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ARTICLE

Migration of Atlantic salmon (*Salmo salar*) smolts in a large hydropower reservoir

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Abstract: Migration rates, delay, timing, and success of acoustic-tagged Atlantic salmon (*Salmo salar*) presmolts (n = 120) and smolts (n = 57) are reported as they moved through the large Mactaquac Generating Station (MGS) reservoir and subsequently the lower Saint John River (SJR). The potential relationship between fish movements and the MGS operations was examined directly and via a hydrodynamic model. Migration rates were 15.4–29.3 km·day^{-1} within the river sections and 5.0–13.3 km·day^{-1} through the reservoir, a significant reduction of 32%–57%. Migratory timing was temporally mismatched with dam operations such that only a few (n = 3) smolts had the option of dam passage via spill. Migration success estimated as apparent survival was high through the reservoir (81%–100%), declined by 8%–32% during passage at the MGS, and additional losses (27%–55%) occurred during the migration to the lower SJR, such that overall survival to the estuary for the groups tagged as autumn presmolts was 61%–65%, and survival for those tagged as spring smolts was 6%–10%.

Résumé : Le présent article fait état des vitesses, retards, moments et succès de la migration de saumons atlantiques (*Salmo salar*) dotés d'étiquettes acoustiques aux stades de pré-saumoneau (n = 120) et de saumoneau (n = 57), durant leurs déplacements à travers le grand réservoir de la centrale électrique de Mactaquac (CEM), puis dans le cours inférieur du fleuve Saint-Jean (FSJ). Le lien potentiel entre les déplacements des poissons et les activités à la CEM a été examiné directement et par l'entremise d'un modèle hydrodynamique. Les vitesses de migration étaient de 15,4–29,3 km·jour^{-1} dans les tronçons du fleuve et de 5,0–13,3 km·jour^{-1} dans le réservoir, pour une baisse significative de 32–57 %. Le moment de la migration était décalé dans le temps par rapport aux activités au barrage, de sorte que seuls quelques saumoneaux (n = 3) avaient l'option de franchir le barrage par l'évacuateur. Le succès de migration, estimé comme étant le taux de survie apparent, était élevé dans tout le réservoir (81–100 %) et diminuait de 8–32 % durant le passage dans la CEM, d'autres pertes (27–55 %) se produisant durant la migration dans le cours inférieur du FSJ, de sorte que les taux de survie globaux une fois l'estuaire atteint pour les groupes étiquetés comme étant des pré-saumoneaux de l'automne étaient de 61–65 %, et pour ceux étiquetés comme des saumoneaux du printemps étaient de 6–10 %. [Traduit par la Rédaction]

Introduction

Migration of diadromous fishes is challenged worldwide by hydropower stations and the reservoirs they create, risking loss of some species such as eels (*Anguilla* spp.), shads (*Alosa* spp.), and salmonids (Liermann et al. 2012; Xu et al. 2017). This paper focuses on the downstream migration of juvenile Atlantic salmon (*Salmo salar*) in a large regulated river. Dam passage of salmonids has been extensively studied (see review Noonan et al. 2012), but less attention has been given to migratory delay or other complications caused by suppressed water currents in large reservoirs (Pelicice et al. 2014). Shifting river habitat from lotic to lentic can create an "ecological trap" (Robertson and Hutto 2006); where flowing water previously provided an ecological cue for direction and a potential transport mechanism, now low flows are found. Inundating sections of a river to create a reservoir for hydropower production decreases water currents, which has been shown to lead to migratory delay for smolts in some salmonid populations (Ruggles 1980; Stich et al. 2015). Migratory delay may increase the risk of predation (Poe et al. 1991) and decrease survival probabilities when smolts cannot reach ocean waters within the physiologically and environmentally determined "smolt window" (McCormick et al. 1998).

In addition to the potential effects of the reservoir on smolt migration, the dam operations can affect fish migrations by controlling how and when passage options such as spillways and bypasses are available (Coutant and Whitney 2000) and by controlling the flow of water through the dam, which could influence the flow patterns in the forebay and reservoir areas (Connor et al. 2003).

Another factor contributing to the migration success and timing of smolts from large river systems is the sometimes-high proportion of populations that employ a presmolt migration strategy of moving downstream into the main stem for the winter. It is thought that the presmolt strategy may be an adaptation in large river systems where the putative smolts may move out of smaller tributaries that may experience more dynamic winter conditions and position themselves closer to the river mouth in preparation

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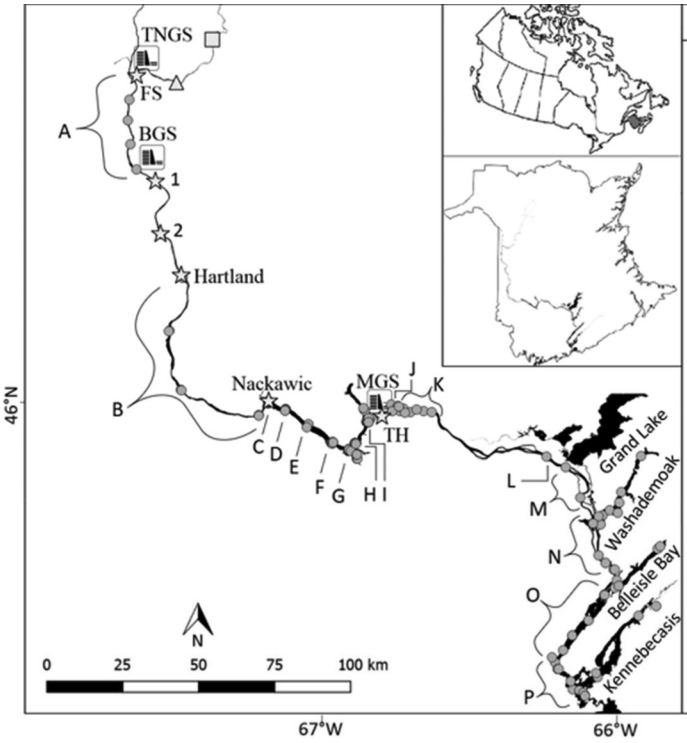
Fig. 1. Locations of receivers (circles), hydropower generation stations (TNGS = Tobique-Narrows, BGS = Beechwood, MGS = Mactaquac), Atlantic salmon presmolt and smolt capture (rotary smolt traps at square, gatewells at BGS), tagging (triangle), and release sites (stars; FS = free-swim, TH = trap-and-haul) along the Saint John River, New Brunswick, Canada. The dead-end tributary Longs Creek is located between reaches G and H. Associated table delineates Cormack–Jolly–Seber groupings with maximum number of receivers in the main stem in any given study year. Map created in QGIS with basemaps provided by GeoNB (2014*a*, 2014*b*) and data points created by the current study.



Reach	Rkm	Number of receivers
A	288-313	5
B	192-250	4
C	187	2
D	182	3
E	175	3
F	167	3
G	162	2
H	158	3
I	150-152	5
J	146	2
K	138-144	5
L	95	1
M	76-89	2
N	53-68	4
O	20-50	8
P	9-15	5

for the smolt migration the following spring (Riddell and Leggett 1981; Buck and Youngson 1982).

As plausible mechanisms exist for how smolt migration may be affected in hydropower regulated rivers, the migration success and rates within the impounded Saint John River (SJR), New Brunswick, Canada, are of high interest for conservation efforts of the endangered Outer Bay of Fundy Atlantic salmon population (Committee on the Status of Endangered Wildlife in Canada 2011). To better understand the relationship between Atlantic salmon smolt migration and the hydropower operations at the largest hydropower facility on the SJR, the Mactaquac Generating Station (MGS), this study quantifies migration rates in relation to water currents within the large hydropower reservoir, as well as examines the migratory timing, specifically of dam passage at the MGS. The main objective was to relate the movements of acoustic-tagged Atlantic salmon smolts to hydropower operations at the MGS to examine the extent to which the fish behavior and survival may be influenced by these operations. The second objective was to quantify any delay attributable to the hydropower operations, whether due to reservoir passage or directly by the MGS, and identify any sections of the SJR that may act as migration bottlenecks.

