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ARTICLE

Transport, Dam Passage, and Size Selection of Adult Atlantic Salmon in the Penobscot River, Maine

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Abstract
Prior to 2012, returning adult Atlantic Salmon *Salmo salar* had to pass through fishways at three dams in the lower section of the Penobscot River, Maine: Veazie Dam (river kilometer [rkm] 48; removed in 2013), Great Works Dam (rkm 60; removed in 2012), and Milford Dam (rkm 62). To facilitate better passage through the lower river, a fish transport program was implemented in 2010 and 2011. Fish were captured at Veazie Dam and were either transported by truck above Milford Dam (TRKD group) or released into the head pond above Veazie Dam (run-of-the-river [ROR] group). To assess the efficacy of transport, we used PIT telemetry to compare the performance and passage of TRKD and ROR fish based on their (1) success in reaching one of the three dams upstream of Milford Dam, (2) time taken to reach an upstream dam (transit time), and (3) success in passing that upstream dam. In both years, the percentage of fish detected at upstream dams was higher for the TRKD group (82.4% in 2010; 78.6% in 2011) than for the ROR group (41.3% in 2010; 22.4% in 2011). In addition, median transit time was faster for TRKD fish (7 d in 2010; 5 d in 2011) than for ROR fish (23 d in 2010; 25 d in 2011). However, passage success through the upstream dams did not differ between the two release groups. Our analysis also revealed a strong, negative size-selective force on dam passage: larger fish were consistently less likely to successfully pass dams than smaller fish. Finally, environmental conditions also influenced passage success. Our analysis shows that the transport of adult Atlantic Salmon can be an effective means by which to increase migration success in systems where upstream passage is poor.

Dams pose a significant risk to the movements and migrations of diadromous fishes (Fay et al. 2006) and have been identified as a major impediment to Atlantic Salmon *Salmo salar* restoration efforts in Maine (NRC 2004). Atlantic Salmon runs in the state represent the last vestiges of viable populations, although these runs are at risk and have been listed as endangered under the U.S. Endangered Species Act (NMFS and USFWS 2000, 2009). Among these populations, the Penobscot River stock has the highest number of adult returns, ranging between 1,000 and 3,000 fish in the last

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decade (Maine Department of Marine Resources [MDMR], unpublished data).

Prior to 2012, returning Atlantic Salmon had to navigate fishways at three dams in the lower section of the Penobscot River: Veazie Dam (river kilometer [rkm] 48; removed in 2013, as explained below), Great Works Dam (rkm 60; removed in 2012), and Milford Dam (rkm 62). To reach the majority of suitable spawning habitat, Atlantic Salmon adults had to ascend at least one additional upstream impoundment (Figure 1). Although fishways were installed at Penobscot River dams to facilitate upstream passage, the fishways are not always effective and can cause significant delays in arrival at spawning areas (Gorsky et al. 2009; Holbrook et al. 2009). As a consequence, managers considered other measures to improve Atlantic Salmon access to the spawning grounds. One option to increase fish passage is the use of live transport (e.g., Clemens et al. 2009). This technique has the potential to increase overall passage rates and decrease migratory delays at dams (Schmetterling 2003). However, for sensitive species (e.g., American Shad *Alosa sapidissima*), live transport may also result in physiological or behavioral stress that could negatively affect spawning success (Halvorsen et al. 2009). Although some evidence suggests that adult Atlantic Salmon do not exhibit a high stress response when transported (Tang et al. 2009), the long-term effects of transport on their behavior have not been characterized. Fish that are subjected to a stressful event may slow or abandon upstream movements, resulting in reduced migratory success (Harris and Hightower 2011).

An understanding of the effectiveness of transport and dam removal in the Penobscot River is important for both short- and long-term management of Atlantic Salmon. Under the Penobscot River Restoration Project (PRRP), the two lowest dams in the system were removed: Great Works Dam was removed in summer 2012, and Veazie Dam was removed in 2013. Additional restoration measures encompassed by the PRRP include the installation of a fish elevator at Milford Dam. Earlier studies indicated extremely poor passage at Great Works Dam (Holbrook et al. 2009). In an effort to improve upstream migration in the short term prior to and during dam removal, a trucking program was implemented by the MDMR to transport adult Atlantic Salmon above the lower dams.

When assessing the efficacy of a live-transport program, it is important to consider not only the number of fish that can successfully reach spawning grounds but also the quality of those fish. In particular, the size of spawning adults could be influenced by such programs. Recent studies have suggested that

