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ARTICLE

Downstream Migration and Multiple Dam Passage by Atlantic Salmon Smolts

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Abstract
The purpose of this study was to investigate behavior and survival of radio-tagged wild and hatchery-reared landlocked Atlantic Salmon *Salmo salar* smolts as they migrated past three hydropower dams equipped with fish bypass solutions in the Winooski River, Vermont. Among hatchery-reared smolts, those released early were more likely to initiate migration and did so after less delay than those released late. Once migration was initiated, however, the late-released hatchery smolts migrated at greater speeds. Throughout the river system, hatchery-reared fish performed similarly to wild fish. Dam passage rates varied between the three dams and was highest at the dam where unusually high spill levels occurred throughout the study period. Of the 50 fish that did migrate downstream, only 10% managed to reach the lake. Migration success was low despite the presence of bypass solutions, underscoring the need for evaluations of remedial measures; simply constructing a fishway is not synonymous with providing fish passage.

Dams in rivers hinder fish migration and reduce connectivity between habitats; this causes fragmentation and sometimes even local extinction of migratory species (Jonsson et al. 1999). For migrating fish, dam passage is associated with both direct and

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delayed mortality (Muir et al. 2001; Ferguson 2005; Ferguson et al. 2006). Delays at hydropower dams also increase susceptibility to predation, energy expenditure, and migration duration and are likely an important cause of reduced migratory success in impounded rivers (McCormick et al. 1999; Muir et al. 2006; Kraabøl et al. 2009). In addition, the accumulated effect of multiple dam passage may result in very low migration success (Norrgård et al. 2012; Brown et al. 2013). Because of this, remedial measures involving fish passage solutions are often deployed to reduce the negative effects of dams (Schilt 2007).

The need for fishways at migration obstacles has been acknowledged for hundreds of years (Montgomery 2004; Waldman 2013). Increased spill levels and other fish passage solutions are used to mitigate the negative effects of hydropower dams on downstream-migrating fish (Noonan et al. 2012; Calles et al. 2013; Adams et al. 2014). Relatively few downstream passage solutions have been evaluated. Because of this, there is a pressing need for evaluating the function of these fish passage solutions, in particular in relation to fish behavior (Castro-Santos et al. 2009; Vowles et al. 2014; Arenas et al. 2015).

Atlantic Salmon *Salmo salar* typically migrate from riverine nursery areas to feeding areas at sea or in large lakes and then back to the river to spawn (Jonsson and Jonsson 2011). Before leaving the river, the juvenile fish become smolts through a series of behavioral, physiological, and morphological changes that adapt them to entry into the marine or lake environment (McCormick et al. 1998). Typically the smolts migrate downstream in spring, with the parr–smolt transformation (“smoltification”) governed by the combined effects of photoperiod and temperature. The onset of migration is primarily triggered by temperature but may in some cases also involve river discharge (Hesthagen and Garnås 1986; McCormick et al. 1998; Whalen et al. 1999; Jonsson and Jonsson 2011). The smolt status of the fish is temporally constrained and loss of smolt characters, including the migratory urge and salinity tolerance, may occur if the fish are delayed or prevented from exiting the river (McCormick et al. 1998).

Releases of hatchery-reared salmonids are widely used to increase harvest, mitigate habitat losses, and otherwise supplement local populations across the range of Atlantic Salmon (Brannon et al. 2004; McClure et al. 2008; Brown et al. 2013). Hatchery environments, however, differ from the natural river in many aspects (e.g., lack of predators, lower mortality, lower structural and hydraulic complexity) resulting in differences in behavior and physiology between wild and hatchery smolts. Hatchery smolts have, for example, been observed to have inferior swimming performance (Pedersen et al. 2008), weaker antipredator response (Jackson et al. 2011), lower in-river migration survival (Aarestrup and Koed 2003), and lower migration speed (Hansen et al. 1984) than wild smolts. One aspect that might affect the behavior, survival, and migration success of released salmonid smolts is the timing of release (Nettles and Gloss 1987; Karppinen et al. 2013). In nature, the timing of migration for wild smolts is assumed to be adapted to local environmental conditions (Antonsson and Gudjonsson 2002). For hatchery smolts, to achieve good migration performance and survival, releases need to be timed to match fish physiology with environmental conditions.

The aim of this study was to quantify the migratory behavior and dam passage performance of both wild and hatchery Atlantic Salmon smolts in the Winooski River, a tributary of Lake Champlain. Lake Champlain and its tributaries historically supported large numbers of landlocked Atlantic Salmon (Webster 1982). Although locally extirpated in the 19th century (Edmunds 1874; Watson 1876; Marsden and Langdon 2012), efforts to reestablish Atlantic Salmon have been ongoing since the 1960s. As part of the restoration plan, fry and smolts are stocked in the Winooski River, where three hydropower dams, equipped with fish bypasses for downstream-migrating fish, separate available nursery areas from the lake (Marsden and Langdon 2012; Chipman et al. 2013). In this study, we used radiotelemetry to study the behavior and survival of Atlantic Salmon smolts during May and June 2014. We tested for the effects of release and tagging time on initiation of migration, migration speed, and survival for wild and hatchery reared smolts. We quantified the effect of hydropower dams on passage rates (i.e., proportion passing per unit time), postpassage delays, and migration survival. We also described the accumulated migratory success for fish passing multiple bypass-equipped hydropower dams.

METHODS

Study area and population.—The Winooski River has a mean annual discharge of 67 m^3/s. Winooski Dam, Gorge Dam, and Essex Dam separate the current Atlantic Salmon nursery and spawning habitats in the Huntington River from Lake Champlain (Figures 1, 2; Table 1). Upstream-migrating spawners are caught at Winooski Dam and transported

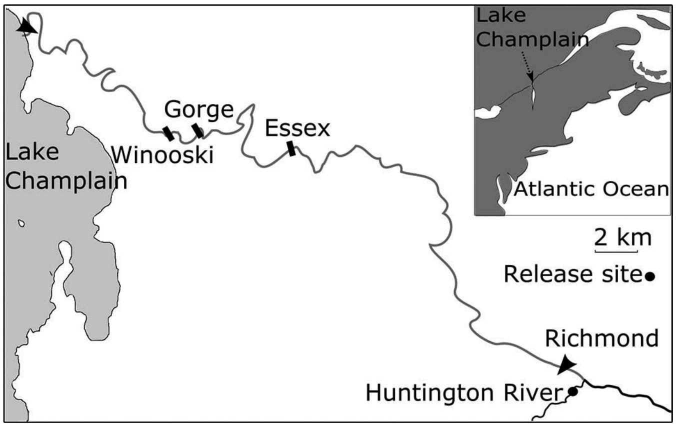

FIGURE 1. Map of the Winooski River with hydropower dams Essex (river kilometer [rkm] 29, measured from the river mouth at Lake Champlain), Gorge (rkm 19), and Winooski (rkm 17) denoted as black bars. The automatic receiver stations at Richmond (rkm 50) and by the mouth (rkm 0) are shown as arrows, and the release site (rkm 56) in the tributary Huntington River is shown as a black circle.