Materials and methods

Study site

The SJR is the longest river in New Brunswick (700 river km (rkm), the distance measured on the centerline of the river, mean width 750 m, mean depth 2 m; Kidd et al. 2011). Discharge ranges from 280 $m^3 \cdot s^{-1}$ in the summer to ~10 000 $m^3 \cdot s^{-1}$ during the spring freshet (Kidd et al. 2011). The SJR has three hydropower generating stations along the main migratory route of juvenile Atlantic salmon as they migrate downstream from the tributary with the most nursery habitat, the Tobique River, to the Bay of Fundy (Marshall et al. 2014; Chateauvert et al. 2018). The migrating presmolts (45%–81% of the smolt population in 2007–2012; Jones et al. 2014) and smolts first encounter the Tobique-Narrows Generating Station (TNGS) located 315 rkm from the Bay of Fundy, followed 30 rkm downstream by the Beechwood Generating Station (BGS) at rkm 285, and finally the MGS after an additional 135 rkm downstream at 150 rkm before they enter the free-flowing section of the SJR to the estuary. Of these three hydropower stations along the main migratory route of smolts, the MGS has the largest reservoir (97 rkm) that is 30–40 m deep, with severely reduced water currents creating a lake-like environment for 37 rkm of its length. Upstream of this reach (Nackawic, reach C; Fig. 1), the river substantially narrows in width and becomes more shallow in depth (<20 m), increasing water velocity. Therefore, this study considered reaches C–I (Fig. 1) to be the lentic section (mean 0.04 $cm \cdot s^{-1}$; M. Ndong, University of New Brunswick, unpublished data) and was termed "reservoir", whereas reach B (Fig. 1) was a more lotic section (mean 0.14 $cm \cdot s^{-1}$; M. Ndong, University of New Brunswick, unpublished data) and was termed "upriver". Downstream of the MGS was termed "downriver" (reaches J–P; Fig. 1). There are two dead-end tributaries within the reservoir where receivers were located to identify whether these areas were of concern for migratory delay. Long Creek is situated at a large, almost 90° bend in the MGS reservoir between reaches G and H (Fig. 1), and the Mactaquac Arm is located northwest of the MGS (Fig. 1).

Fish and tagging

Atlantic salmon presmolts and smolts from both wild and hatchery origin were acoustic-tagged and tracked during 2014–2016 to determine downstream movement rates and success (Table 1). Tagging was performed on the presmolt life stage during their autumn outmigration, which allowed for acclimatization

Table 1. River age (years), weight (g), and fork length (cm) (mean ± SE) of wild, hatchery-born (i.e., hatchery smolts; HS), and captive-reared (CR) Atlantic salmon presmolts and smolts tagged between 2014 and 2016.

Tagging date	Origin	*N*	River age (years)	Weight (g)	Fork length (cm)
21–26 May 2014	HS	20	—	41.7±1.7	16.8±0.2
29 May – 1 June 2014	Wild	20	—	41.4±2.3	17.2±0.3
17–20 Nov. 2014	Wild	5	2.0	67.7±12.9[a]	19.3±1.2[a]
8 Dec. 2014	CR[b]	15	1.6±0.2	39.4±2.0	15.6±0.2
19 May – 2 June 2015	Wild	20	2.3±0.1	41.0±1.6	16.5±0.2
28 Oct. – 25 Nov. 2015	Wild (FS)	50	1.8±0.1	40.4±0.9	16.2±0.1
28 Oct. – 25 Nov. 2015	Wild (TH)	50	1.7±0.1	40.6±0.8	16.1±0.1
27 Oct. – 9 Dec. 2015	Wild (DT)	50	—	44.6±1.2[c]	16.3±0.1
5 Nov. – 10 Dec. 2015	Wild (UT)	50	—	42.9±1.6[c]	16.2±0.2
31 May 2016	HS	7	1.0±0.0	48.7±2.2[d]	17.5±0.3[c]
15–27 May 2016	Wild	30	2.3±0.1	44.9±2.4[d]	17.4±0.3[c]

Note: FS, free-swim; TH, trap-and-haul; DT, dummy-tagged; UT, untagged.

[a]Wild presmolts were significantly larger than all other presmolt groups.

[b]Wild presmolts held at the Mactaquac Biodiversity Facility for ~1 month prior to acoustic tagging.

[c]Dummy-tagged and untagged control groups were measured after 3 weeks in the hatchery, where they were fed a commercial pellet feed to daily satiation, resulting in slight weight increases in comparison with experimental groups.

[d]Smolts tagged in spring 2016 were significantly larger than all other smolt groups.

over the winter before being tracked in the spring, limiting misinterpretations of the data due to potential tagging impacts that might skew results (Cooke et al. 2011).

Presmolts and smolts of wild origin were preferred, but in cases where wild fish were not captured in sufficient numbers, spring smolts born in captivity (F_1 hatchery smolts raised from wild brood stock; HS) were used to supplement the tagging efforts (Table 1). In addition, migrating wild presmolts (n = 15) collected for the Tobique River adult captive-rearing program (Jones et al. 2004) were used in autumn 2014 to supplement tagging. These wild-origin, captive-reared smolts (CR) spent <1 month at the Mactaquac Biodiversity Facility (4 rkm downstream of the MGS) in large cobble-bottomed enclosures with river water flow-through to simulate the natural environment prior to tagging and release back into the wild environment (Table 1). Wild fish from the Tobique River were sourced from rotary smolt traps (Fig. 1) or from the BGS gatewells, which are the areas leading to the turbine and spillway gates. Overall, the study included 27 HS and 70 wild smolts tagged over multiple spring seasons and 15 CR and 105 wild presmolts tagged over multiple autumn seasons (with an additional 100 wild presmolts in control groups; Table 1).

In spring 2014, the first 10 HS fish were tagged at the Mactaquac Biodiversity Facility and transported by truck for 2 h and additionally for 1 h by boat to a release site 4 rkm downstream of the BGS (site 1; Fig. 1). Thereafter, fish were transported by truck for 3 h to a more accessible release site 20 rkm downstream of BGS (site 2; Fig. 1), avoiding additional handling that was required for boat transport. Wild smolts from the BGS gatewells were tagged on site then transported for 2 h 40 min to release site 2. In autumn 2014, presmolts from the BGS gatewells were tagged on site and transported for 15 min to release site 1. CR fish were tagged at the Mactaquac Biodiversity Facility, held for 3 days, then transported for 2 h to either the BGS tailrace while the immediate turbine was off (n = 7) or to release site 1 (n = 8). In the first 10 days of spring 2015, fish were transported for ~30 min to a holding tank with gravity-fed flow-through from a nearby brook (triangle, Fig. 1) where they were observed for 24 h before tagging and allowed to recover for another 24 h before being released at site 2. To reduce transport time, we either tagged fish captured (starting 29 May) at the capture or release site (2) and observed for 1–4 h before release. During all transport, fish were provided with aeration either in a 45 L cooler or a large transport tank.

In autumn 2015, a study on the migration success of presmolts in relation to a newly constructed bypass structure at the TNGS was initiated (A.B. Babin, S. Peake, R. Jones, R.A. Curry, and T. Linnansaari, unpublished data). In that study, the efficacy of a free-swim (released just downstream of TNGS) versus a trap-and-haul (released just downstream of MGS) strategy was compared by assessing apparent survival probabilities of 50 presmolts within each group to the SJR exit. Data from these groups in regard to migration rates were retained for use in the current study. Control groups of dummy-tagged and untagged presmolts (n = 50 each) were held over winter to estimate the prevalence of tag loss and natural mortality. These fish were sourced from the rotary smolt traps, transported for 20 min to the gravity-fed holding tank, and observed for 24 h before tagging. Tagged fish were then transported for 30 min for the free-swim release group or for 2 h for the trap-and-haul group. Control fish were held at the Mactaquac Biodiversity Facility.

