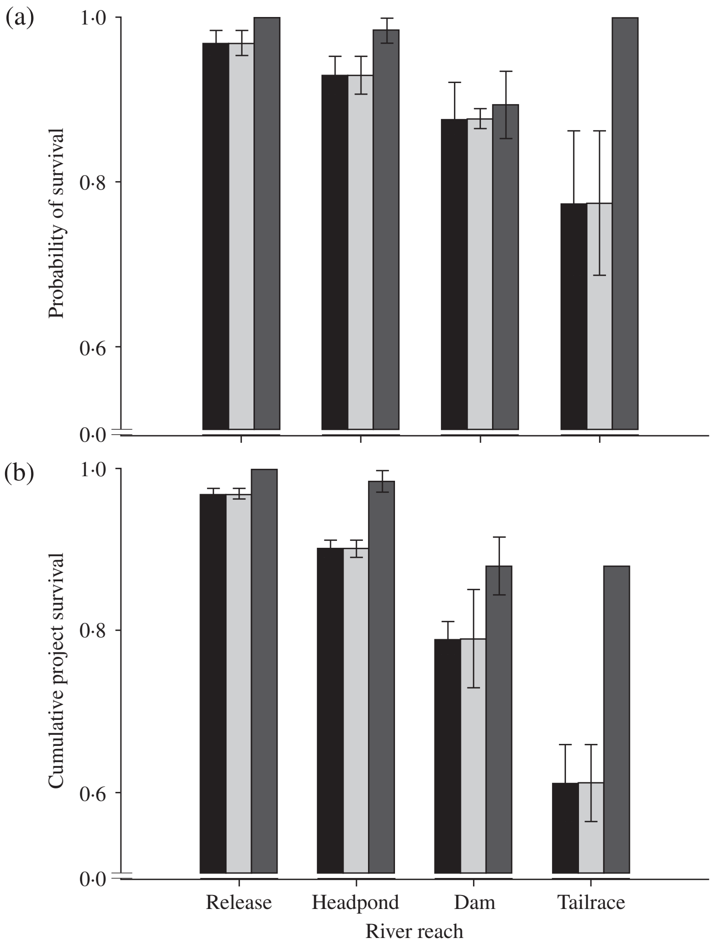


FIG. 7. (a) Reach-specific and (b) cumulative survival of radio-tagged *Salmo salar* smolts through the Milford Dam powerhouse and spillway during 2010 and 2012 radio-telemetry studies. Model selection suggested that there was no difference between survival through the powerhouse and spillway in 2012, as is indicated by the high degree of overlap between the two estimates. ■, survival through spillway in 2012; □, survival through the powerhouse route during 2012; ■, survival through the powerhouse path in 2010.

MOVEMENT AND SURVIVAL THROUGH THE MAIN-STEM PENOBSCOT

Milford Dam represents a potential impediment to restoring effective downstream passage of *S. salar* in the main-stem of the Penobscot River. It also offers the greatest opportunity for improvement of smolt passage in the lower river. By virtue of its location in the catchment (the lowest remaining dam in the main-stem), Milford Dam affects the success of diadromous fish migrations more than many of the other dams in the system. A high percentage (75–94%) of the total of number of migrating *S. salar* smolts in the Penobscot catchment passes Milford Dam each year. Smolt survival through Milford Dam averaged 91% over the 6 years of this study. Survival at Milford Dam is among the lowest of dams in the system (Holbrook *et al.*, 2011). Survival past

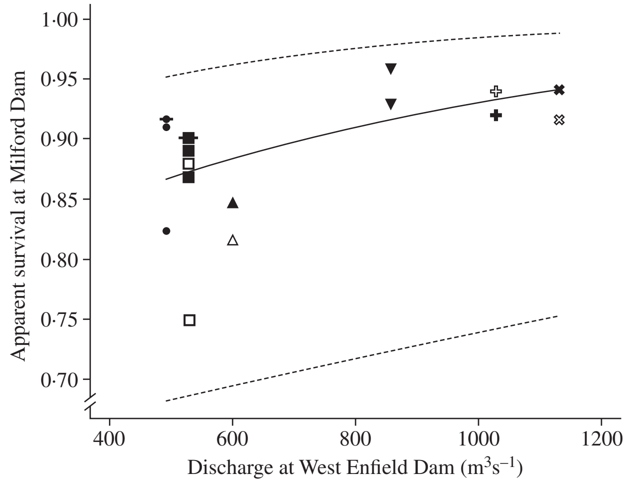


FIG. 8. Simple linear regression used to characterize the relationship between mean daily discharge at West Enfield Dam during the smolt run for each year and estimated annual probabilities of *Salmo salar* smolt survival during passage of Milford Dam by each release cohort of acoustic- and radio-tagged fish. A logit transformation was used on the response in the analysis and as such the *y*-axis is labelled with probabilities but is scaled on the logit. Symbols represent survival estimates from 2005 (▼), 2006 (✖), 2009 (▲), 2010 (■), 2011 (✚) and 2012 (•). Within each year, open symbols correspond to survival estimates for wild smolts and closed symbols are for hatchery-reared smolts. Radio-telemetry estimates in 2010 and 2012 are indicated by strike-through.