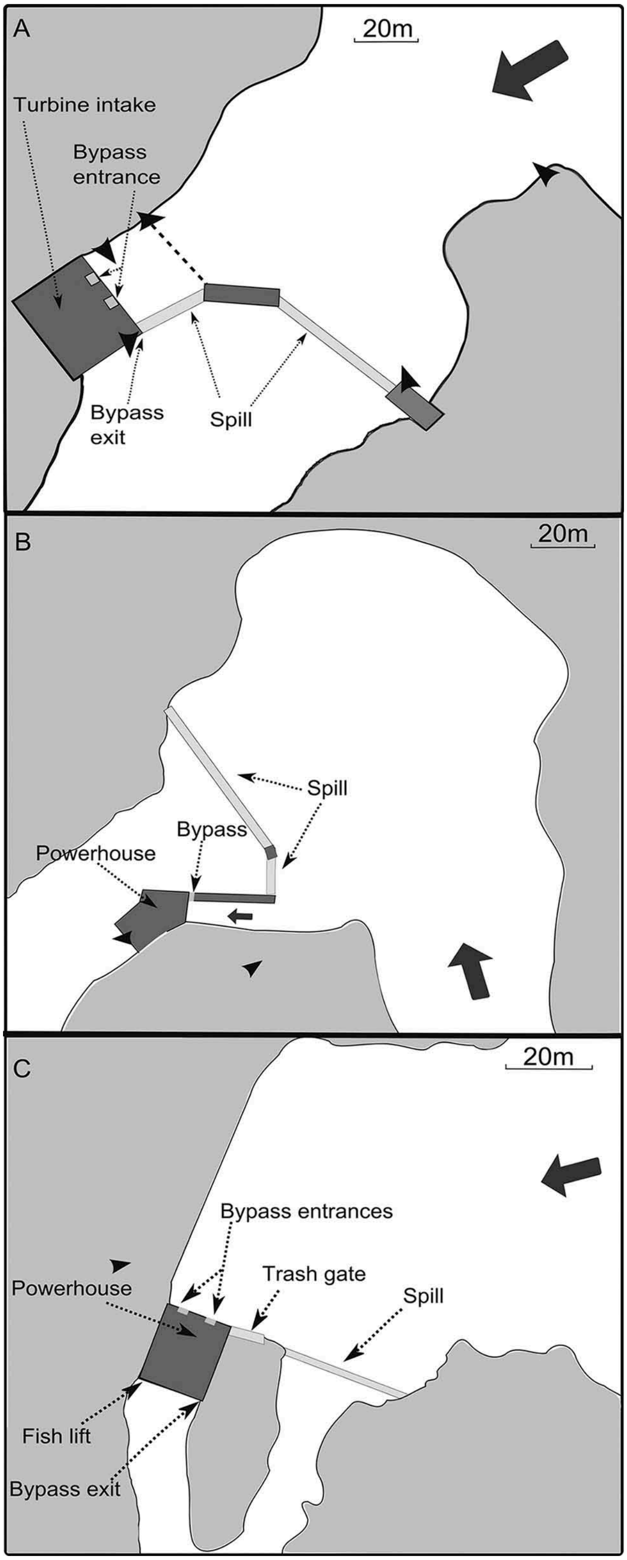

FIGURE 2. Maps of **(A)** Essex, **(B)** Gorge, and **(C)** Winooski hydropower dams, showing the turbine intake or powerhouse, the bypass entrances, and the spill gates. Yagi antennas are displayed as black triangles. In addition, dropper antennas were placed in the turbine intakes and in the bypass to determine the passage route at Essex Dam.

upstream, past the three dams, and released upstream of Essex Dam. Bypasses are installed at all three dams for downstream-migrating smolts and postspawners. In addition, "esthetic spill" is provided at Gorge Dam (≥1.4 m^3/s) and Winooski Dam (≥4.8 m^3/s).

Essex Dam operates as a daily peaking facility, whereas Gorge Dam and Winooski Dam operate in tandem with Essex Dam as run-of-the-river facilities (Table 1). At all three dams the turbine intakes are protected by an intake rack with 25-mm spacing. At Essex Dam, two bypass entrances (designed discharge = 2.8 m^3/s) are located in the upper portion of the intake racks. Here the racks extend to a depth of 3 m, with no physical structures separating the fish from the intake tubes below this point. During the study, only the easternmost bypass entrance was open (estimated discharge = 1.4 m^3/s) as the other entrance was closed due to problems with debris clogging. At Gorge Dam, a single bypass entrance (1.4–1.7 m^3/s) is located next to and perpendicular to the intake rack. At Winooski Dam, two bypass entrances located in the upper portion of the intake racks typically pass 2% of the total river discharge. Water not used in energy production is spilled via overflow spillways (Figure 2; Table 1). During the study period mean total discharge in the river was 63 m^3/s (SD = 36 m^3/s, range = 16–197 m^3/s). Spill discharge in relation to total discharge was 20% at Essex Dam, 79% at Gorge Dam, and 15% at Winooski Dam. (Figures 2, 3; Green Mountain Power, Essex, Vermont, and Burlington Electric Department, Burlington, Vermont, personal communication).