In spring 2016, wild fish from the rotary smolt traps (n = 18) and the BGS gatewells (n = 12), as well as HS fish (n = 7) were observed for 24 h before and after tagging before releasing the wild fish in Hartland (upper reach B; Fig. 1) and the HS fish in Nackawic (reach C; Fig. 1).

Acoustic (69 kHz) V7 tags (Vemco, Halifax, Nova Scotia) that were used were 7 mm in diameter, 20 mm in length, weighing 1.6 g in air and 0.75 g in water. The tag:body weight ratio was kept under 5% (mean 3.95% ± 0.69%) to avoid tagging effects on swimming performance and survival (Thorsteinsson 2002). Tagging was performed using 40 ppm clove oil as anesthetic (eugenol as active ingredient; ethanol in 1:10 ratio used as carrier; water temperatures ranged from 0.3 to 7.3 °C in autumn and from 11.5 to 16.9 °C in spring, 206 ± 111 s), with surgery lasting 162 ± 76 s for an acoustic tag to be inserted into the body cavity and closed using two monofilament sutures (Monosof 6-0, ce-2 needle). Scale samples were also taken from the standard sampling position for aging (Shearer 1992). When tagging presmolts in autumn, tags were programmed to ping at least every 230–370 s for ~30 days to ensure the tag was functional and the fish had moved from the release site, then turned off to conserve battery life throughout the winter and resume pinging every 30–90 s during spring migration starting in April, lasting ~62–82 days. Owing to a logistical error, the tags placed in the presmolts in autumn 2014 were reactivated late in spring 2015 when the smolt migration had already begun. Therefore, some upriver and reservoir movements were not detected due to tag inactivity, but their presence can be inferred from detections downriver. For this reason, the 2014–2015 presmolt group was not included in the apparent survival

analysis; however, movement data of those smolts that were detected after tag reactivation were used in other analyses. Smolts tagged in spring always had tags pinging every 30–90 s that were estimated to last 132 days.

Presmolts and smolts were passively tracked downstream through the SJR and MGS reservoir using a network of passive VR2W receivers (47 in spring 2014, 17 in autumn 2014, 38 in spring 2015, 59 in autumn 2015, 76 in spring 2016; Fig. 1). Range-testing of the receiver setup was performed and reported in a separate study (Babin et al. 2019), documenting mean detection ranges of 246–307 m for V7 tags using VR2W receivers. The fish were also actively tracked throughout the river for a total of 63 hydrophone hours using a VR100 receiver to confirm final positions when outside of the detection range of passive receivers. Active tracking was restricted to daylight hours and wind speeds below 25 $km \cdot h^{-1}$. Through a data partnership with the Ocean Tracking Network, smolts were detected by an additional $n = 12$ passive receivers in the downriver section during spring 2015, as well as by one receiver in the Saint John Harbour (spring 2016) and two receivers within the Halifax Line (spring 2015).

All experimental protocols were approved by the University of New Brunswick Animal Care Committee in accordance with the guidelines provided by the Canadian Council on Animal Care, and scientific licenses were granted by Fisheries and Oceans Canada (License 325657).

Hydrodynamic model

Fish movements were examined in relation to water velocity and direction by modelling these variables through time and space. The numerical model Delft 3D (Delft3D-FLOW 4.01.00; Deltares 2013) used hourly inputs of tailrace discharge from the BGS, total discharge through the MGS, incoming tributary discharges, wind speed and direction, and bathymetric data to estimate surface (5 m) water velocities ($cm \cdot s^{-1}$, angle from downstream) every 2 h during the study period at the same locations as the acoustic receivers (Haralampides et al. 2018; M. Ndong, K. Haralampides, G. Yamazaki, and R.A. Curry, unpublished data). The bathymetry data used to set up the model were collected by the Ocean Mapping Group from the University of New Brunswick using a multibeam system (Bremner et al. 2016), and the topographic data were obtained from the Province of New Brunswick (GeoNB 2005). From these, a curvilinear grid was developed to represent the river. Discharge and water level calibration and validation data were provided by New Brunswick Power for the BGS and MGS. Based on historical data, the initial water level depth in the MGS reservoir was set to 40.5 m. The computational model was calibrated by comparing the predicted and observed water levels at various locations in the reservoir and the predicted and observed discharge at the MGS. The model predictions were then validated against an independent set of observed data by comparing the water levels at rkms 167 (reach F; Fig. 1) and 233 (reach B; Fig. 1) and several other locations, as well as the discharge at the MGS. There was good agreement between the observed data and the Delft3D model results ($r^2 > 0.99$; M. Ndong, K. Haralampides, G. Yamazaki, and R.A. Curry, unpublished data).

Statistical analyses

Differences in weight and length were considered separately for presmolts and smolts, since the latter would have had an extra winter of growth before measurement. Two-way ANOVAs were used to compare weight or length among tagging years and origin (wild versus HS or CR) and among tagging years and river age for presmolts. Tukey's honestly significant differences test was used for post hoc tests.

The fate of each individual was determined based on the presence, duration, and location of detections. This was possible due to the extensive receiver network that was found to produce excellent encounter probabilities upstream of the MGS through Cormack–Jolly–Seber modeling (see below) and from the tested detection range of 246–307 m for V7 tags using VR2W receivers (Babin et al. 2019), ensuring that movements could be inferred from the presence or absence of detections. Three categories of the fate of fish were defined:

(1) Tag loss or mortality — presmolts and smolts were presumed to have either lost their tag or died when they were never detected, detections were near continuous at a single receiver line for the duration of the battery life of the tag, or detections ceased abruptly within the battery life of the tag, indicating that the tag or fish had been lost in an area outside the detection range of any receivers. Tag loss or mortality could be attributed to natural causes such as overwintering stress, tagging effects, dam or reservoir related impacts, or predation. In one case detections indicated active fish movements for a period of time before presumed tag loss; therefore, these data were included in all analyses except survival analyses.

(2) Unsuccessful migrants — smolts were considered to have been unsuccessful in migrating downstream of the reservoir when the last detection came from a receiver upstream of the MGS (reach I; Fig. 1).

(3) Successful migrants — smolts detected downstream of the MGS were known to have passed the dam, but if they were not detected greater than 7 rkm downstream, they were considered to have experienced delayed mortality from dam passage. Although, it is possible that fish experienced natural mortality in this area unrelated to the effects of dam passage. If a fish was detected on the lowermost receivers located 9–20 rkm from the mouth of the SJR (lower SJR; reach P; Fig. 1), it was considered to have successfully migrated out of the river.

Overwintering locations were inferred from the detection patterns of presmolts tagged in autumn. The location of the last detection before the programmed tags turned off for the winter was contrasted with the location of the first transmission in the spring. If detection locations were from the same river reach, then the fish was assumed to have overwintered in that area, whereas if the detections indicated directed downstream movement, then the overwintering location was assumed to have been upstream of the first spring detection.

Migration success is discussed by reporting the absolute number of fish that reached key locations (reservoir, dam passage, and lower SJR < 20 rkm from the river mouth) and the number and location of suspected mortalities. Migratory timing to key locations is visualized and discussed between groups and in relation to whether the spillway gates at the MGS were open and available for fish passage.

Cormack–Jolly–Seber (Lebreton et al. 1992; Bowerman and Budy 2012) models were constructed to estimate survival (Φ) and encounter (p) probabilities during the spring migration of four groups: 2014 smolts, 2015–2016 free-swim presmolts, 2015–2016 trap-and-haul presmolts, and 2016 smolts. When predation was apparent (e.g., abrupt movement away from the main migratory pathway to a side channel or bay), only those detections determined to have been observed from a smolt were included in the apparent survival analysis. Cormack–Jolly–Seber models use the number of unique tags detected on receivers and the detection efficiency of the receivers to estimate survival for each reach (Lebreton et al. 1992; Bowerman and Budy 2012). The models assumed that during the spring migration, tagged individuals were representative of the population, survival probabilities did not differ between tagged and untagged individuals, each tagged individual had equal but independent probabilities of survival and detection, no tags were lost, sampling was instantaneous, and movement was generally unidirectional (downstream). While each detection was recorded "instantaneously" by receivers, the detections from the pooled receivers within each reach would

Table 2. Model type and formula, sample size (*N*), and coefficient estimates, standard errors (SE), *z* values (ordinal regression model, ORM) or *t* values (linear mixed effects models, LMEM; and linear mixed effects, LME, logistic regression model), and *p* values.