this dam is also lower than the combined effects of dams in the alternative migration route (the Stillwater Branch in 2005–2012) through the Marsh Island hydropower complex (this study). Estimated survival through Milford Dam is also low relative to salmonid smolt survival in larger dams with greater generating capacity throughout Pacific Coast systems such as the Columbia River (Ferguson *et al.*, 2007; Skalski *et al.*, 2009). Taken together, these facts illustrate that Milford Dam is the most limiting impediment to *S. salar* smolt migrations in the lower 100 km of the Penobscot River. Furthermore, if passage at Milford Dam is not improved, then the new regulation for passage at this dam (96%) will not be met in the future.

Smolt survival through Milford Dam was estimated under a wide range of discharges during the 6 years of this study, and survival through the dam was found to be positively related to discharge experienced by fish during the smolt run each year. This observation is consistent with observations on other systems in which higher survival is observed past impoundments under higher flow conditions (Connor *et al.*, 2003; Smith *et al.*, 2003). These findings indicate that there may be some potential for regulation of upstream discharge at dams in the upper Penobscot River to be useful as a tool for managers to improve downstream passage success of *S. salar* smolts in the lower river (Connor *et al.*, 2003). For example, by increasing discharge at regulated dams upstream of those examined in this study during peak migration, smolt survival might be improved at Milford Dam through one or more mechanisms.

While path choice through dams can often influence survival, it is notable that there did not appear to be any differences in path-specific estimates of survival between smolts that used the powerhouse or the spillway at Milford Dam. The probabilities of survival through the powerhouse (88%) and the spillway (88%) were strikingly similar, and they agreed well with the annual survival estimated for acoustically tagged smolts through Milford Dam (91%). This suggests that the mechanism resulting in increased survival during high discharge is not likely to be related to passage path (powerhouse or spillway) through Milford Dam, and could potentially be a result of decreased passage time (Smith *et al.*, 2003) and thus reduced exposure to physical injury at dam structures and predators above and below the dam (Venditti *et al.*, 2000; Antalos *et al.*, 2005) during high-discharge events (Raymond, 1979). Similarly, mortality experienced by smolts at Great Works and Veazie Dams did not appear to be directly related to turbine passage because mortality during 2005–2010 at these facilities was similar to mortality during years in which turbines were shut down during the smolt run (2011 and 2012).

In future assessments of the results of the PRRP, it is important to understand and differentiate between the acute effects of management actions on individual species and the integrated effects of the project as a whole. The benefits of conservation efforts in the Penobscot River are likely to be species-specific and responses to restoration efforts will also be specific to life-history stages for any species. The removal of Great Works and Veazie Dams is expected to improve upstream passage of adult *S. salar* (Holbrook *et al.*, 2009; National Marine Fisheries Service, 2012) and will increase access to nearly 100% of historical habitat for other species such as Atlantic sturgeon *Acipenser oxyrinchus* Mitchill 1815, shortnose sturgeon *Acipenser brevirostrum* leSueur1818, Atlantic tomcod *Microgadus tomcod* (Walbaum 1792) and striped bass *Morone saxatilis* (Walbaum 1792) (Trinko Lake *et al.*, 2012). Thus, restoration efforts in the Penobscot River are expected to provide benefits to adult *S. salar* in addition to various life-history stages of several other species. The results of this study, however, suggest that the benefits afforded to *S. salar* smolts through the PRRP will be minimal in the lower main-stem Penobscot because estimated smolt survival at the two dams that were removed in the main-stem, Great Works Dam (99%) and Veazie Dam (98%) was already high prior to the removal of those dams during the period studied. Rather for smolts using the main-stem of the river, improved passage will depend largely upon anticipated improvements to downstream passage at Milford Dam.

MOVEMENT AND SURVIVAL IN THE STILLWATER BRANCH

Although only 6–25% of fish uses the Stillwater Branch, survival through this migratory route historically has been high relative to survival through the main-stem Penobscot River around Marsh Island. In most years, survival was near 100% at Orono and Stillwater Dams prior to PRRP actions. The estimated survival of 1·00 at the Orono facility in all years indicates that there may have been some difficulty in estimating survival at this dam due to the small number of fish using the Stillwater Branch; however; inspection of empirical relocation data at sites above and below the dam also suggest that survival was near 1·00 at this facility in all years. Even estimates of minimum survival based on empirical data (0·97) that ignore detection probability suggest that the rate of survival km^{-1} (0·99 km^{-1}) was indistinguishable from survival in free-flowing reaches of the river (0·99 km^{-1}; Holbrook *et al.*, 2011). In all years of this study but one, mean passage success at each dam in the Stillwater Branch was higher than the minimum standards for passage (96%) that will be required under the species protection plans for the two dams (National Marine Fisheries Service, 2012). If downstream passage success through the Stillwater Branch is reduced below historically high survival rates by the addition of generating capacity, the net result of the restoration project for *S. salar* smolts will be an overall reduction in survival through the Stillwater Branch, even if performance standards for downstream passage are met. This is because the criteria of 96% survival could result in a cumulative survival of 92% through the Stillwater Branch. Based on historically high (and therefore difficult to estimate) survival in the Stillwater, combined with the small numbers of fish that use the migratory route each year, studies that stock tagged fish directly in the Stillwater may provide the most useful method for assessing changes in passage success at these dams.