Tagging.—Fry-stocked (i.e., naturally reared, from here on we call these "wild") and hatchery-reared smolts were all tagged and released in the Huntington River about 500 m from its confluence with the Winooski River (Figure 1). Hatchery smolts were reared for 1 year at ambient temperatures in the Dwight D. Eisenhower National Fish Hatchery (U.S. Fish and Wildlife Service, North Chittenden, Vermont) and transported to the Huntington River on the day of tagging. Wild smolts were caught in a rotary screw trap located just upstream of the release site and tagged within 1 d of capture (except for one fish that was held for 2 d before tagging). The smolts were surgically implanted with coded radio transmitters (7.8 mm × 6.7 mm × 17.0 mm, 1.35 g; Sigma Eight, Newmarket, Ontario). The transmitters weighed on average 2.8% (range = 1.3–6.0%) of the fish's body mass, which is considered an acceptable percentage (Brown et al. 1999; Newton et al. 2016). Before tagging, fish were anaesthetized with MS-222 (tricaine methanesulfonate). Transmitters were placed in the body cavity through an incision made on the ventral side of fish. The transmitter antenna was made to exit the body cavity through a separate small opening posterior to the incision and trailed back along the body of the fish. The incision was closed by suturing. A continuous flow of water was maintained over the gills of the fish during the whole procedure, shifting from water containing anesthesia to fresh river water towards the end of

TABLE 1. Hydropower dams separating current Atlantic Salmon nursery and spawning habitats in the Huntington River from Lake Champlain. Measurements of capacity, turbine type, dam head (Google Earth; Green Mountain Power), required spill, and relative spill (mean spill discharge in relation to total discharge) are given for each dam during the study period.

		Hydropower generation			Spill	
Dam	rkm	Capacity (m^3/s)	Turbine type	Head (m)	Required (m^3/s)	Relative (%)
Essex	29	67	Francis	20	0.0	20
Gorge	19	48	Norcan variable pitch	8	1.4	79
Winooski	17	85	Kaplan (Sulzer-Bevel)	12	4.8	15

the surgery (Liedtke and Rub 2012). The whole procedure lasted approximately 10 min. After tagging, fish were acclimatized in a cage in the river for 1 h before being released. Posttagging holding time was minimized to reduce the negative effects of confinement (Jepsen et al. 2002; Portz et al. 2006). All fish were released between 0915 and 1430 hours.

Eighty-one smolts of wild (n = 21, two groups) and hatchery origin (n = 60, three groups) were tagged and released in the Huntington River in May and June 2014. The hatchery fish were tagged and released on May 6 (n = 14), May 12 (n = 20), and May 15 (n = 26), whereas wild fish were tagged as they were caught and divided into an early (May 8–21; n = 13) and a late (June 2–5; n = 8) group based on tagging dates (Figure 2). The mean ± SD fork length of the radio-tagged smolts was 169 ± 16 mm (range = 127–220 mm) and hatchery fish were on average 17 mm larger than wild fish (Wilcoxon–Mann–Whitney: $P < 0.01$; Figure 4).

Stationary receivers and manual tracking.—Stationary automatic receivers (Model Orion; Sigma Eight) were used to track fish movements. The most upstream receiver, with a six-element Yagi antenna, was placed by the Winooski River in the town of Richmond, 6 km downstream of the release site. Arrays of receivers with six-element Yagi antennas were also placed upstream and downstream of the three dams. In addition, "dropper" antennas (whip antennas made of stripped lengths of coaxial cable) were placed in the turbine intakes and in the bypass at Essex Dam. This configuration allowed us to track arrival and passage at all three dams and route selection at Essex Dam (Evans and Stevenson 2012). Two receivers with six-element Yagi antennas were placed by the mouth of the Winooski River to register arrival to the lake. Fish that did not arrive at the upper dam were manually tracked with handheld antennas and receivers (Model SRX 400; Lotek Wireless, Newmarket, Ontario) in the upper parts of the study area between Essex Dam and an upstream barrier to movement in the Huntington River. Detection efficiency was estimated for each site as $\text{Detected}_{\text{Common}} \times (\text{Detected}_{\text{DownstreamArray}} + \text{Detected}_{\text{Common}})^{-1}$, where $\text{Detected}_{\text{Common}}$ is fish detected at a given site and at the next array downstream and $\text{Detected}_{\text{DownstreamArray}}$ is fish detected only at the downstream array (Zydlewski et al. 2006).

Physiological sampling.—To determine and compare the migratory state of hatchery and wild smolts, blood and gill samples were taken in the hatchery and in the wild to measure gill Na^+,K^+-ATPase (enzyme number 3.6.1.36; IUBMB 1992) activity and plasma thyroid hormones, both of which increase during the normal smolt development of landlocked Atlantic Salmon (Nilsen et al. 2003). Smolts were anesthetized with MS-222 (100 mg/L; pH 7.0), and blood was collected from the caudal vasculature in heparinized 1-mL syringes and centrifuged at 3,200 × g for 5 min at 4°C. Plasma was removed and stored at –80°C for later analyses. Gill biopsies (four to six primary filaments) were cut from the first or second gill arch and placed into 100-L ice-cold SEI (250 mmol/L sucrose, 10 mmol/L Na_2EDTA, and 50 mmol/L imidazole; pH 7.3) and stored at −80°C for later analysis.

Hatchery-reared smolts were sampled on January 28 and April 28. On April 29 smolts were released into the Huntington River. A subset of these were captured in the smolt trap and sampled on May 4. Wild fish were sampled between May 15 and 22, the approximate midpoint of migration for wild fish. To minimize stress on tagged fish, blood and gill samples were taken only on untagged fish. Consequently, fish sampled for physiology were not used in the telemetry study.

Na^+,K^+-ATPase activity was determined with a kinetic assay run in 96-well microplates at 25°C and read at a wavelength of 340 nm for 10 min as described in McCormick (1993). Gill tissue was homogenized in 150 μl of SEID (SEI buffer and 0.1% deoxycholic acid) and centrifuged at 5,000 × g for 30 s. Two sets of duplicate 10-μl samples were run, one set containing assay mixture and the other assay mixture and 0.5-mM ouabain. The resulting ouabain-sensitive ATPase activity is expressed as μmoles ADP × mg protein^{-1} × h^{-1}. Protein concentrations are determined using BCA (bicinchoninic acid) Protein Assay (Pierce, Rockford, Illinois). Both assays were run on a THERMOmax microplate reader using SOFTmax software (Molecular Devices, Menlo Park, California).