Model type	*N*	Coefficient	Estimate	SE	*z*/*t*	*p*
(*a*) ORM: success index ~ tide + temperature_avg + water_velocity_avg + fish_km_day + proportion_upstream						
	N = 64	Tides ebb vs. flood	−0.16179	0.35405	−0.457	0.648
		Tides overall	−4.85893	0.98379	−4.939	<0.001
		Temperature_avg	−0.83411	0.48017	−1.737	0.082
		Water_velocity_avg	0.06902	0.36907	0.187	0.852
		Fish_km_day	0.27384	0.34296	0.798	0.425
		Proportion_upstream	−0.18623	0.35170	−0.530	0.597
(*b*) LMEM: fish_km_day ~ reach + (1|fish_id)						
	N = 159 from 76 fish	Reach	4.162	1.078	3.860	<0.001
(*c*) LMEM: fish_km_day ~ reach × temperature_avg × water_velocity_avg + (1|fish_id)[a]						
	N = 867 from 65 fish	Reach	0.5308	2.2648	0.234	0.815
		Temperature_avg	10.8308	3.0467	3.555	<0.001
		Water_velocity_avg	2.6082	1.9935	1.308	0.191
(*d*) LMEM: velocity_difference ~ reach + (1|fish_id)						
	N = 1279 from 65 fish	Reach	6.044	1.309	4.618	<0.001
(*e*) LME logistic regression model: fish_direction ~ reach × water_angle + (1|fish_id)[a]						
	N = 1279 from 65 fish	Reach	0.014	0.005	2.666	0.008
		Water_angle	0.006	0.008	0.082	0.935

[a]Interactions (not shown) were nonsignificant.

span a longer period of time that was considered an "instant" within the context of the smolt window. Survival probabilities and encounter estimates were assessed for 15 reaches with detections of all the receivers within each reach being pooled to reduce model overfitting (Fig. 1), and encounter probabilities were pooled within study years. Detection probability (aka encounter estimates) was considered reliable when >50%. Survival over each reach was estimated as $k = \Phi^d$, where k is the survival probability of a reach, Φ is the survival estimate per rkm, and d is the distance (reach length; rkm) of each reach. A null model whereby survival and encounter probabilities were not allowed to vary by reach was constructed for base comparison. The comparison of models with or without spatial variability was based on Akaike's information criterion corrected for small sample sizes (AIC_c), and the model with the lowest AIC_c was selected as the best model (Akaike 1973; Burnham and Anderson 2002). Cumulative apparent survival probabilities were compared between the presmolt and smolt groups using a χ^2 test.

Overall migration success was coded as an index as follows: 0 = no dam passage, 1 = dam passage, 2 = movement downstream of the MGS (reach J), 3 = mid-way downriver (reach L), 4 = arrival to the lower SJR (top of reach P), 5 = exit of the lower SJR (bottom of reach P), 6 = outside of SJR (Fig. 1). An ordinal regression model (Table 2*a*) was used to identify the variables affecting migration success, including the fixed effects of tides, average water temperature throughout the migration, average water velocities in the reservoir, the fish's migration rate through the reservoir, and the proportion of time the fish spent traveling in the reversed direction upstream of the MGS. Fish that reached the lower SJR were assigned an ebb or flood state based on their last detection, whereas those that did not reach the lower SJR were assigned a null tide state because the tidal effect was not expected to be strong enough to affect fish movements upstream of this area. Continuous variables were scaled using *z* scores to account for differences in units, and candidate variables were assessed for multicollinearity prior to analysis. Water temperature values were taken from temperature loggers deployed at mid-column alongside the receivers. A proportion (21%) of fish movements could not be directly linked with concurrent water temperatures, in which case temperature values were interpolated based on the closest spatial and temporal locations.

Linear mixed effects models (LMEM; Tables 2*b*–2*e*) were used to identify the variables affecting migration rates and the proportion of time fish spent swimming upstream. These models allowed for different intercepts for each fish via the random effects, candidate variables were assessed for multicollinearity prior to analysis, and continuous variables were scaled using *z* scores to account for differences in units.

The first LMEM compared overall migration rates (km·day^{-1}) within the upriver, reservoir, and downriver reaches (Table 2*b*). These rates were calculated as (*i*) upriver: from the first detection indicating the initiation of migration (directed downstream movements) to the first detection as they entered the reservoir (reach C); (*ii*) reservoir: from the last detection as they first entered the reservoir (reach C) to the first detection near the MGS (reach I); and (*iii*) downriver: from the last detection as they were first detected downstream of the MGS (reach J) to the first detection at the last receiver they were observed at downriver (Fig. 1). One-way ANOVAs were used to compare overall migration rates between wild and HS or CR fish and between years. Migration rates were further examined by only considering downstream movements between receivers within the upriver and reservoir reaches. These fine-scale movements (km·day^{-1}) were related to concurrent water temperatures and velocities (m·s^{-1}) through a second LMEM (Table 2*c*). A third LMEM (Table 2*d*) was used to determine whether smolts were moving passively (fish migration rate < water velocity) or actively (fish migration rate > water velocity) in the upriver and reservoir reaches by subtracting water velocities from fish velocities (km·day^{-1}) for each movement between receivers.

The proportion of time that fish spent traveling in the reversed direction to their out-migration and the minimum extra rkm that they swam upstream of the MGS was calculated. The proportion of time was based on observed travel times for each individual fish, and the distance covered was based on centerline distances between receivers, meaning they were minimum distances and did not take into account the potential back-and-forth movements outside of the detection area of the receivers. Fish direction (upstream or downstream) between receivers was examined using an LME logistic regression model in relation to the associated maximum water angle from downstream in the upriver and reservoir reaches (Table 2*e*). Water angle was an output of the hydrodynamic model and varied depending on wind strength and direc-

tion, as well as changes in dam operations that could either pull the water toward the dam or have a backwater effect when gates were closed.

Migratory delay was partitioned to components in relation to the causing mechanism (i.e., delay likely due to the slower than prereservoir water currents, time spent searching within dead-end tributaries, and searching for the downstream exit as well as dam passage itself). A pre-MGS reservoir migration rate was estimated for each tagged fish by applying their respective up- or downriver migration rates to the distance of the reservoir (37 rkm), providing a duration of time that the fish would have been expected to be able to traverse this distance if the water was flowing at a river rate as opposed to a slow-moving reservoir. These expected durations were compared with the observed duration of time each fish used to travel over that distance (from Nackawic to their first encounter with the MGS) to provide an estimate of delay. Observed and expected durations based on up- and downriver migration rates were compared using paired *t* tests. Delay due to dam passage was quantified in two ways: (*i*) the duration of time between the first detection at the MGS and the last detection before passing the MGS and (*ii*) the duration of time between the last detection upstream and the first detection downstream of the MGS. During the time between the first detection at the MGS and the last detection before passing the MGS, detections were examined to estimate the number of times each fish presumably attempted to pass the dam. An attempt for dam passage was defined as being detected near the MGS (up to 1 rkm away; first attempt), moving away from the MGS (at least 3 rkm), then returning to near the MGS (second attempt).

Analyses were done in R Studio (version 1.1.423; RStudio, Inc., packages car, lme4, lmerTest, ordinal), with the exception of Cormack–Jolly–Seber analyses done in Program MARK (version 8.2; White and Burnham 1999). Normality plots were analyzed where appropriate, and statistical significance was assumed at $p \leq 0.05$.