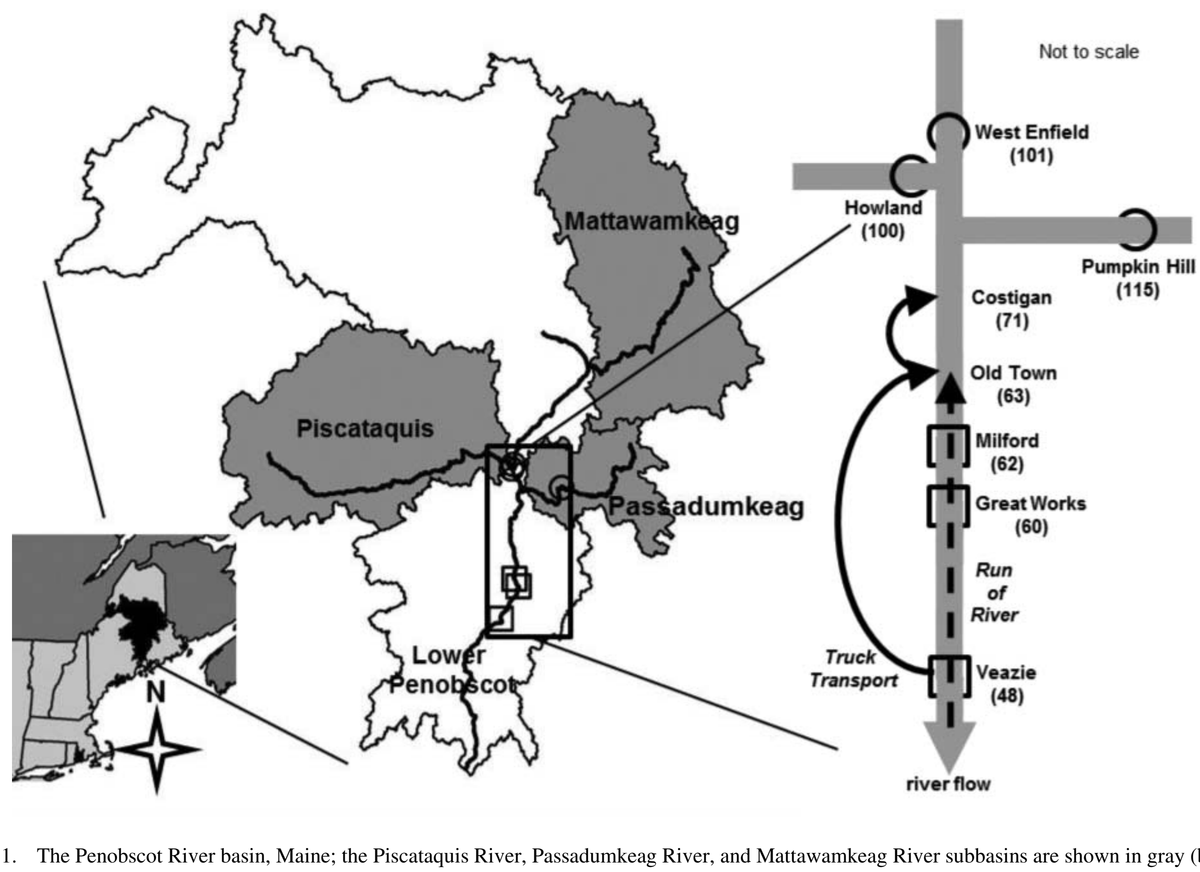

FIGURE 1. The Penobscot River basin, Maine; the Piscataquis River, Passadumkeag River, and Mattawamkeag River subbasins are shown in gray (black lines = main-stem river reaches; squares = lower dams; circles = upper dams). The schematic on the right shows (1) the truck transportation (solid lines) of Atlantic Salmon (arrows = release sites); and (2) the passage route (dashed lines) for run-of-the-river fish through fishways at the three lower dams (values in parentheses represent the river kilometer for each study site; not to scale).

migration barriers can act as a selective force on fish size and can ultimately shift life history traits (Carlson and Quinn 2007; Haugen et al. 2008). Many studies have investigated the benefits of transporting fish (Wagner et al. 2004; Evans et al. 2008; Clemens et al. 2009), but few have looked at the potential influences of transport on life history traits, such as the size of successful spawners. To fully quantify the ability of a transport program to influence spawning success, it is important to assess how important life history attributes, such as size, are affected.

Beginning in 2010, the MDMR began transporting some of the adult Atlantic Salmon from the trap at Veazie Dam to a release site upstream of Milford Dam. Using PIT technology installed at the major dams, we were able to (1) assess whether the upstream transport of adult Atlantic Salmon impeded upstream migratory behavior and (2) determine whether size influenced migration speed or the probability of passage by comparing "run-of-the-river" (ROR) fish (those that passed the lower dams) with fish that were transported around the dams by truck (TRKD fish).

METHODS

Study site.—The Penobscot River watershed drains an area of approximately 22,000 km^2. The river is approximately 563 km long and has three major tributaries: the Piscataquis, Passadumkeag, and Mattawamkeag rivers (Figure 1). There are several dams located on the main-stem Penobscot River and its tributaries. Upstream fish passage at all of the major dams is provided via Denil-type or vertical-slot fishways. In this paper, we refer to Veazie, Great Works, and Milford dams as the "lower dams," which occur near the head of tide. To reach the majority of spawning habitat, adult Atlantic Salmon must pass through fishways at one of the three "upper dams": Pumpkin Hill, West Enfield, or Howland Dam (Figure 1).

In 2010, a PIT telemetry study was initiated to determine passage success at and transit times to the major dams in the Penobscot River system. To detect fish that entered or exited the fishways at each dam, we installed stationary PIT antennas at the bottom (lower antennas) and top (upper antennas) of each fishway in a manner similar to that described by Gorsky et al. (2009). Arrays were installed at all lower dams except Great Works Dam, which was slated to be removed, and also at all upper dams. We built our antennas using 10-AWG (American wire gauge)-equivalent Litz wire encased in high-density polyethylene pipe following the design of Kazyak and Zydlewski (2012). To power the antennas, we used a FishTRACKER reader (Model FS1001M; Destron Fearing, St. Paul, Minnesota).

Fish tagging and release.—During May–October, adult Atlantic Salmon were captured at a fish trap located at Veazie Dam, the lowermost dam in the system (Figure 1). All adults were measured for FL (nearest cm) without anesthesia and without removing the fish from the water. All fish were PIT tagged by injecting a 12-mm Biomark tag into the dorsal musculature, again without removing the fish from the water. Handling of each fish generally took less than 1 min.

The majority of our analyses focused on comparing two groups released at separate locations. The first release group (ROR group) consisted of adult Atlantic Salmon that were released into the head pond just above Veazie Dam. These ROR fish had to ascend fishways at Great Works Dam and Milford Dam to reach Milford Dam's head pond (Figure 1). The second group (TRKD group) consisted of individuals that were transported around the lower dams (i.e., Great Works and Milford dams). The decision to transport fish was primarily based on environmental conditions. In particular, fish were not transported if water temperatures were above 21°C. The TRKD fish were placed into 800-L containers at a maximum density of 20 fish/tank; the containers were filled with river water that was infused with oxygen. The fish were subsequently trucked upstream and released at rkm 71 (Costigan, Maine), with the exception of a small portion of fish (110 total) that were released at rkm 63 (Old Town, Maine) in 2011 (see Figure 1).

In 2010 and 2011, the transport of adult Atlantic Salmon was not initiated until after June 1. However, a number of ROR fish ($N = 170$ in 2010; $N = 222$ in 2011) were released in May under different environmental conditions. Additionally, the PIT antenna arrays were not in place at upper dams until June 2010. To avoid possible biases that could result from differences in release dates, we restricted analyses to fish captured at Veazie Dam between June 1 and July 15 in 2010 and 2011. We analyzed data for each year separately because in 2010, we experienced antenna problems that led to poor detection efficiencies at some dams.

Environmental data.—The discharge and temperature of the Penobscot River at West Enfield (rkm 100) were measured by the U.S. Geological Survey (USGS), and the data were obtained through the USGS National Water Information System (http://waterdata.usgs.gov). Average daily discharge and average temperature on the day of release were calculated and assigned to each fish.