Plasma T_4 and T_3 concentrations were measured by a direct radioimmunoassay as described by Dickhoff et al. (1978) and modified by McCormick et al. (1995). Sensitivity as defined by the dose–response curve was 1–64 ng/mL for T_4 and 0.5–

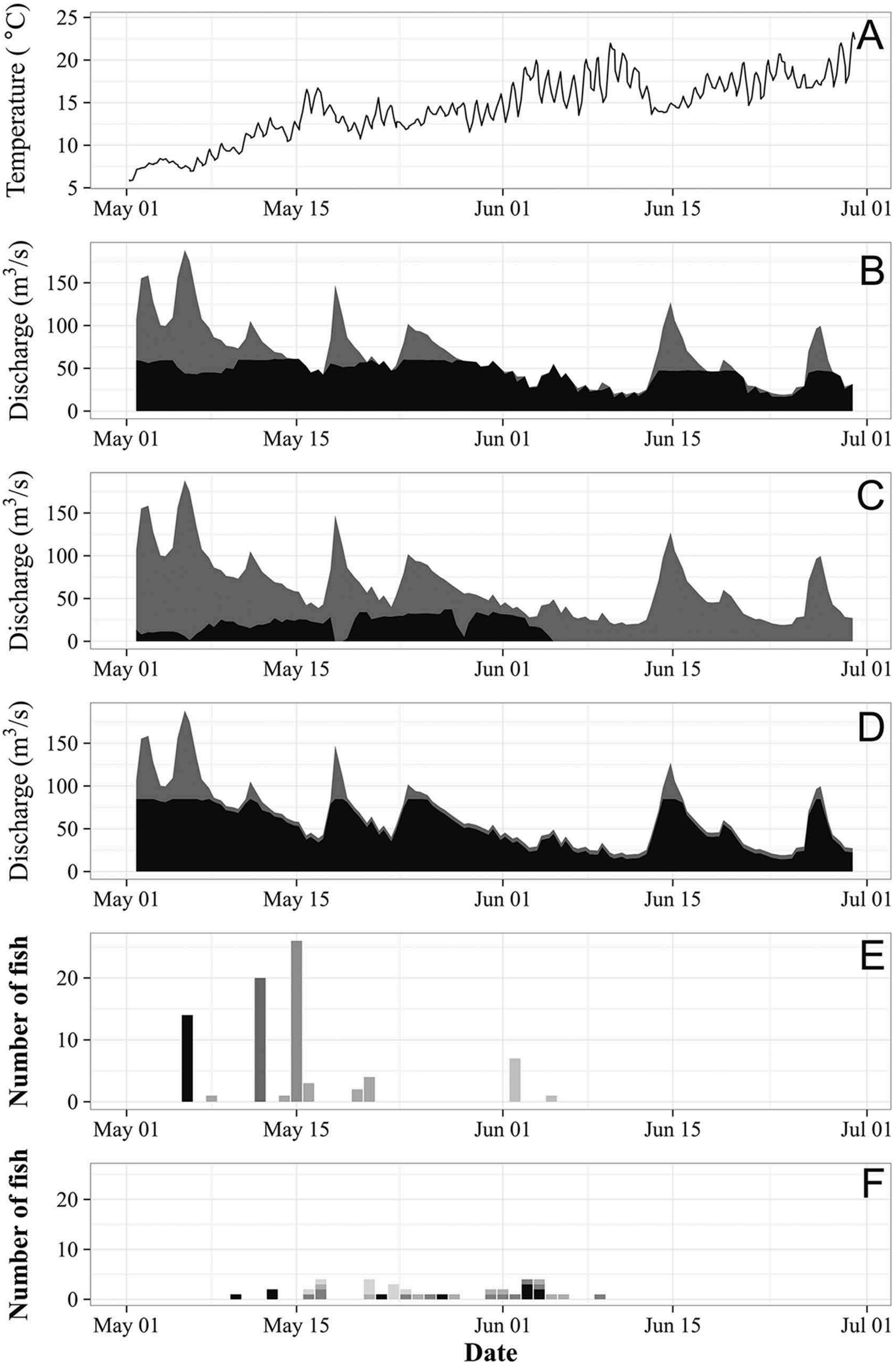

FIGURE 3. Graphs of **(A)** the seasonal pattern (May–June 2014) for river temperature (°C) and the total discharge (m^3/s), turbine flow (black), and flow through the spill gates (gray) for **(B)** Essex Dam, **(C)** Gorge Dam, and **(D)** Winooski Dam. Additional graphs show **(E)** the number of wild fish (lightest gray) and hatchery fish (black, dark gray, and gray) from the five groups tagged over the course of the study and **(F)** the number of fish from the five groups arriving at Essex Dam over the course of the study (data are first arrivals only).

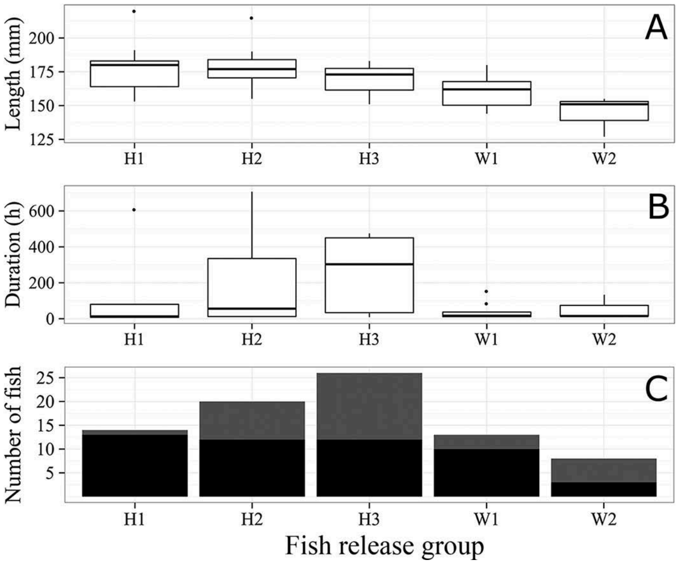

FIGURE 4. Box plots showing **(A)** fish length (mm) and **(B)** travel time (h) from the release location to Richmond, and a graph of **(C)** the number of fish that arrived at Richmond (black) or were lost (gray) for the five release groups. The abbreviations H1, H2, and H3 indicate hatchery-reared fish that were tagged and released on three different occasions (May 6, 12, and 15, respectively), and W1 and W2 indicate wild-reared fish grouped by tagging dates (May 8–21 for W1 and June 2–6 for W2). For the box plots, the horizontal line in each box indicates the median, the box dimensions represent the 25th to 75th percentile ranges, the whiskers show the 10th to 90th percentile ranges, and the black dots indicate outliers.

16 ng/mL for T_3. Intra-and interassay coefficients of variation for these assays were 4–11% and 3–5%, respectively.