Results

Wild presmolts were significantly heavier (two-way ANOVA, $F_{[1,116]} = 44.738$, $p < 0.001$) and longer (two-way ANOVA, $F_{[1,116]} = 71.710$, $p < 0.001$) than CR fish. Those tagged in 2014 were significantly heavier (two-way ANOVA, $F_{[2,116]} = 4.488$, $p = 0.013$) than those tagged in 2015 in the free-swim group (Tukey HSD, $p = 0.016$) and the trap-and-haul group (Tukey HSD, $p = 0.02$), but these groups did not differ by length (two-way ANOVA, $F_{[2,116]} = 1.453$, $p = 0.238$). Freshwater age-2+ presmolts were ~4 g heavier (two-way ANOVA, $F_{[1,78]} = 7.305$, $p = 0.008$) and 0.6 cm longer (two-way ANOVA, $F_{[1,78]} = 12.242$, $p < 0.001$) on average than age-1+ presmolts.

Smolt weight (two-way ANOVA, $F_{[1,81]} = 0.008$, $p = 0.928$) and length (two-way ANOVA, $F_{[1,81]} = 1.297$, $p = 0.258$) did not differ by origin, but those tagged in 2016 were significantly heavier by 4 g (two-way ANOVA, $F_{[2,81]} = 4.591$, $p = 0.013$) and longer by 1 cm (two-way ANOVA, $F_{[2,81]} = 6.243$, $p = 0.003$), on average, than those tagged in 2014 (Tukey HSD, weight: $p = 0.020$, length: $p = 0.041$) or 2015 (Tukey HSD, weight: $p = 0.038$, length: $p = 0.003$).

Dummy-tagged and untagged presmolt control groups held over the 2015–2016 winter season (A.B. Babin, S. Peake, R. Jones, R.A. Curry, and T. Linnansaari, unpublished data) indicated that overwinter mortality and tag loss was expected to be 36%. Of the autumn-tagged presmolt and spring-tagged smolt groups released upstream of the MGS, 20 (14%) tags were never detected and 53 (36%) individuals were determined to have either lost their tag or experienced mortality. Of the one autumn-tagged presmolt group that was released downstream of the MGS, 5 (10%) tags were never detected and 34 (78%) were determined to have either lost their tag or experienced mortality. With one exception of clear fish movements before presumed tag loss, detections of these individuals were removed from analyses to avoid methodological bias on the results.

Table 3. Model selection of Cormack–Jolly–Seber survival (Φ) and encounter (*p*) probabilities with (*s*) and without (.) spatial variability.

Model	AIC_c	w_i	Evidence ratio
$\Phi(s)p(s)$	970.1952	1.00000	5.19×10^{37}
$\Phi(s)p(.)$	1124.3836	0.00000	17 126
$\Phi(.)p(.)$	1143.8804	0.00000	1

Note: Evidence ratio describes the likelihood of the best model being correct over the least plausible model. Also shown are Akaike information criteria corrected for small sample sizes (AIC_c) and relative plausibility of each candidate model (i.e., model weight, w_i).

Overwinter

Overwintering locations were determined for the presmolts for the two winters in 2014–2015 (released at site 1; Fig. 1) and 2015–2016 (released at the tailrace of the TNGS; Fig. 1). Two fish from the former group remained within the BGS reservoir over winter. The upriver section (reach B; Fig. 1) was used for overwintering by eight presmolts, whereas the majority of fish ($n = 18$) overwintered in the upriver-top of reservoir transition area (reaches B–C; Fig. 1). Entry into the MGS reservoir was infrequent, but one fish was detected entering the reservoir in the winter with its first spring detection just 17 rkm upstream of the MGS, and another presmolt overwintered within the reservoir only 12 rkm upstream of the MGS (reach G; Fig. 1). No winter movement through the MGS was documented in this study. In the 2015–2016 group released downstream of the MGS, only two moved downstream of their release site during the winter, being detected up to 17 rkm away (reach K; Fig. 1); however, neither of these fish were detected in the spring.

Migration success and timing

Overall, of all the tagged smolts successfully tracked in the reservoir ($n = 73$), 69 (95%) successfully navigated the reservoir and approached the MGS, 55 (80%) of which were able to pass the MGS, and 27 (49%) of those further reached the lower SJR.

Cormack–Jolly–Seber estimates of detection efficiency and survival were best explained with spatial variability (Table 3). Encounter estimates were less than 50% in areas outside of the reservoir that were covered by a single receiver (mainly in the downriver reach) but were greater than 50% for lines of multiple receivers within the reservoir (Fig. 2A).

Overall, apparent survival probabilities were 95% ± 0.01% (SE) to 100% as they entered the reservoir (reaches B–C; Fig. 2B) and remained stable within each group as they travelled through the reservoir, with the exception of the 2016 smolt group that declined by 12.5% (reaches C–I; Fig. 2B). Apparent survival probabilities declined by 8% ± 0.02% to 32% ± 0.05% during dam passage (reaches I–J; Fig. 2B), with smaller losses (8% ± 0.02%) in the group tagged as presmolts, and the greater losses (2014: 32% ± 0.05%, 2016: 20% ± 0.04%) being incurred by the groups tagged in the spring. Downriver, survival probabilities declined by 27%–55% (reaches J–P; Fig. 2B). It appeared as though the last reaches (N–P; Fig. 1) incurred losses of 10%–20% for most groups but was higher for the 2014 smolts (53%). Cumulative survival probabilities to the lower SJR ranged from 60% to 65% for groups tagged as autumn presmolts, which was significantly higher than the range for groups tagged as spring smolts (6%–10%; $\chi^2 = 8.717$, df = 1, $p = 0.003$; Fig. 2). Two CR fish from the 2014–2015 presmolt group continued on to the Bay of Fundy and were detected off the Halifax Line (9 and 26 June).

The index of migration success was not affected by average water temperature ($p = 0.082$; Table 2*a*) or velocity ($p = 0.852$; Table 2*a*), individual migration rates through the reservoir ($p = 0.425$; Table 2*a*), or the proportion of time that individual fish

Fig. 2. Cormack–Jolly–Seber (A) estimated probability of encounter (%) and SE in 2014 (open circles) and 2016 (closed circles) and (B) estimated cumulative probability of survival (%) and SE during the spring migration in 15 river reaches to scale according to reach length (Fig. 1) of Atlantic salmon smolts tagged as autumn presmolts (grey lines; 2015–2016 presmolts free-swim shown by open squares, trap-and-haul shown by closed squares) or spring smolts (black lines; 2014 = open circles, 2016 = closed circles). The shaded section represents the MGS reservoir, and the dashed vertical line represents the location of the MGS. The SE bar exceeding the *y* axis is attributed to the 2014 smolts (N–O = 58.3).