Overall comparison of release groups.—In comparing the two release groups of Atlantic Salmon, we focused on (1) the probability of migration to an upper dam (successful arrival) and (2) passage success at the upper dams given successful arrival at an upper dam. Because our main interest was in relative differences between groups, we used logistic regression to analyze arrival and passage probabilities in lieu of a more complex capture–mark–recapture analysis. Our main assumption was that detection probability did not vary between release groups; therefore, observed differences in arrival and passage probabilities at dams were assumed to be primarily attributable to between-group differences in passage rates rather than to between-group differences in detection rates. To assess possible variation in detection probability between release groups, we first summarized the total number of individuals within a release group that were detected upstream of an antenna array and therefore had passed the array; we then calculated the proportion of fish with known upstream passage that were detected by the antenna array. Sample sizes were low for some arrays, limiting our ability to calculate detection efficiency for all arrays in all years.

To analyze arrival success at the upper dams, arrival was treated as a binary response variable: fish that were detected at an upper dam were assigned a value of 1, whereas all other individuals were considered an apparent failure and were assigned a value of 0. We use the term "apparent failure" to indicate that some fish successfully migrated to one of the upper dams but were not detected. If a fish was detected as migrating downriver (i.e., a fallback event) at one of the lower dams prior to reaching an upper dam, the fish was also considered an apparent failure and was assigned a value of 0, and any subsequent detections of that individual were ignored. A number of categorical and continuous predictor variables were included in the regression models, including release group (categorical variable), FL (continuous individual covariate), and temperature and discharge (continuous environmental covariates). To help facilitate the interpretation of modeled intercepts, all continuous covariates were standardized within each year and release group to a mean of 0 and an SD of 1 for use in the model (Gelman and Hill 2007). We did not include the arrival dam as a potential categorical predictor; however, a chi-square test was used to identify group differences in the proportion of fish arriving at each upper dam.

We used logistic regression to analyze adult passage success at the three upper dams. To assess the passage success of each fish, we only considered the upper dam at which it was first detected. If a fish was detected at the upper PIT antenna of the upper dam, that individual was assigned a value of 1. All other fish were considered apparent failures and were assigned a value of 0, including individuals that were subsequently detected at an upper dam other than the dam of first detection. The percentages of fish that eventually passed at an alternate dam were small and similar between the TRKD group (3.1%) and the ROR group (4.3%). We used the same set of variables described above to evaluate passage success. Additionally, the dam at which passage was first attempted was used as a categorical predictor variable, as there was some evidence that passage rates differed among dams.

Analysis of run-of-the-river fish passage through the lower dams.—To understand where ROR Atlantic Salmon might experience passage delays within the lower river, we conducted a separate analysis on this release group. Similar to the analyses described above, we used logistic regression to assess (1) arrival success at Milford Dam given release into the Veazie Dam head pond and (2) passage success at Milford Dam given successful arrival at that dam. As in previously described models, FL was included as a continuous individual covariate, and water temperature and river discharge were used as continuous environmental covariates.

Model selection.—For each set of logistic regression analyses, we considered a number of plausible models that were applicable to the particular analysis (see Table 1). Because the fish were released in batches and they often migrate in groups, there was the potential for a lack of independence that could cause overdispersion in the data, subsequently biasing the results (Burnham and Anderson 1998). To adjust for a lack of independence, we used quasi-binomial models in Program R to fit all logistic regression models (Kéry 2010). Akaike's information criterion corrected for small samples sizes (AIC_c) was used to determine the support for each model (Burnham and Anderson 1998). To adjust for possible overdispersion in the data, we used the quasi-AIC_c ($QAIC_c$), which adjusts AIC_c values by using an estimate of overdispersion (Burnham and Anderson 1998).

TABLE 1. Summary of logistic regression models applied to analyses of adult Atlantic Salmon arrival and passage success at various dams in the Penobscot River system, Maine (+ = additive effect; × = interaction effect). Explanatory variables include release group (RG; i.e., run of the river [ROR] or truck transported), dam (DAM), fork length (FL), water temperature (TEMP), and discharge (FLOW). The subset of models applied to each particular set of analyses is indicated by numbers in the "Analysis" column (1 = analysis of arrival success from release to the upstream dams; 2 = analysis of passage at the upstream dams given arrival at the dams; 3 analysis of arrival at Milford Dam given release in the Veazie Dam head pond [ROR only]; 4 = passage at Milford Dam given arrival at that dam [ROR only]).

Model	Analysis
RG	1, 2
FL	1, 2, 3, 4
FLOW	1, 2, 3, 4
TEMP	1, 2, 3, 4
DAM	2
TEMP + FLOW	1, 2, 3, 4
RG + FL	1, 2
RG + FLOW	1, 2
RG + TEMP	1, 2
RG + TEMP + FLOW	1, 2
FL + TEMP + FLOW	1, 2, 3, 4
RG + FL + TEMP + FLOW	1, 2
RG + DAM	2
RG + DAM + FL	2
RG + DAM + FL + TEMP + FLOW	2
DAM + FL	2
DAM + FL + TEMP	2
DAM + FL + FLOW	2
RG × FL	1, 2
(RG × FL) + DAM	2
(RG × FL) + FLOW	1, 2
(RG × FL) + TEMP	1, 2
(RG × FL) + TEMP + FLOW	1, 2
(RG × FL) + DAM + TEMP + FLOW	2

Transit time.—Transit time was calculated for individual Atlantic Salmon that were successful in reaching one of the upper dams. Transit time was calculated for (1) the interval from release to first detection at an upper dam and (2) the interval from successful passage at Milford Dam to first detection at an upper dam. Because transit times were nonnormally

TABLE 2. Environmental variables measured at capture and the release group characteristics for adult Atlantic Salmon that were captured at Veazie Dam (Penobscot River) and used in the analysis of dam passage (summarized weekly). Release groups are divided into run-of-the-river (ROR) fish and truck-transported (TRKD) fish.

Release group	Week	Dates	Mean water temperature (°C)	Mean flow (m^3/s)	Number released	Average FL (cm)
			2010			
ROR	1	Jun 1–7	18.8	284.7	41	67.5
TRKD					0	
ROR	2	Jun 8–14	18.5	392.2	209	57.2
TRKD					0	
ROR	3	Jun 15–21	21.0	180.0	43	63.1
TRKD					33	60.5
ROR	4	Jun 22–28	23.2	150.6	24	59.4
TRKD					14	56.8
ROR	5	Jun 29–Jul 5	23.1	260.5	39	59.1
TRKD					106	57.4
			2011			
ROR	1	Jun 1–7	17.3	602.0	173	69.8
TRKD					0	
ROR	2	Jun 8–14	19.9	321.3	466	68.7
TRKD					169	70.3
ROR	3	Jun 15–21	19.6	264.1	19	59.9
TRKD					488	68.7
ROR	4	Jun 22–28	20.7	251.3	24	64.5
TRKD					567	66.9
ROR	5	Jun 29–Jul 5	22.6	202.5	11	69.2
TRKD					127	66.9

distributed, release groups were compared by using nonparametric Kruskal–Wallis (K–W) tests.