Definitions and statistical analysis.—Migratory onset (initiation of migration) was determined by detection at Richmond or at downstream receivers and includes elements of both posttagging survival and migration (Figure 1). Survival through a reach of the river is defined by radio detections at the reach's downstream end. Survival percentages, distance-based mortality rates, and migration speeds were calculated from Richmond to arrival at Essex Dam, from arrival at Essex Dam to arrival at Gorge Dam, from arrival at Gorge Dam to arrival at Winooski Dam, and from arrival at Winooski Dam to arrival at the mouth of the river. Passage route survival at Essex Dam was defined by arrival at Gorge Dam. Overall migration survival was defined as the proportion of those smolts that initiated migration that subsequently arrived at the lake. Postpassage delays at Essex Dam and Winooski Dam were defined as the time from passage to departure from the area downstream of the dam (500–1,000 m). Dead and drifting fish were excluded by including only fish that were later detected at downstream antennas in these delay calculations.

The effects of release or tagging date on initiation of migration and arrival to the upper dam were analyzed separately for hatchery and wild fish. Logistic regression was used to test for the effects of release or tagging date on the initiation of migration and for survival to Essex Dam for fish initiating migration. The effects of release or tagging date on duration from release to arrival at Richmond and on travel time from Richmond to Essex Dam were tested with survival analysis (survreg with Weibul distribution; Therneau and Lumley 2016). Day versus night migration was quantified from the time of arrival at Richmond and at Essex Dam, and the difference between wild and hatchery fish tested with Fischer's exact tests. Due to the low number of fish between the upper dam and the lake, we compared dams and river reaches instead of groups of fish for everything downstream of Essex Dam.

We used accelerated failure time regression to compare passage rates at the three dams (survreg; Therneau and Lumley 2016). This is a form of a parametric time-to-event analysis (survival analysis) method that quantifies covariate effects on passage rates in the presence of censoring and competing risks. Here, we included fish ID as a frailty term to test for effects of dam on passage rate. Failure to pass (upstream movements or lost fish) was included as censored events (Hosmer et al. 2008:132–168; Castro-Santos and Perry 2012).

Differences in survival among passage routes were tested with logistic regression. Nonparametric rank tests were otherwise used to describe differences between groups of fish throughout the study. For two-group comparisons, we used Wilcoxon–Mann–Whitney tests. Differences in survival between reaches including different dams were tested using multiple pairwise Fisher's exact tests, whereas the difference in migration speed through the same reaches were tested with a Kruskal–Wallis test followed by Tukey post hoc tests (Pohlert 2014). Differences in levels of gill Na^+,K^+-ATPase, plasma T_4, and plasma T_3 over time in hatchery fish and between hatchery and wild fish caught in the rotary screw trap were tested with Student–Newman–Keuls tests. Statistical tests were performed using R (R Core Team, Vienna; packages Hmisc version 3.17, PMCMR version 4.0, and Survival version 2.38).

RESULTS

Migration Onset

A total of 50 fish, 37 hatchery (61.7%) and 13 wild (61.9%), arrived at the Winooski River in Richmond, 6 km downstream of the release site in the Huntington River (Figure 4). One fish passed the receiver station undetected (98% detection efficiency) and was therefore only included as having initiated migration and not in quantifying duration from release to onset of migration, travel speed, and timing of migration. Among hatchery smolts, a greater proportion of early released fish arrived at Richmond compared with those released late (logistic regression: P = 0.01; Figure 4). Duration from release to initiation of migration was longer later in the season than early in the season for hatchery fish (survreg: $\beta = 0.15 \pm 0.06$, $P = 0.01$; Figure 4). For wild fish, there was a similar trend of early tagged fish being more likely to migrate than fish tagged late. The sample size (n = 21) was small however, and no statistically significant difference was detected (logistic regression: $P = 0.2$; Figure 4). The few wild fish tagged late in the season and initiating migration took relatively long to do so, but the effect of release time was nonsignificant (survreg: $P = 0.85$; Figure 4). There was no significant difference between hatchery and wild fish in the onset of migration (Fischer's exact test: $P = 1$) or duration from release to onset of migration (Wilcoxon–Mann–Whitney test: $P = 0.24$; Figure 4). Fish not initiating migration disappeared except for two fish that were repeatedly found at the same location in the river. Failure to initiate migration is assumed to reflect mortality. Of the 49 fish detected at Richmond, 47 passed the receiver at night with no difference between hatchery and wild fish (Fischer's exact test: $P = 1$).

Migration

A total of 40 fish (30 hatchery, 10 wild) arrived at Essex Dam, the upper dam, between May 10 and June 9, and there was no effect of release date on the migration survival of hatchery fish ($P = 0.91$) or wild fish ($P = 0.13$); survival of the two groups was also nearly identical (81% versus 76%; Fisher's exact test: $P = 1$; Figure 5). Migration speed from Richmond to Essex Dam was significantly faster for hatchery fish released late than for hatchery fish released early (survreg: $\beta = -0.13 \pm 0.06$, $P = 0.02$; Figure 5). There was no effect of tagging date on migration speed for wild fish (survreg: $P = 0.41$), and wild fish were faster than hatchery fish (Wilcoxon–Mann–Whitney test: $P < 0.01$; Figure 5). Fish arrived both during daytime (n = 21) and at night (n = 19), with no difference between fish of hatchery and wild origin (Fischer's exact test: $P = 1$).

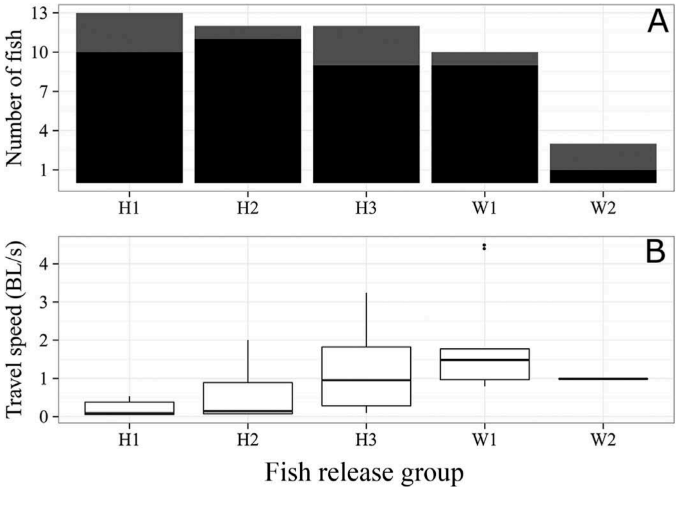

FIGURE 5. Graphs of **(A)** migration success (successful fish in black, lost fish in gray) and **(B)** migration speed in body lengths per second by tagging group between Richmond and Essex Dam. The abbreviations H1, H2, and H3 indicate hatchery-reared fish that were tagged and released on three distinct occasions (May 6, 12, and 15, respectively), whereas W1 and W2 indicate wild-reared fish that were grouped by tagging dates (May 8–21 for W1 and June 2–6 for W2). See Figure 4 for box plot description.