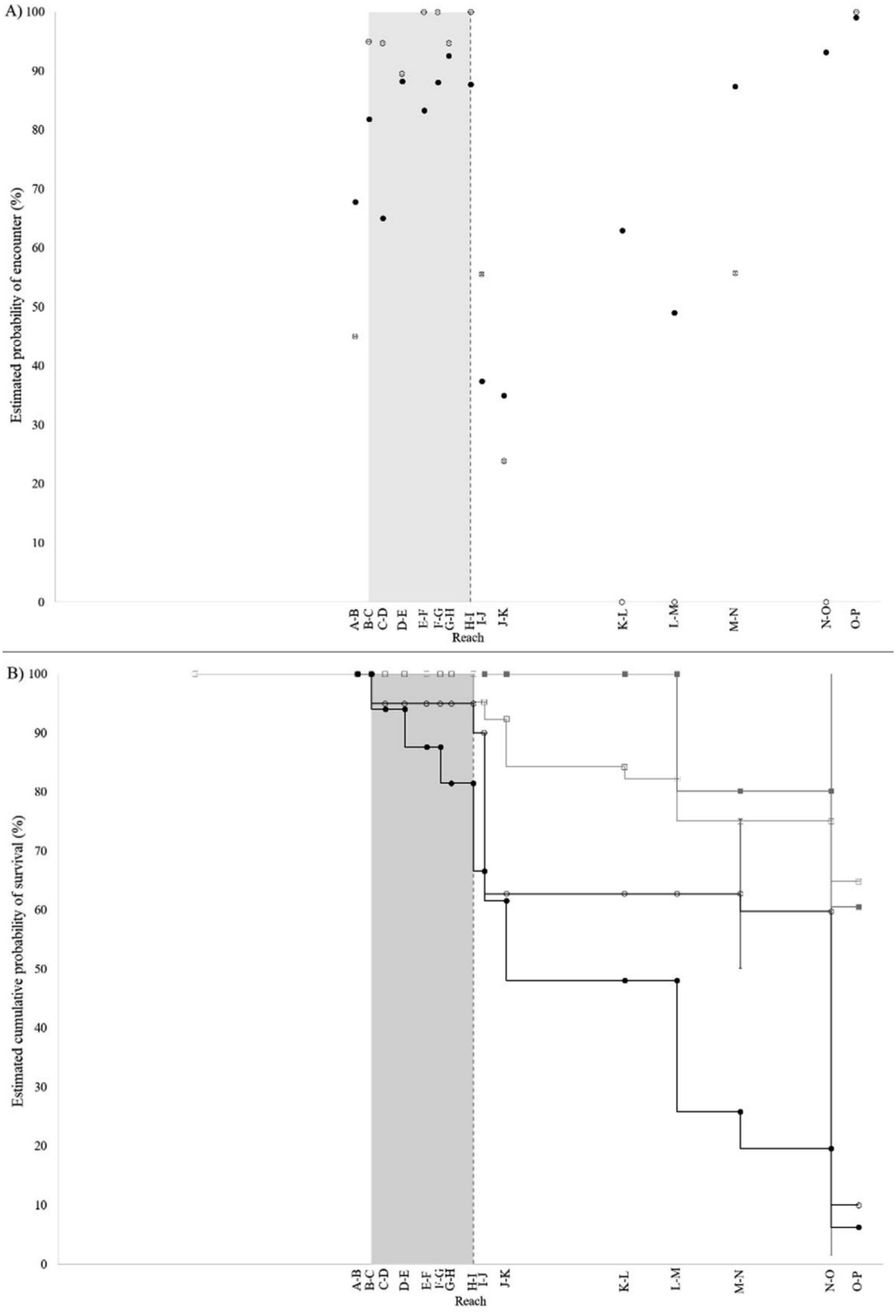
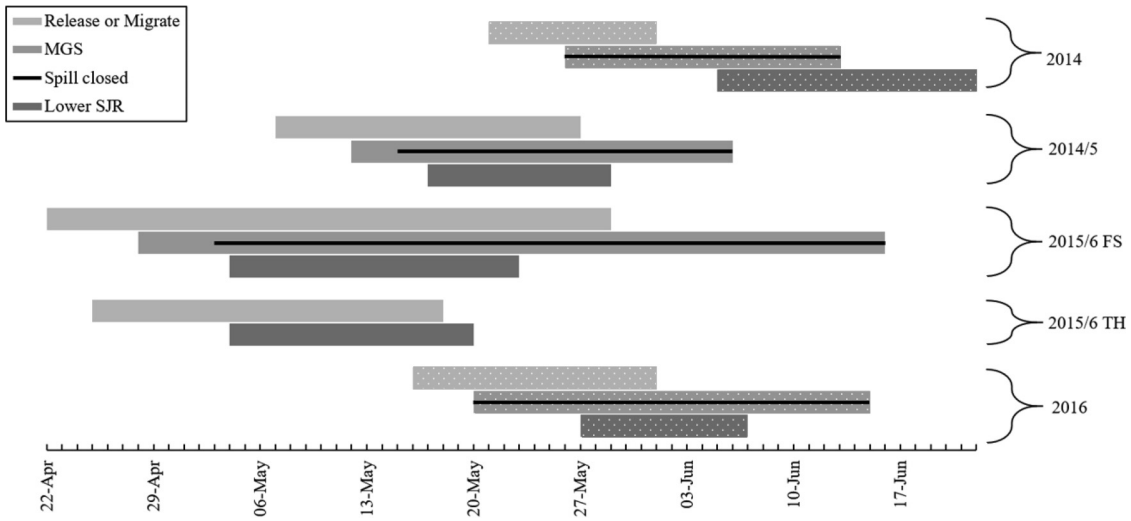


Fig. 3. Migration timing of Atlantic salmon tagged as presmolts (solid bars; 2014–2015, 2015–2016, FS = free-swim, TH = trap-and-haul) or smolts (textured bars; 2014, 2016) including release (smolts) or initiation of spring migration (presmolts; light grey), arrival to the MGS (medium grey), and arrival to the lower Saint John River (SJR; dark grey). The horizontal black line represents the time range over which the spillway gates typically used during high waters of the spring freshet are closed and unavailable for fish passage.



spent traveling upstream instead of downstream (p = 0.597; Table 2*a*). Migration success was significantly different according to whether the fish was assigned a tidal state (ebb or flood) if it reached the lower SJR or not (null; $p < 0.001$; Table 2*a*), but migration success was not significantly different between ebb and flood states for those fish that did reach the lower SJR (p = 0.648; Table 2*a*).

Areas of atypical smolt movements included Grand Lake (n = 1), Washademoak Lake (n = 5), Belleisle Bay (n = 6), and Kennebecasis Bay (n = 1; Fig. 1). In addition, five smolts were detected by downstream receivers and, subsequently, upstream receivers. The most extreme example was one smolt that was detected in reach P then subsequently in reach J without any detections from the 16 receivers between these reaches (Fig. 1).

The timing of migration initiation and arrival to the MGS of each tagging group is visualized in Fig. 3. Fish tagged as autumn presmolts initiated their spring migration (identified by directed downstream movements) earlier than fish tagged in the spring as smolts (22 April – 29 May versus 16 May – 1 June) with associated median water temperatures of 8.0–11.1 °C (SE: 0.5–0.8 °C) for smolts tagged as autumn presmolts and 10.1 ± 0.2 °C for smolts tagged in the spring. Presmolt groups entered the reservoir earlier (reach C; Fig. 1; 25 April – 30 May versus 18 May – 12 June) and reached the MGS (28 April – 16 June versus 20 May – 12 July) and the lower SJR (4–29 May versus 28 May – 22 June) sooner in comparison with groups tagged as spring smolts. Reaching the MGS earlier in the year allowed three fish tagged as presmolts the option of passing via spill (either the outer diversion sluiceway or the spillways within the forebay), although there were only 4–6 days to do so before the spill was closed (22 May 2014, 15 May 2015, 3 May 2016). Fish tagged as smolts did not encounter the MGS before spill was closed. Those that successfully passed the MGS experienced median water temperatures of 9.3–16.1 °C (SE: 0.5–0.8 °C) near the MGS, and those that remained in the reservoir experienced median water temperatures of 9.6–18.0 °C (SE: 1.0–1.1 °C) and up to 20.4 °C near the end of the tracking period.

Migration rate and delay

Juvenile salmon migrants traveling through the reservoir experienced lower migration rates (medians 5.0–13.3 km·day^{-1}) when compared with sections upriver (18.7–23.4 km·day^{-1}) or downriver (15.4–29.3 km·day^{-1}; Fig. 4). Migration rates were significantly different between reaches (LMEM, $p < 0.001$; Table 2*b*), but did not significantly differ between wild and HS or CR origin (one-way ANOVA, $F_{[1,157]}$ = 2.003, p = 0.159). Individual fish accounted for 1.04% of the variation in overall migration rates.

When only downstream movements between receivers were considered, there was no effect of reach (LMEM, p = 0.815; Table 2*c*) or concurrent water velocities (LMEM, p = 0.191; Table 2*c*); however, greater water temperatures were found to have a positive and significant effect (LMEM, $p < 0.001$; Table 2*c*). Individual fish only accounted for 1.12% of the variance between downstream migration rates.