*Comparisons of fork length.—*Differences in FL between release groups and among dam locations were compared within each year by using a two-way ANOVA. The α value was set at 0.05 for this and all other statistical comparisons.

RESULTS

Number of Fish Tagged and Released

We tracked the passage of 509 Atlantic Salmon adults in 2010 and 2,040 adults in 2011 (Table 2). Release dates ranged from June 1 to July 7. Average FL was larger in 2011 (mean = 68.2 cm; SD = 9.3) than in 2010 (mean = 59.0 cm; SD = 9.1). Daily water temperatures during release ranged from 16.3°C to 24.8°C (mean = 21.5°C; SD = 2.8), while daily mean discharge ranged from 129.4 to 747.6 m^3/s (mean = 265.2 m^3/s; SD = 141.3).

Comparison of Arrival to Upper Dams

Overall, we found that transport above Milford Dam increased an Atlantic Salmon adult's probability of reaching one of the upper dams in both 2010 and 2011 (Table 3). The percentage of fish detected as exhibiting fallback after release was consistently lower for the TRKD group than for the ROR

TABLE 3. Summary of the number of PIT-tagged adult Atlantic Salmon in each release group (run of the river [ROR] or truck transported [TRKD]), the number (%) detected as arriving at one of the upper dams, the number (%) detected as passing an upper dam, and the number (%) detected as exhibiting fallback in the Penobscot River system during 2010 and 2011.

Year	Release group	Number released	Number detected as arriving upstream	Arrival success (%)	Number detected as passing upstream	Passage success (%)	Number detected as falling back	Fallback (%)
2010	ROR	356	147	41.3	95	64.6	19	5.3
	TRKD	153	126	82.4	63	50.0	4	2.6
2011	ROR	693	155	22.4	104	67.1	81	11.7
	TRKD	1,351	1,062	78.6	634	59.7	25	2.4

TABLE 4. Estimated probability of detection for adult Atlantic Salmon at lower and upper antennas installed at various dams in the Penobscot River system during 2010 and 2011. Run-of-the-river (ROR) fish were released above Veazie Dam; trucked (TRKD) fish were released above Milford Dam. The total number of fish detected at the antenna, the number detected above the antenna, the number missed by the antenna, and the estimated detection probability are presented.

Year	Release group	Dam	Detected at the antenna	Detected above the antenna	Missed (undetected) at the antenna	Detection probability
			Lower antenna			
2010	ROR	Milford	39	166	127	0.24
	ROR	West Enfield	99	64	21	0.83
	TRKD	West Enfield	70	22	1	0.96
	ROR	Howland	68	85	33	0.61
	TRKD	Howland	29	52	29	0.44
2011	ROR	Milford	212	260	48	0.82
	ROR	West Enfield	122	74	12	0.84
	TRKD	West Enfield	844	542	64	0.88
	ROR	Howland	48	43	8	0.81
	TRKD	Howland	267	188	37	0.80
	ROR	Pumpkin Hill	16	6	0	1.00
	TRKD	Pumpkin Hill	103	41	7	0.83
			Upper antenna			
2010	ROR	Milford	108	141	58	0.59
2011	ROR	Milford	184	138	25	0.82
	ROR	West Enfield	57	5	0	1.00
	TRKD	West Enfield	478	68	11	0.83
	ROR	Howland	77	8	2	0.75
	TRKD	Howland	153	21	3	0.86

group (Table 3). The detection probability at PIT antennas associated with the upper dams varied between years but was consistently greater than 80% at lower antennas during 2011 for both release groups and at all dams (Table 4). In addition, the between-group difference in detection probability at the lower antennas was 2% at West Enfield Dam and 1% at Howland Dam. Detection probabilities for both antennas at Pumpkin Hill Dam and for the upper antennas at Howland and West Enfield dams were more variable due to low samples sizes. In 2010, detection probability at West Enfield Dam was greater than 80% for both release groups but was 13% higher for TRKD fish than for ROR fish (Table 4).

Fork length and release group were important predictors of postrelease arrival at an upper dam (Tables 5, 6). In particular, the significant FL × release group interaction indicated that FL (1) did not influence the probability that TRKD fish would arrive at the upper dams but (2) did have a strong influence on the probability for ROR fish. At average temperatures and flows, ROR fish of all sizes had a lower probability of arrival than TRKD fish (Figure 2a). In addition, larger ROR fish had a substantially lower success rate, indicating that Great Works and Milford dams had a strongly negative size-selective influence on adult passage. Environmental conditions also influenced passage success. For both years, the top models included negative effects of both water temperature and discharge (Table 6). Arrival success was greater at cooler temperatures and at lower flows, particularly in 2010 (Table 6).

The proportions of fish detected at each of the upper dams or at multiple upper dams were similar between release groups (χ^2 test: df = 3, $P = 0.44$ [2010] and 0.40 [2011]). Generally, the greatest numbers of fish were detected at West Enfield Dam followed by Howland Dam. Relatively few fish approached Pumpkin Hill Dam (Table 7). Roughly 25% of the fish were detected at multiple upper dams.

Comparison of Passage at Upper Dams

Contrary to trends in arrival at the upper dams, a consistently higher proportion of ROR fish was detected as successfully passing the upper dams in both 2010 and 2011 (Table 3). Analysis of the 2010 data indicated that release group was again an important predictor of passage: ROR fish had a higher passage probability than TRKD fish, even after we controlled for the effects of FL, dam, water temperature, and discharge (Tables 8, 9). A closely competing model ($\Delta QAIC_c = 0.5$) indicated a significant FL × release group interaction. In 2011, release group was not included in the top model, indicating that the differences observed between the two release groups in that year were not evident after controlling for the effects of FL and dam. Similar to our results for arrival at the

TABLE 5. Comparison of logistic regression models for the probability of Atlantic Salmon arrival at one of the three upper dams in the Penobscot River system for both trucked (TRKD) and run-of-the-river (ROR) fish after release in 2010 and 2011. Top models and their associated quasi-Akaike's information criterion ($QAIC_c$) values are presented ($\Delta QAIC_c$ = difference in $QAIC_c$ value between the given model and the best-performing model). Effect abbreviations are defined in Table 1.