Hydropower Passage

Of the 50 fish initiating migration, only 5 fish (4 hatchery and 1 wild) reached the lake. The accumulated survival was almost identical between hatchery and wild fish (Fischer's exact test; $P = 1$). Detection efficiency was estimated to be 100% at all three dams, whereas the downstream receivers used to estimate postpassage delay had detection efficiencies of 75% downstream of Essex Dam and 100% downstream of Winooski Dam. The sample size for fish passing Essex Dam and moving farther downstream was low (n = 26), and the groups were relatively well mixed; hence all fish were combined into a single group when analyzing passage rates, postpassage delay, migration speed, and river reach survival.

Of the 40 fish that arrived at Essex Dam, 26 passed the dam while 14 fish disappeared (n = 4) or returned upstream (n = 10) (see also Nyqvist et al., in press). For fish that passed the dam, median delay from arrival to passage was 6.8 h (interquartile range [IQR] = 0.9–33.7 h; range = 0.2–618 h; n = 26). Median postpassage delay was 2.9 h (IQR = 1.4–163 h; n = 9). Percent survival was lowest through the bypass (38 %) and greatest through the turbines (67%). Although this result is alarming, it is important to note that sample size was low and the differences in survival between routes were not statistically significant (logistic regression: $P > 0.26$; Figure 6). The fish that did not manage to pass took a median of 7.6 d (IQR =

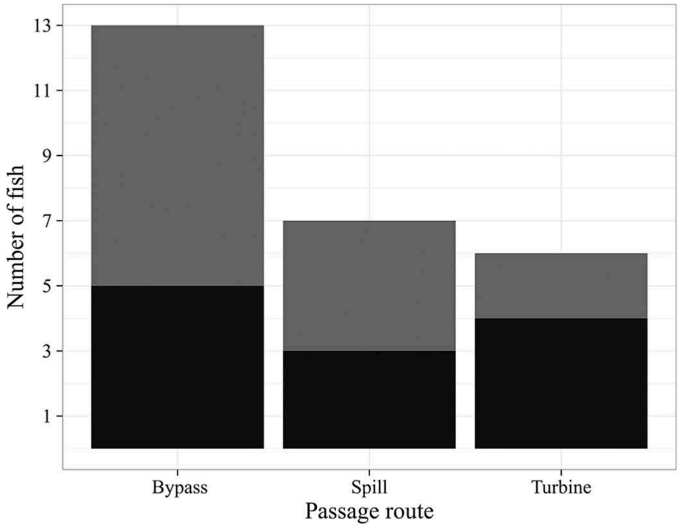

FIGURE 6. Number of fish passing Essex Dam via the bypass, spill, and turbines divided into those fish that arrived downstream of the dam (black) and those that failed to arrive (gray).

2.8–10.7 d; range = 0.4–26.7 d) from first arrival to last rejection of the forebay.

A total of 12 fish (9 hatchery and 3 wild) arrived at the forebay of Gorge Dam. Passage was relatively rapid at Gorge Dam (median = 29 min; IQR = 2–163 min; n = 12) and all fish that arrived in the forebay also passed the dam. In two extreme cases, fish were present at the dam for 4 and 15 d. Both of these fish were later detected downstream of the lowermost dam and one of them reached the lake.

A total of 11 fish (8 hatchery and 3 wild) arrived at Winooski Dam, the lowermost dam on the river, and 9 of these were observed to pass the dam while 2 disappeared without downstream detections. Median time from approach to passage was 257 min (IQR = 3–570 min; n = 9). One fish took 6 d to pass the dam; this fish did not survive to the lake. Median postpassage delay was 27 min (IQR = 22–35 min; n = 5).

Comparison between Dams

Passage rate was highest at Gorge Dam followed by Winooski Dam, and the lowest passage rate was observed at Essex Dam (Figure 7). This corresponds with passage times at Essex Dam being on average 45.6 times longer than at Gorge Dam (survreg with Weibull distribution; Gorge Dam versus Essex Dam: $\beta = -3.82 \pm 1.09$, $P < 0.01$), and 8.1 times longer than at Winooski Dam (survreg with Weibull distribution; Winooski Dam versus Essex Dam). Survival from the dam to the next downstream transition, either the next dam or the lake, in both relative numbers and per kilometer was lowest through the reach that included Essex Dam and higher at the other two dams. The proportion of fish surviving Essex Dam and Gorge Dam (Table 2) reaches were significantly different (Fischer's exact test: P = 0.002), whereas the other pairs were not (Winooski–Lake versus Gorge–Winooski and Winooski–Lake versus Essex–Gorge; P > 0.22). Survival per kilometer was higher in the free flowing reach than at any of the reaches including dams (Table 2). Migration speed was higher from the Winooski Dam to the lake than in the reach including Essex Dam (Kruskal–Wallis: P = 0.02; Tukey post hoc test: P = 0.015), with no significant difference between the other reaches (Tukey post hoc test: P > 0.11). Postpassage delay was longer at Essex Dam than at Winooski Dam (Wilcoxon–Mann–Whitney test: P = 0.01). At Gorge Dam our study design did not allow us to quantify postpassage delay.

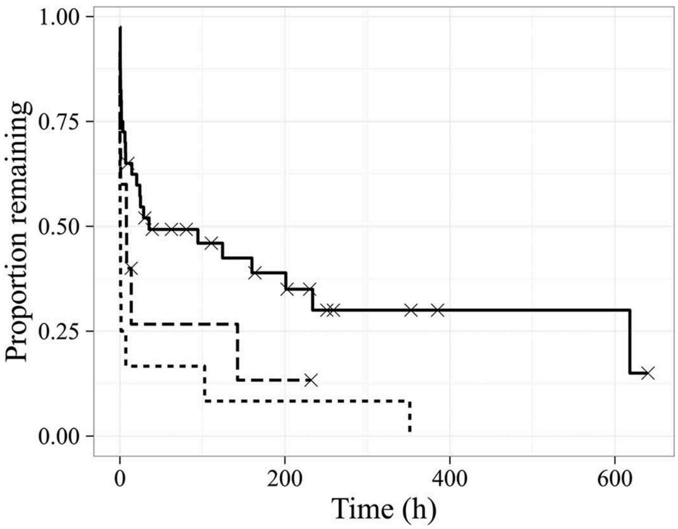

FIGURE 7. Kaplan–Meier curves for the time from arrival at the forebay to passage at Essex Dam (solid line), Gorge Dam (line with short dashes), and Winooski Dam (line with long dashes). Fish that failed to pass or return upstream are included as censored observations (marked as an X).