Velocity differences were significantly different between reaches (LMEM; $p < 0.001$; Table 2*d*), with smolts more often swimming actively in the reservoir than upriver (93% versus 68%). Individual fish accounted for 8.26% of the variance in velocity differences.

The majority of the tracked fish (n = 46 of 84) spent 17%–49% of their time swimming upstream in areas upstream of the MGS during the migratory period (Fig. 5). Compared with the minimum distance the fish would need to travel to exit the reservoir (37 rkm), swimming upstream added medians of 24–302 ± 14–217 extra rkm and up to 519 extra rkm to the migration. Swimming upstream was less common once fish had passed the MGS (median 11%–41% ± 2%–14% of time; 7–64 ± 7–55 extra rkm).

Fish direction was not detectably affected by the water direction as measured by the maximum angle away from the downstream direction (LMEM, p = 0.935; Table 2*e*), but upstream movement between receivers was more common in the reservoir than upriver (35% versus 3%; LME logistic regression model, p = 0.008; Table 2*e*). Individual fish accounted for 3.51% of the variance in fish direction (upstream or downstream) between receivers.

Many (n = 33) migrating fish journeyed into and spent time within the dead-end Longs Creek tributary (Table 4). One tagged fish each spring was last detected in Longs Creek. Another dead-end tributary, the Mactaquac Arm to the east of the MGS, was also entered by two smolts (both tagged in the spring of 2016) that visited once for a total of 11.3 h and 1.4 days.

Expected durations to traverse the MGS reservoir for all three studied springs ranged between 1.8 and 2.8 days (Table 5). However, the observed durations to pass the reservoir were longer than expected (paired t test; versus upriver $p < 0.001$, versus downriver p = 0.009; Table 5). The tagged fish migrating in spring 2014

Fig. 4. Median migration rate (km·day^{-1}) of Atlantic salmon tagged as autumn presmolts or spring smolts as they migrated through the Saint John River from 2014 to 2016. FS = free-swim, TH = trap-and-haul. Error bars represent standard error, and sample sizes are shown.

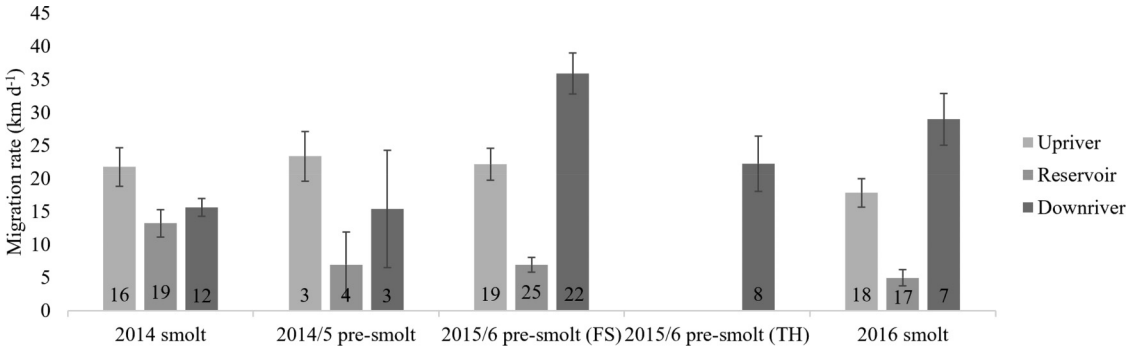


Fig. 5. Median proportion of time Atlantic salmon smolts spent swimming upstream (dark grey) within the MGS reservoir in 2014–2016 and the accompanying minimum distance of extra rkm added to the migration due to this movement (greater than the 37 rkm of the reservoir; light grey); error bars represent standard error, and sample sizes are shown.

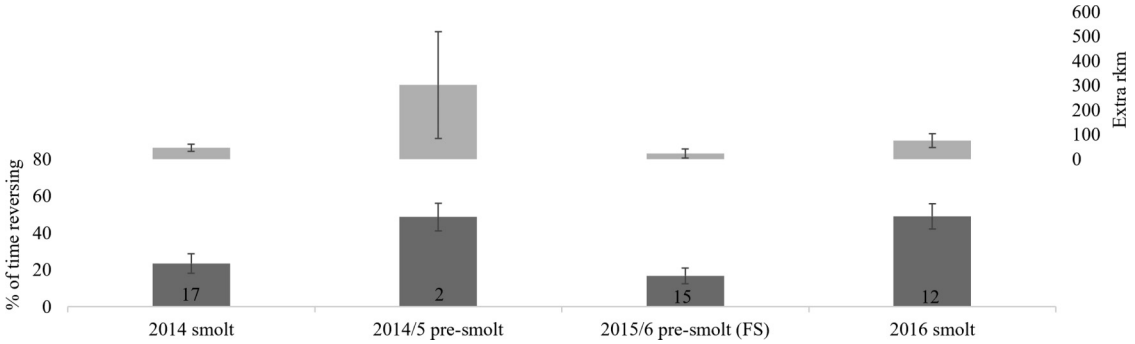


Table 4. Number of tagged Atlantic salmon smolts that entered or bypassed Longs Creek, with the number of tagged smolts that entered upon their first encounter, and the mean ± standard error duration of time spent in the tributary.

Tagging group	*N* bypassed	*N* entered	*N* first encounter	Duration (days)
2014 smolt	4	15	9	0.8±0.1
2014–2015 presmolt	2	2	1	1.3±0.8
2015–2016 presmolt	15	10	6	1.5±0.3
2016 smolt	8	6	4	2.5±0.8
Total	29	33	20	

and 2015 migrated at similar rates (one-way ANOVA, $p = 0.957$) and took ~4.5 days to traverse the reservoir, whereas the reservoir migration was significantly slower for tagged fish migrating in 2016 (by an additional 3.5 days; one-way ANOVA, $p = 0.005$; Table 5). Overall, migratory delay within the reservoir could be determined for $n = 53$ migrating smolts, estimated as 3.74 ± 0.94 days based on upriver migration rates and 3.54 ± 0.88 days based on downriver migration rates.

During each of the three studied springs, tagged smolts took multiple attempts to approach the MGS (up to seven attempts), with most attempts taking place during daylight hours (pooled 76%). The median time spent at the MGS prior to passage varied between years (2014: $n = 14$, 18.7 ± 28.5 h, range 7 min to 16 days; 2015: $n = 2$, both 30 min; 2016 presmolt group: $n = 21$, 40 min ± 13.49 h, range 2 min to 9 days; 2016 smolt group: $n = 7$, 14 h ± 6.1 days, range 43 min to 43 days). The last detection upstream of the MGS and first detection downstream of the MGS ranged between 2 min and 8 days (median 8.0 ± 10.9 h) for all years studied.

Discussion

The outer Bay of Fundy population of Atlantic salmon is under severe decline, partially due to challenges associated with dam operations (Clarke et al. 2014). This study found that migration success was fairly high throughout the MGS reservoir (81%–100%), but declined during dam passage (63%–92% cumulative survival probability), with the greater losses being incurred by groups acoustic-tagged as spring smolts in comparison with those tagged during the presmolt life stage. Cumulative apparent survival to the lower SJR was also greater for groups tagged as autumn presmolts over groups tagged as spring smolts (60%–65% versus 6%–10%). While the apparent survival through the reservoir was generally good, the migration rates were suppressed within the reservoir (5.0–13.3 km·day^{-1}) compared with river reaches (15.4–29.3 km·day^{-1}), causing migratory delay (3–4 days). Migratory timing in the spring was largely mismatched with the availability of fish passage through the spillways such that only a few fish tagged as autumn presmolts had the option of spillway passage due to their generally earlier migratory timing, whereas all fish tagged as spring smolts were forced to pass via the turbines.

Much of the comparative research comes from Pacific salmon species with relatively large populations (Raymond 1968, 1979; Williams et al. 2005), as well as other Atlantic salmon populations (Stich et al. 2015; Honkanen et al. 2018). However, the results herein could also be useful for researchers of other migratory fish impacted by hydropower systems, such as eels that can experience migratory delay in reservoirs with consequences for condition (Acou et al. 2008), and shad that may benefit from impounded reaches creating new spawning and rearing habitats (Hinrichsen et al. 2013).