Year	Rank	Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight
2010	1	RG + (RG × FL) + TEMP + FLOW	553.1		0.97
	2	RG + (RG × FL) + TEMP	560.9	7.8	0.02
	3	RG + (RG × FL)	562.6	9.5	0.01
	4	RG + (RG × FL) + FLOW	564.1	11.0	0
	5	RG + FL + FLOW + TEMP	566.9	13.8	0
2011	1	RG + (RG × FL)	2,116		0.34
	2	RG + (RG × FL) + TEMP	2,117	1.0	0.2
	3	RG + (RG × FL) + TEMP + FLOW	2,117.1	1.1	0.2
	4	RG + (RG × FL) + FLOW	2,117.4	1.4	0.17
	5	RG + FL	2,119.9	3.9	0.05

upper dams, FL had a negative effect on passage success at the upper dams during 2010 and 2011 for both release groups (Figure 2b; Table 9).

Among-dam variation in passage for both 2010 and 2011 was also supported by the analysis (Table 9). In 2010, a higher percentage of fish was detected as passing Howland Dam (86%; $N = 98$) than West Enfield Dam (59%; $N = 99$). The pattern in 2011 was similar; the percentage of fish detected as passing Howland Dam (72%; $N = 222$) was higher than the percentages detected as passing West Enfield Dam (61%; $N = 828$) and Pumpkin Hill Dam (39%; $N = 33$).

Environmental factors were not included in the most supported model for 2010, although there was a small difference in $QAIC_c$ values ($\Delta QAIC < 2$) between the best model and the models that included environmental variation. Therefore, an effect of environmental conditions during 2010 found limited support in the data. The 2011 data yielded greater evidence that environmental effects influenced passage. The most supported model for 2011 included water temperature as an important variable; increasing temperature had a negative effect on passage (Table 9).

TABLE 6. Model-averaged coefficient estimates and SEs of the most supported model from Table 5, along with *P*-values from that model. Effect abbreviations are defined in Table 1 (TRKD = trucked release group; ROR = run-of-the-river release group).

Year	Effect	Estimate (SE)	*P*-value
2010	Intercept (TRKD)	1.68 (0.23)	<0.001
	FL	0.18 (0.24)	0.46
	FLOW	−0.43 (0.14)	<0.01
	TEMP	−0.85 (0.24)	<0.001
	RG (ROR)	−2.46 (0.30)	<0.001
	RG (ROR) × FL	−1.03 (0.27)	<0.001
2011	Intercept (TRKD)	1.27 (0.07)	<0.001
	FL	−0.12 (0.07)	0.12
	RG (ROR)	−2.56 (0.13)	<0.001
	RG (ROR) × FL	−0.27 (0.10)	<0.01

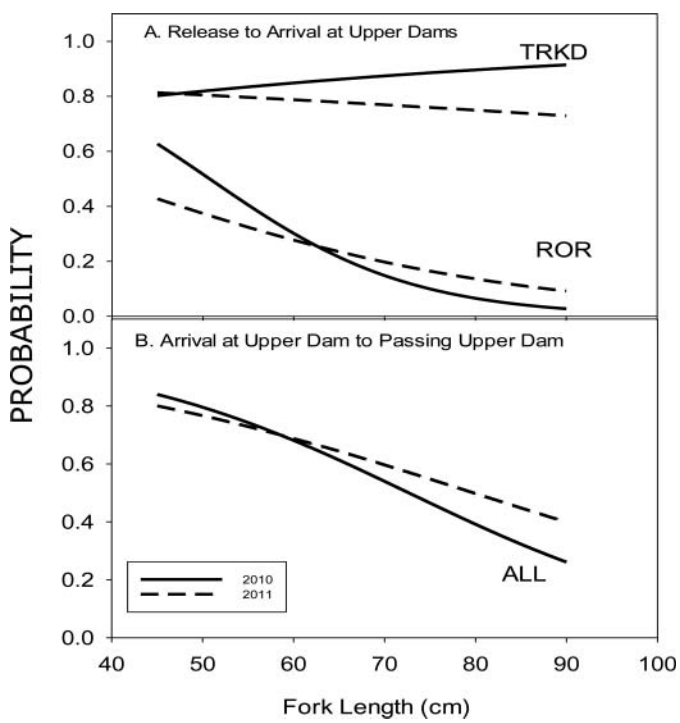

FIGURE 2. Probability of **(A)** successful arrival at an upper dam and **(B)** successful passage at an upper dam in the Penobscot River system relative to the FL (cm) of adult Atlantic Salmon that were released above Veazie Dam (run-of-the-river [ROR] release group) or transported by truck above Milford Dam (trucked [TRKD] release group) during 2010 and 2011. Predictions are from logistic models in which flow and temperature were held constant at average values.

TABLE 7. Number of PIT-tagged adult Atlantic Salmon in the trucked (TRKD) release group or the run-of-the-river (ROR) release group that were detected by an antenna at an upper dam (Howland, West Enfield, or Pumpkin Hill) in the Penobscot River system, 2010 and 2011. The “Multiple dams” column indicates the number of fish that were detected by PIT antennas at two or more upper dams.

Year	Release group	Number released	Howland Dam	West Enfield Dam	Pumpkin Hill Dam	Multiple dams
2010	ROR	356	59	57	1	54
	TRKD	153	31	42	2	29
2011	ROR	693	37	111	7	28
	TRKD	1,351	169	646	27	187

TABLE 8. Comparison of logistic regression models for the probability of successful passage at the first upper dam approached for both trucked (TRKD) and run-of-the-river (ROR) Atlantic Salmon adults in 2010 and 2011. Top models and their associated quasi-Akaike’s information criterion ($QAIC_c$) values are presented ($\Delta QAIC_c$ = difference in $QAIC_c$ value between the given model and the best-performing model). Effect abbreviations are defined in Table 1.

Year	Model rank	Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight
2010	1	RG + DAM + FL	207.4		0.26
	2	RG + (RG × FL) + DAM + TEMP	207.9	0.5	0.2
	3	RG + DAM + FL + TEMP + FLOW	208.3	0.9	0.17
	4	RG + (RG × FL) + DAM + TEMP + FLOW	209.4	2.0	0.09
	5	RG + (RG × FL) + DAM + TEMP	209.9	2.5	0.07
2011	1	DAM + FL + TEMP	1,387.6		0.41
	2	DAM + FL + TEMP + FLOW	1,389.6	2.0	0.16
	3	DAM + FL	1,390.3	2.7	0.11
	4	RG + (RG × FL) + DAM + TEMP	1,390.7	3.1	0.09
	5	RG + DAM + FL + TEMP + FLOW	1,391.2	3.6	0.07

Passage Success through Lower Dams for Run-of-the-River Fish

In both years, less than 50% of the ROR Atlantic Salmon released above Veazie Dam were detected at or above Milford Dam. Data for Milford Dam in 2010 were somewhat limited by the low detection probability (<60%) at both antennas (Table 4). However, detection probability at Milford Dam was considerably higher (>80%) during 2011. Despite this increase in detection probability, the overall percentage of ROR fish detected at Milford Dam was still lower in 2011 (37.5%) than in 2010 (47.2%). Fork length was consistently identified as an important factor for both the 2010 data and the 2011 data (Tables 10, 11). In both years, the relationship between arrival at Milford Dam and FL was negative, indicating a decreased probability of arrival for larger fish (Table 11). Environmental conditions at the time of release were also important variables in both 2010 and 2011 (Table 11). Water temperature and discharge were each negatively correlated with arrival probability in 2010. For 2011, an effect of water temperature was not evident, but discharge continued to have a negative effect on arrival probability.