Physiology

Na^+,K^+-ATPase and T_4 levels indicated that smolts were physiologically prepared to migrate during the study period. Na^+,K^+-ATPase activity did not increase substantially in the hatchery between January and April (Table 3). However, after release and recapture in the smolt trap in early May gill Na^+, K^+-ATPase activity was 50% higher than at the time of release a week earlier. Gill Na^+,K^+-ATPase activity of hatchery-reared smolts was significantly lower than that of naturally reared smolts (Table 3).

Plasma T_4 levels were sevenfold higher in smolts captured in the smolt trap than in the hatchery a week earlier, while plasma T_3 levels were twofold higher. Plasma T_4 levels were higher in hatchery-reared than naturally reared smolts, whereas plasma T_3 levels were similar (Table 3).

DISCUSSION

In this paper, we present a study on downstream migration and dam passage performance for wild-reared and hatchery-reared landlocked Atlantic Salmon smolts in the Winooski River. Encouragingly, hatchery-reared fish performed similarly to wild fish. Hatchery fish released late in the season, however, were more likely to fail to initiate migration than hatchery fish released early. In addition, among the fish that did migrate downstream only 10% managed to swim through the 50 km of river and pass all three hydropower dams to reach the lake. Hence, the study highlights both the importance of hatchery release timing and the potential negative effect of multiple dam passages for migrating fish.

For the hatchery-reared fish, the likelihood to initiate migration was greater for fish released earlier than for fish released later. Although many fish failed to initiate migration, almost all (93%) of early released hatchery fish successfully initiated downstream migration, compared with 55% and 38% for the two later groups. The smolt phase during which juvenile Atlantic Salmon migrate downstream is limited in time, and loss of smolt characters, including the migratory urge,

TABLE 2. Fish survival over river reaches with and without dams. Measurements indicate the number of fish arriving at the reach, number of fish physically passing the dam within the reach, number of fish surviving migration through the reach, percent survival (survive/arrive × 100) through the reach, mortality per kilometer of river, and migration speed within the reach. Mortality includes failure to pass, passage mortality, postpassage mortality, and natural river mortality. The migration speed is presented as the median (with IQR given in parentheses).

Reach	Length (km)	Gradient (%)	Dam	Arrive	Pass	Survive	Survival (%)	Mortality/km (%)	Migration speed (km/d)
Richmond to Essex Dam	21	0.05	No	50		40	80	1	7 (2–20)
Essex Dam to Gorge Dam	10	0.27	Essex	40	26	12	30	11	2 (1–7)
Gorge Dam to Winooski Dam	2	0.75	Gorge	12	12	11	92	4	6 (3–25)
Winooski Dam to lake	17	0.08	Winooski	11	9	5	46	5	38 (28–46)

occurs if fish do not leave the river in a timely manner (McCormick et al. 1998). The physiology data, however, showed relatively strong smolt characteristics in early May. As it typically takes many weeks to lose smolt characteristics at the temperature experienced by these fish, it seems unlikely that many of the fish released only 2 weeks later had started to desmoltify. Instead, higher temperatures might have increased the stress related to release and handling (Cooke et al. 2011), leading to a reduced migratory urge and survival in some fish. The later-released hatchery fish that did initiate migration also took longer to do so. It might be that migration onset was delayed by stress, and therefore these fish were more susceptible to predation. The fact that these fish were not detected during manual tracking surveys supports this interpretation. Extensive migratory failure has been observed for other hatchery-released salmonids (Spicer et al. 1995; Larsen et al. 2015), and release timing might be crucial for the success of hatchery programs. While we show negative effects of late releases, very early releases have also been shown to result in low initiation of migration and thereby low survival in other rivers (Karppinen et al. 2013). In the Winooski River, large hatchery releases typically occur during the first week of April, earlier than the experimental releases in this study. The early hatchery releases aim to avoid stress associated with increased temperatures and the accompanying desmoltification among the released smolts and to take advantage of low predation from cormorants *Phalacrocorax* sp. before the return of large numbers of these birds in late spring (Nicholas Staats, U.S. Fish and Wildlife Service, personal communication).

Smoltification is governed by photoperiod and temperature, with downstream migration triggered by temperature and at some places discharge (Hesthagen and Garnås 1986; McCormick et al. 1998; Whalen et al. 1999; Jonsson and Jonsson 2011). Interestingly most of the wild-reared smolts were caught later than when the hatchery-reared fish were released, with catches continuing into June. There was, however, a similarity in movement patterns between wild and hatchery fish, with most early tagged smolts and few late-tagged smolts continuing to migrate also among the wild fish. The wild fish were caught in a rotary screw trap; hence, most of them were assumed to be migrating downstream (Volkhardt et al. 2007). Perhaps the delay and stress caused by the trapping in combination with higher temperatures late in the season resulted in desmoltification (McCormick et al. 1998). The late-caught wild fish were also smaller than the early caught wild fish and could have experienced more negative effects of tagging (Jepsen et al. 2002).

TABLE 3. Gill Na^+,K^+-ATPase (μmoles ADP·mg protein^{-1}·h^{-1}), plasma T_4 (ng/mL), and plasma T_3 (ng/mL) in wild and hatchery-reared Atlantic Salmon. Values are presented as the mean ± SE. Different letters indicate significantly different mean values within the hatchery-reared group (Student–Newman–Keuls test: $P < 0.05$). An asterisk indicates a significant difference between the wild and hatchery-reared fish captured in the smolt trap.