Proportional use of the Stillwater Branch by out-migrating smolts was variable during the 6 years of this study, and as many as 25% of migrating smolts used this route each year. Operational and structural changes at Stillwater and Orono Dams in the Stillwater Branch increase total energy production from 4·3 to 10·2 MW, more than doubling the capacity of these dams over the pre-restoration configuration. Legal provisions exist that will allow for modest increases to discharge in the Stillwater Branch from the current level of 30% of upstream (main-stem) discharge to 40% of upstream discharge (Federal Energy Regulatory Commission, 2004). While the proportional use of the Stillwater Branch by smolts is clearly related to bulk flow in the lower river (Fig. 5), the importance of the proportional distribution of flows between the main-stem and the Stillwater Branch in this relationship remains unclear. In the future, data about relative distributions of flow through each branch of the lower river could provide invaluable information about effects of management on smolt passage.

The effects of operational and structural changes in the Stillwater Branch Dams have the potential to affect smolt survival in the lower river in two ways. First, if discharge through the Stillwater Branch is increased, it is hypothesized that a greater proportion of migrating smolts will use this migration route. Second, with increased generation and number of turbines, it is hypothesized that Stillwater Branch smolt survival could decrease below historic rates, especially at Orono Dam where mean annual survival was near 100% during all 6 years of this study. Thus, as in the main-stem of the Penobscot River, it seems likely that there will be no net gain in smolt survival through the Stillwater Branch through the actions of the PRRP. In the future, monitoring changes in discharge in the Stillwater Branch, concurrent with smolt survival, will be imperative for evaluating the success of the restoration project with respect to *S. salar* smolts.

UNCERTAINTY IN RESTORATION

Predicting the influence of large-scale conservation efforts for any given species involves some understanding of the uncertainty surrounding expected results (Simenstad *et al.*, 2006; Millar *et al.*, 2007). Despite the utility of basin-scale restoration as a conservation tool (Opperman *et al.*, 2011), the results of this study indicate that the individual effects of specific dams have important, site-specific and species-specific consequences for restoration of downstream fish passage (improvements in fish survival, in this case) within large-scale conservation projects. This demonstrates the importance of monitoring individual sites for adaptive management and governance within basin-wide restoration projects (Gunderson & Light, 2006; Opperman *et al.*, 2011; Trinko Lake *et al.*, 2012). In the Penobscot River, management agencies will have a good, working knowledge of the baseline conditions for survival of smolts by which progress can be measured. Few systems have such an unambiguous quantification of both the sites and magnitudes of loss during downstream migration.

Continued monitoring of passage through the hydropower complex in the lower river will provide the ability to assess management strategies and hydropower operations through the complex. Importantly, uncertainty in the effectiveness of downstream passage facilities and proportional discharge through the Marsh Island hydropower complex strongly suggests that monitoring will be fundamental for understanding biological changes in the river in response to ongoing changes in dam operation, and ultimately for determining the effects of the PRRP on the success of *S. salar* smolt passage in the lower Penobscot River.

Even in natural systems, the transition into the lower river and estuary of coastal systems is known to be a period of high mortality for *S. salar* smolts, owing to high rates of predation (Blackwell *et al.*, 1997; Kocik *et al.*, 2009) and increased susceptibility to both physical and physiological stressors (McCormick *et al.*, 1998). The mortality experienced during this transition can be exacerbated owing to the direct and indirect effects of dams such as disorientation, migratory delays (Mathur *et al.*, 2000; Keefer *et al.*, 2012), increased exposure to predators (Poe *et al.*, 1991; Blackwell & Juanes, 1998) and physical injury (Stier & Kynard, 1986; Zydlewski *et al.*, 2010) caused during dam passage.

This study only examined acute mortality at dams in the lower Penobscot. It is possible that smolts experiencing different conditions through the two migration routes in the lower river also express different responses to the stressors encountered during estuary migration and seawater entry. Fish passing dams that have increased rates of mortality may also experience elevated rates of delayed mortality downstream (Schreck *et al.*, 2006). In the future, these considerations may become increasingly important in determining the overall effects of changes in the main-stem of the Penobscot River and the Stillwater Branch, and may hold previously unrecognized benefits for improvement of downstream migration of *S. salar* smolts.

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