TABLE 9. Model-averaged coefficient estimates and SEs of the most supported model from Table 8, along with *P*-values from that model. Effect abbreviations are defined in Table 1 (ROR = run-of-the-river release group; PH = Pumpkin Hill Dam; WE = West Enfield Dam; HW = Howland Dam).

Year	Coefficient	Estimate (SE)	*P*-value
2010	Intercept (HW)	1.44 (0.34)	<0.0001
	RG (ROR)	1.15 (0.42)	<0.05
	DAM (WE)	−1.29 (0.36)	<0.001
	FL	−0.31 (0.16)	<0.05
2011	Intercept (HW)	0.90 (0.16)	<0.0001
	DAM (WE)	−0.50 (0.17)	<0.001
	DAM (PH)	−1.58 (0.40)	<0.0001
	FL	−0.41 (0.07)	<0.0001
	TEMP	−0.22 (0.10)	<0.05

Passage success at Milford Dam (for fish that successfully arrived at the dam) was relatively high. In 2010, nearly all (>97%) of the fish that arrived at Milford Dam passed the dam successfully, so an analysis of passage was not conducted. During 2011, passage success was 80% ($N = 221$). Fork length continued to have a significant negative effect, whereas discharge had a significant positive effect (Tables 12, 13). Water temperature was not included in the top model, but $QAIC_c$ weights suggested some support for a model that included water temperature (Table 12).

TABLE 10. Comparison of logistic regression models for the probability of successful arrival at Milford Dam (Penobscot River) for run-of-the-river Atlantic Salmon adults after their release into the Veazie Dam head pond in 2010 and 2011. Top models and their associated quasi-Akaike's information criterion ($QAIC_c$) values are presented ($\Delta QAIC_c$ = difference in $QAIC_c$ value between the given model and the best-performing model). Effect abbreviations are defined in Table 1.

Year	Model rank	Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight
2010	1	FL + TEMP + FLOW	432.4		0.51
	2	FL	434.1	1.7	0.23
	3	FL + TEMP	434.5	2.1	0.18
	4	FL + FLOW	436.1	3.7	0.08
	5	TEMP	481.7	49.3	0
2011	1	FL + FLOW	881.5		0.71
	2	FL + TEMP + FLOW	883.4	1.9	0.27
	3	FL + TEMP	888.8	7.3	0.02
	4	FL	891.6	10.1	0
	5	FLOW	902.9	21.4	0

The ROR fish still experienced a decreased probability of reaching the upper dams even after they were detected as passing Milford Dam. In 2010, 68% ($N = 94$) of the ROR fish that made it to the upper antenna at Milford Dam arrived at one of the upper dams, whereas 82% ($N = 153$) of TRKD fish arrived at an upper dam. In 2011, 63% ($N = 177$) of ROR adults that reached the upper antenna at Milford Dam were subsequently detected at an upper dam, while 79% ($N = 1{,}351$) of TRKD fish were detected as arriving at one of the upper dams.

Transit Time

During both 2010 and 2011, ROR fish took significantly longer to reach the upper dams (K–W test: $P < 0.0001$ for both years) than TRKD fish (Figure 3). Median transit time from Veazie Dam to the upper dams was fivefold greater for ROR fish than for TRKD fish (Figure 3). In 2010, the median transit time was 5 d (SD = 34.4) for TRKD fish and 23 d (SD = 44.4) for ROR fish. In 2011, the median transit time was 7 d (SD = 33.2) for TRKD fish and 25 d (SD = 44.8) for ROR fish. In both years, there was substantial variation in transit time, as evidenced by the large difference between the minimum and maximum transit times for each release group (Figure 3).

TABLE 11. Model-averaged coefficient estimates and SEs of the most supported model from Table 10, along with P-values from that model. Effect abbreviations are defined in Table 1.

Year	Coefficient	Estimate (SE)	P-value
2010	Intercept	−0.43 (0.18)	<0.05
	FL	−0.85 (0.12)	<0.0001
	TEMP	−0.67 (0.04)	<0.05
	FLOW	−0.31 (0.14)	<0.05
2011	Intercept	−0.37 (0.09)	<0.0001
	FL	−0.40 (0.10)	<0.0001
	FLOW	−0.29 (0.10)	<0.001

For ROR fish that successfully passed Milford Dam, the transit time to the upper dams differed among years (Figure 3). In 2010, the median transit time from Milford Dam to the upper dams was significantly longer for ROR fish (20 d; SD = 39.3) than for TRKD fish (K–W test: $P < 0.0001$). In 2011, the median transit time for ROR fish was 7 d (SD = 35.5) and did not differ from the median for TRKD fish (K–W test: $P = 0.71$).

Comparison of Fork Lengths

We detected a significant release group × location interaction for both 2010 data ($P < 0.01$) and 2011 data ($P < 0.01$). For both release groups, the average FL of Atlantic Salmon decreased from the date of release to arrival or passage at an upstream dam in both 2010 and 2011, although the decrease was more pronounced for ROR fish than for TRKD fish (Figure 4). From release to successful passage at an upper dam, average FL decreased by 5.9% for ROR fish and by

TABLE 12. Comparison of logistic regression models for the probability of successful passage at Milford Dam (Penobscot River) given arrival at the fishway entrance for run-of-the-river Atlantic Salmon adults in 2011 (a model for 2010 is not shown because >97% of the fish passed successfully). Top models and their associated quasi-Akaike's information criterion ($QAIC_c$) values are presented ($\Delta QAIC_c$ = difference in $QAIC_c$ value between the given model and the best-performing model). Effect abbreviations are defined in Table 1.