Sample date	Gill Na^+,K^+-ATPase	Plasma T_4	Plasma T_3
Hatchery reared			
Jan 28 (*n* = 12)	3.8 ± 0.3 z	2.0 ± 1.1 z	7.6 ± 0.8 z
Apr 28 (*n* = 12)	3.4 ± 0.3 z	3.0 ± 1.2 z	5.4 ± 0.8 z
May 4 (smolt trap, *n* = 13)	4.8 ± 0.3 y	21.8 ± 1.3 y	10.1 ± 1.2 z
Wild			
May 15–22 (smolt trap, *n* = 4)	7.4 ± 0.3 *	9.7 ± 3.7 *	10.9 ± 1.7

Once the fish initiated migration, the mortality of 1% per kilometer in the reach upstream of Essex Dam is near the median among mortality rates reviewed by Thorstad et al. (2012). Of those late-released hatchery fish that did migrate, migration in this reach was faster than for fish released earlier. Higher temperatures at later dates could explain some of the faster migration for fish released late compared with fish released early (Videler 1993). This explanation, however, may be unlikely as the difference between release groups in mean temperatures experienced in the river reach was only 1°C. An alternative explanation is that when fish approach the end of their smolt window, they either stop migrating or they migrate more intensely. In other words, migratory urge (also known as *zugunruhe*; Dingle 2006) might increase until it ceases. A similar pattern has been seen in hydropower passage rate in migrating lampreys (family Petromyzontidae; Castro-Santos et al. 2017) and in transition from nocturnal to day and night migration in salmonid smolts (McCormick et al. 1998) and offers an interesting perspective on the behavior of migrating animals.

Our study design could not effectively separate residualization from mortality over the whole river system (Buchanan et al. 2009). The migration of Atlantic Salmon smolts, however, is considered obligate, and fish that failed to reach the lake during the migration likely did so with very high fitness costs (Cunjak and Therrien 1998; Huusko et al. 2007; Zydlewski et al. 2017). Hence, we classified survival as successful migration. The highest survival was observed through the free-flowing reach and the lowest through the reach that included the uppermost dam. Reaches including dams started from the forebay of a dam and ended at a receiver array located at a substantial distance downstream (another forebay for the two upper most dams). For reaches including dams, mortality estimates consequently include failure to pass, direct passage mortality, and postpassage mortality, as well as natural river mortality (Calles and Greenberg 2009; Roscoe and Hinch 2010; Zydlewski et al. 2017). This approach likely overestimates the absolute number of dam-related mortalities but underestimates the per kilometer mortality in reaches affected by dams, especially for the uppermost and lowermost dam with longer postpassage reaches. Future studies are needed to better understand dam-related mortality in the Winooski River. Such studies should have larger sample sizes, additional automatic stationary receivers, and consider releasing fish in multiple locations (but see Zydlewski et al. 2017 for insights on release location and sample size).

Of the 40 fish that arrived at Essex Dam, the upper dam, only 5 survived to reach the lake 30 km and three dams downstream. The accumulated passage and migration success, despite the existence of bypasses, was low but within the range of reported survival (3–59%) from multiple dam passages in other regulated river systems (Williams et al. 2001; Calles and Greenberg 2009; Norrgård et al. 2012). Contrary to what might have been expected (Aarestrup et al. 2014), hatchery-reared and wild-reared fish experienced similar survival ratios throughout the system. For the fish that did initiate migration, the substantial migration failure is thus likely the combined effect of delays, direct passage mortality, postpassage mortality (particularly at the uppermost dam; Calles and Greenberg 2009), and natural river mortality. The low migration success observed indicates that installing a fishway does not always promote successful fish passage.

Passage performance was particularly low at Essex Dam, the uppermost dam, with fish losses due to failure to pass, as well as passage and postpassage effects. Fishways passing few fish have been widely reported, often together with calls for evaluation of existing fishways (Bunt et al. 2012; Noonan et al. 2012). Fish behavior in the forebay of this dam, including failure to pass and route selection, is analyzed in depth in another paper (Nyqvist et al., in press). Here, in addition, we were able estimate passage-route-specific survival at this dam. Although our low sample size limited our ability to see any significant difference between passage routes in survival to downstream sites, the results indicate that passage through the bypass was not preferable to passage via the other two routes. This result warrants further study on the immediate aftereffects of bypass passage and spill passage, such as predation or injuries associated with passage through these routes (Ward et al. 1995; Skalski et al. 2002; Deng et al. 2007).

The positive relationship between spill and survival has been seen in other rivers (Čada et al. 1997; Stich et al. 2014), and increased spill is explicitly used to pass fish at some dams (Colotelo et al. 2012; Adams et al. 2014). In our study, passage rate and the proportion of fish that successfully migrated past a dam to continue downstream was lowest at the upper dam and highest at the middle dam, with the lower dam being intermediate. During a large part of the study period, the hydropower plant at the middle dam was not in operation, resulting in very high levels of spill at this dam. This most likely contributed to the high passage rate and migration survival seen at this dam. Also, the relatively high passage rate at the lower dam could be associated with spill as some water was constantly spilled (aesthetic spill) at this site. At the same time, the relatively high spill passage mortality observed at the Essex Dam highlights the importance of also studying and improving spill passage survival. All in all, the potentially positive effect of spill on passage performance could be used in management as the smolts' migration typically is short in duration and triggered by predictable environmental cues (Jonsson and Ruud-Hansen 1985; Antonsson and Gudjonsson 2002; Jonsson and Jonsson 2011). By modeling, experience, or direct observations, one could time increased spill levels with the bulk of the smolt run to safely pass migrating smolts with short delays (Calles et al. 2013). This, of course, would come with a cost of reduced hydroelectric generation. Although, with careful evaluations it may be possible to optimize the benefits while minimizing costs.

Postpassage delay is seldom reported in fish passage evaluations but could be an important source of mortality for the migrating fish. The passed fish may be delayed and preyed upon due to injuries and stress acquired in dam passage (Mesa 1994; Ferguson et al. 2006; Schreck et al. 2006). As our method limited our ability to distinguish between live, dead drifting, and predator-consumed smolts, we limited the quantification of postpassage delay to fish that later arrived at downstream locations. Because postpassage mortality likely increases with postpassage delay, our estimates should be seen as conservative. Still, we observed substantial delays downstream of the upper dam. At the lower dam, on the other hand, postpassage delays were shorter, indicating that site-related characteristics influence postpassage delay. The effects of dam passage do not end with passage survival (Marschall et al. 2011; Roscoe et al. 2011; Stich et al. 2015), and postpassage delay and mortality warrant further attention in fish passage evaluations.

To conclude, this study shows the importance of the timing of release for the initiation of migration of hatchery-reared Atlantic Salmon smolts. It also demonstrates low accumulated downstream passage and migration survival for Atlantic Salmon smolts in a system where multiple dam passage is required. Passage performance varied substantially between the three dams, and particularly low passage performance, including failure to pass, was observed at the upper most dam. Low accumulated migration success occurred despite the presence of bypass solutions at all three dams. This underscores the need for fish passage evaluations, showing that simply constructing a fish passageway is not synonymous with providing fish passage.

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