Model rank	Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight
1	FL + FLOW	149.2		0.53
2	FL + FLOW + TEMP	150.9	1.7	0.22
3	FL	152.7	3.5	0.09
4	FL + TEMP	152.8	3.6	0.09
5	FLOW	154.0	4.8	0.05

TABLE 13. Model-averaged coefficient estimates and SEs of the most supported model from Table 12, along with *P*-values from that model. Effect abbreviations are defined in Table 1.

Coefficient	Estimate (SE)	*P*-value
Intercept	1.78 (0.25)	<0.0001
FL	−0.58 (0.24)	<0.05
FLOW	0.51 (0.22)	<0.05

1.2% for TRKD fish during 2010; average FL decreased by 5.3% for ROR fish and by 2.4% for TRKD fish during 2011.

DISCUSSION

Our assessment of the live transport of adult Atlantic Salmon above the lower dams in the Penobscot River yielded several important results. First, transport increased arrival success and decreased transit time to upper dams in the system, illustrating that the implementation of fish transport was successful with respect to management goals. Second, upon arrival at the upper dams, a fish's status as having been transported did not strongly influence passage. Third, relative to the TRKD group, ROR fish experienced considerable migratory delays, which were associated with the increased difficulty of ascending migratory barriers. Fourth, FL was negatively correlated with passage, revealing that dams exerted size-selective pressure on migrating adults. Finally, environmental variation was found to have potential influences on migration and passage.

Passage Rates and Transit Times

In 2010 and 2011, TRKD fish had a consistently greater probability of reaching the upper dams than ROR fish, even after we controlled for the effects of individual size and environmental conditions at the time of release. Furthermore, there was no evidence that transporting the fish led to an increase in fallback rates. The transport of fish around migration barriers can be a relatively low-cost tool to increase connectivity and decrease migratory delay (Schmetterling 2003; Evans et al. 2008); however, results can vary depending on the species and the life stage. For example, stress associated with handling and transport led to increases in fallback behavior among American Shad (Harris and Hightower 2011). Studies of Chinook Salmon *Oncorhynchus tshawytscha* have determined that although transporting smolts around hydroelectric facilities can increase in-stream survival, the effects can be stressful and may result in greater mortality after release (Halvorsen et al. 2009). Schmetterling (2003) reported that a high proportion of adult Cutthroat Trout *O. clarkii* and Bull Trout *Salvelinus confluentus* successfully continued their upstream migration after they were transported around a barrier. In addition, Tang et al.

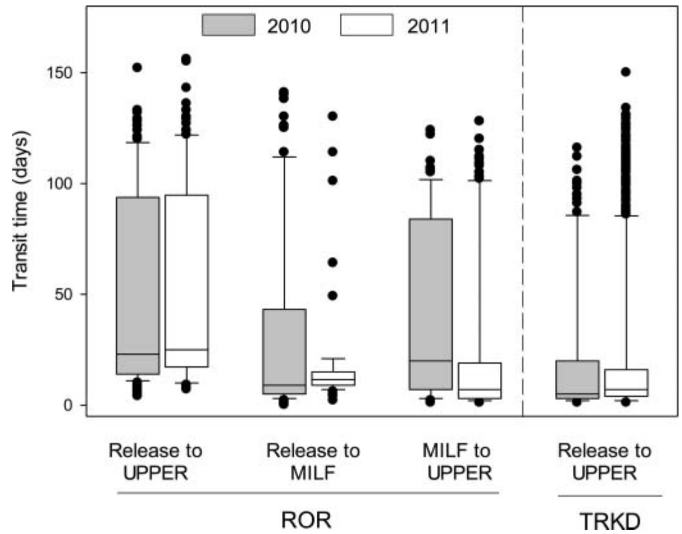

FIGURE 3. Box-and-whisker plots of transit time (d) for PIT-tagged adult Atlantic Salmon (TRKD = trucked release group; ROR = run-of-the-river release group) that were tracked in the Penobscot River system during 2010 and 2011 (horizontal line within each box = median transit time; ends of box = 75% quantiles; ends of whiskers = 95% quantiles; black circles = outliers). For the ROR and TRKD groups, "Release to upper" represents the time for released fish to arrive at any upper dam. For ROR fish only, the "Release to upper" transit time is broken into its two components: "Release to MILF" (i.e., from the time of release to successful passage at Milford Dam); and "MILF to upper" (i.e., from successful passage at Milford Dam to initial arrival at an upper dam).

(2009) found that adult Atlantic Salmon did not appear to suffer from high levels of physiological stress when transported. Results from the present monitoring study suggest that adult Atlantic Salmon responded well to live transport and were likely to continue migrating upstream after release.

In addition to increasing arrival success, live transport decreased the transit time for adult Atlantic Salmon in this study. Transit time for ROR fish was 14–16% greater (i.e., a slower rate of transit) than that of transported fish. Most of this delay appeared to occur in the lower river between Veazie and Milford dams. Hydroelectric facilities in the Penobscot River impede passage and increase migratory delays, often in suboptimal habitats and environmental conditions (Holbrook et al. 2009). Studies of adult Atlantic Salmon migrating in rivers without dams have shown that most adults migrate rapidly (i.e., in a few days) through the lower river (Økland et al. 2001). For the adult Atlantic Salmon that were transported around Milford Dam in our study, transit time was comparable to movement through unimpounded river reaches.

Transportation of the fish did not seem to directly influence passage success at the upper dams after we controlled for other variables. During both years, FL was a significant predictor of passage success, with some indication that differences among dams and variation in environmental conditions also influenced passage. In 2010 but not in 2011, release group was a factor that affected passage success as well. The release group effect in

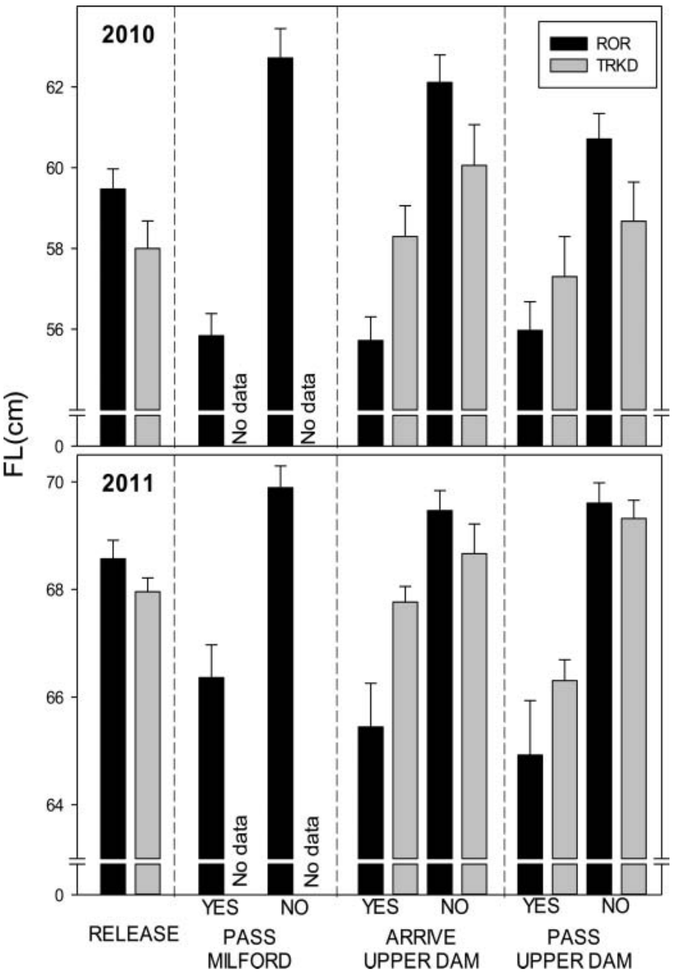

FIGURE 4. Average (+SE) FLs at release for truck-transported (TRKD) and run-of-the-river (ROR) adult Atlantic Salmon; FLs of individuals that did or did not (1) pass Milford Dam, (2) arrive at an upper dam, or (3) successfully pass an upper dam in the Penobscot River system during 2010 and 2011 are also shown.

2010 may have been the result of lower-quality data. For example, we had less data with which to model the potential effects of the release group × FL interaction. Detection probability was more variable in 2010, particularly at Howland Dam; therefore, the apparent release group effect for 2010 may partly be an artifact of the data. Analysis of passage success for the ROR group indicated that fish released above Veazie Dam experienced low passage success and significant delays in migrating through the lower river. During 2010 and 2011, a significant percentage of ROR fish were never detected upstream after their release into the Veazie Dam head pond. Earlier studies indicated that Great Works Dam presented a significant challenge to the upstream migration of Atlantic Salmon (Holbrook et al. 2009). Our analysis further revealed that passage success through the lower dams was influenced by FL and the environmental conditions at release. Although we did not directly monitor fish passage at Great Works Dam, our results together with those from prior studies indicate that the dam was a significant impediment to adult Atlantic Salmon migration.

Our data suggest that ROR fish arriving at Milford Dam have an improved chance of successfully migrating to the upper dams, although they may still experience some delay or migration failure depending on the river conditions and fish size. In 2010, a large majority of fish that arrived at Milford Dam successfully continued to the upstream dams; however, their transit time from Milford Dam to the upper dams was longer than the transit time for the TRKD fish (i.e., released above Milford Dam). In 2011, there was no difference in transit time between the TRKD fish and the ROR fish that passed Milford Dam, but the probability of reaching the upper dams was about 10% lower for ROR fish that passed Milford Dam than for TRKD fish. Overall, the passage rates at Milford Dam were relatively high, but our data also suggested that once the fish reached the top of the fishway, they still experienced some difficulty or delay. The analysis of environmental conditions suggested that warmer temperatures and lower flows could negatively influence passage rates. Passage through the lower river without undergoing delays at Great Works Dam may also benefit the fish in terms of their passage rates at dams farther upstream.

Size Effect

Our results demonstrated that dams on the Penobscot River are size selective. This result is consistent with previous studies reporting differences in passage among size-classes of adult Atlantic Salmon (e.g., Laine et al. 2002). The lack of such an effect for TRKD fish underscores the benefit of bypassing two dams—Great Works and Milford dams—and their associated impoundments. The relatively high passage rate of ROR fish at Milford Dam suggests that this dam has a lesser impact than Great Works Dam once had, but negative size selection appears to be a common effect of dams in the system rather than an effect that is localized to a single site.

Size selection can have both immediate and long-term consequences for population dynamics. In a naturally reproducing population, poorer passage of larger fish would reduce the number of large females, thereby directly limiting egg deposition. Selection against large fish could shift the life history characteristics of the population to a smaller size at maturity and a younger age at maturity. Negative size selection by migration barriers in both natural and human-altered systems has been documented as resulting in shifts to a smaller size at maturation (e.g., Sockeye Salmon *O. nerka*: Carlson and Quinn 2007; sea-run Brown Trout *Salmo trutta*: Haugen et al. 2008). Evidence suggests that in the Penobscot River, the ratio of smaller adults (1 sea winter) to larger adults (>1 sea winter) is relatively high (Friedland et al. 1996; Martinez et al. 2001), and this trend is increasing over time (Juanes et al. 2004). Changes in growth conditions have been implicated (Friedland and Hass 1996; Friedland et al. 1996), but size selection at dams may be a contributing factor.

Environmental Factors

Analysis of data for ROR fish indicated that environmental conditions had a significant influence on rates of passage at the lower dams. Several studies have demonstrated that environmental conditions can adversely affect the behavior of migrating Atlantic Salmon, consequently influencing their overall migration success (Laine et al. 2002; Richard et al. 2014). This information is important to consider when implementing a fish transport program to maximize spawner success.

Assumptions of the Analysis

When PIT tag technology is used to assess the efficacy of transport, it is important to consider the numerous factors that could bias the results and confound conclusions. Our comparison of arrival success and passage success at dams assumed that detection probability did not vary between the release groups. Our assessment of detection probability at the antennas did not reveal any substantial variation between ROR and TRKD groups. In addition, we found that fish from the two release groups arrived at the upper dams in approximately equal proportions. Therefore, variation in the arrival dam should not confound the conclusions about group differences in arrival success at the upper dams. A number of alternative methods could have been used to analyze these data; in terms of our main objectives, however, we do not feel that a change in methods would have significantly altered our primary conclusions that (1) live transport of adult Atlantic Salmon greatly increased their migration success to the upper dams and decreased their transit time; and (2) larger adults experienced a lower passage rate than smaller adults.

By the time of writing, Great Works and Veazie dams had been removed from the Penobscot River. Lundqvist et al. (2008) used a modeling approach to show that the removal of migratory barriers can increase Atlantic Salmon populations by 500% via decreasing migratory delays and improving access to quality spawning habitat. The PRRP offers a large-scale test of managers' ability to increase Atlantic Salmon populations via dam removal. Although the transport of fish is generally not viewed as a sustainable restoration solution (Clemens et al. 2009), the present study demonstrates that live transport can be a successful management tool for use with Atlantic Salmon; this mitigation strategy also avoided significant size-selection effects. The ultimate influence of a live-transport program on spawning success will therefore depend upon where the fish are released and the environmental conditions existing at the time of release.

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