Juvenile fall Chinook salmon (*Oncorhynchus tshawytscha*) in Lower Snake River reservoirs have been observed to pass through dams in the winter, during which time the passage options are the

Table 5. Observed–expected duration (days; median ± SE) that smolt groups (FS = free-swim) spent traversing the MGS reservoir (37 rkm) based on individual up- and downriver migration rates (km·day^{-1}).

		Based on upriver		Based on downriver	
Tagging group	Observed (days)	Expected (days)	Delay (days)	Expected (days)	Delay (days)
2014 smolts	2.7±1.0	1.7±0.5	0.3±1.2	2.3±0.2	0.8±1.2
2014–2015 presmolts	4.5±1.4	1.5±0.4	2.3±1.6	12.2±9.8	–9.6±10.9
2015–2016 FS presmolts	5.1±1.6	1.5±0.3	3.5±1.7	0.9±0.2	3.8±0.8
2016 smolts	7.2±1.4	2.2±0.4	6.4±1.6	1.2±0.7	5.7±3.9

turbines or specific bypasses (that the MGS lacks) because spill is typically restricted to the spring freshet (Tiffan et al. 2012). In the current study, the inferred overwintering location of presmolts was observed to be in the upriver to top of reservoir transition area, as the tagged fish were generally not detected moving into the reservoir until spring. There was evidence for a few fish choosing to overwinter within the reservoirs, either upstream of the BGS or the MGS, and some fish (the 2015–2016 free-swim presmolt group) passed the MGS before their tags reactivated, but the passage likely occurred early in the spring as was observed for the other groups tagged as presmolts. The presmolts that were transported to overwinter downstream of the MGS remained near the release site with only two fish moving downstream (up to 17 rkm), neither of which were detected in the spring.

Reservoir passage of juvenile Chinook salmon has been reported to be associated with greater survival probabilities than dam passage (e.g., 69%–86% versus 14%–33%; Beeman et al. 2013). Previous Atlantic salmon presmolt and smolt migration and passage studies on the SJR have mainly focused on assessment of the TNGS and BGS reservoirs and dam passage success (see review by Chateauvert et al. 2018), with only a few acoustic-tagged individuals making it into the MGS reservoir with sufficient battery-power remaining to allow for tracking (Carr 1999). Findings in Carr (1999) suggested that the hydropower reservoirs of the SJR may act as "ecological traps" for migrating smolts, with generally high proportions (39%–50% for TNGS, 12.5%–100% for BGS) of acoustic-tagged presmolts remaining in the first two reservoirs encountered by migrating fish. As the TNGS (but not the BGS) dam passage incurred additional mortality, the ability to assess migration success in the MGS reservoir was limited and haphazard (Carr 1999). Still, a small number of individuals were tracked (n = 5 and n = 6 in 2 years), and Carr (1999) observed 0% migration success through the MGS reservoir, suggesting that it may play a role in determining survival of smolts through the SJR system. Based on these data, Carr (2001) hypothesized that tributary coves (backwater areas) may be major bottleneck locations where smolt migration ceases. This study found apparent survival probabilities were fairly stable throughout the reservoir (95%–100%; except for a 12.5% decline among the 2016 smolt group). None of the tagged groups experienced greater mortality probabilities while passing the reservoir than when passing the MGS. Previous studies in the SJR have estimated smolt mortality due to reservoir and dam passage as 24.7% at the TNGS, 13.6% at the BGS, and 15.9% at the MGS (Carr 2001), reaching up to 45.3% for smolts emigrating past the three dams cumulatively (Carr 1999; Chateauvert et al. 2018). This study represents the first estimates using telemetry for apparent survival at the MGS reservoir and dam, with dam passage through the MGS being found to reduce survival probabilities by 8%–32%. This encompasses the previous estimates that were based on coded wire tag mass markings for estimating passage success at the MGS (Carr 2001; Chateauvert et al. 2018). These losses suggest that the MGS facility, but not the reservoir, may be a considerable migration bottleneck for Atlantic salmon smolts in the SJR system. It should be noted, however, that fish that were tagged as autumn presmolts incurred smaller losses than those tagged as spring smolts. This could be in part due to the earlier arrival timing at the MGS when they could utilize the potentially safer spillway for passage. The earlier arrival of smolts tagged as presmolts, in turn, may be a true ecological phenomenon but could also be a methodological artifact related to the timing of tagging and potentially delays it may cause (see below).

Temperature is a major driver of the timing of smoltification and downstream migrations in juvenile salmonids, with the peak of migration thought to occur once water temperatures reach 10 °C (McCormick et al. 1998). This was congruent with the current study, regardless of whether fish were tagged in the autumn as presmolts or in the spring as smolts. As the smolt window continued and the fish approached the MGS, successful migrants experienced water temperatures up to 18.6 °C, and those that remained in the reservoir experienced water temperatures up to 20.4 °C. Both individual downstream migration rates and migration success indices were positively correlated with water temperature.

When comparing the migratory timing of fish tagged as smolts in the spring versus those tagged as presmolts in the autumn, it appears as though smolts that waited until spring to initiate their migration moved later in the season than those that moved into the main stem in the autumn. However, the apparent differences in migratory timing between the autumn and spring smolt groups could be partially attributable to the difficulty in maintaining rotary smolt traps during the high waters of the spring freshet, delaying the capture, tagging, and release of spring smolts. The timing differential could also be partially attributable to tagging effects (Greenstreet and Morgan 1989). Those fish tagged in the autumn as presmolts would presumably have fully recovered from tagging before the spring migration, whereas those tagged in spring during the smolt life stage would have experienced the stressful tagging event just before release. Therefore, the delay observed among spring smolt groups may have been partially due to the recovery from tagging stress. The presmolt tagging groups reached the dam 8–29 days earlier, providing a short time frame of 4–6 days during which spill through the diversion sluiceway or spillway gates was an option for downstream passage. Once the spring smolt groups reached the MGS, spill passage was no longer available in any of the studied years. Passing via spill is often preferable over turbine passage due to the decreased risk of injury and mortality (Bell et al. 1967; Budy et al. 2002). The groups tagged as autumn presmolts also reached the lower SJR 10–30 days earlier than groups tagged as spring smolts. It is unknown to what extent the differences in timing of reaching the estuary aligned or misaligned with the theoretical ecological window that is optimal for survival (McCormick et al. 1998). Delay to sea entry outside of the "smolt window" could impact the return rate as adults (Scheuerell et al. 2009).

Migration rates of wild juvenile salmonids in free-flowing and low-flow waters are highly variable, ranging from 0.01–43.5 km·day^{-1} (Aarestrup et al. 1999; Smith et al. 2003), with rates of smolts that have spent time in captivity being even more variable (0.05–82 km·day^{-1}; Beeman et al. 2013; Manel-La et al. 2011). A previous study examining presmolts within the SJR system found variable migration rates that were significantly reduced in the

TNGS, BGS, and MGS reservoirs compared with the free-flowing reaches (1.4–25.2 versus 6.4–33.5 km·day^{-1}; Carr 1999). Similar to the current study, Carr (1999) observed that wild and hatchery smolts moved at similar rates with the exception of one year within the BGS reservoir where HS migration rates were only 47% of the migration rates of wild smolts. Another previous study found that the smolt travel time from the BGS to the MGS was ~10 days moving at ~13.5 km·day^{-1} (Washburn and Gillis Associates Ltd 1995). The migration rates found by the current study were congruent with previous estimates for both the free-flowing sections (medians 15.4–29.3 km·day^{-1}) and the reservoir (medians of 5.0–13.3 km·day^{-1}), with no significant effect of smolt origin. Overall, the smolts migrating in spring of 2014 and 2015 navigated the reservoir in ~4.5 days, whereas the migration through the MGS reservoir was slower in 2016, taking ~8 days. If the fish had been traveling at their respective up- or downriver migration rates, they could have traversed the reservoir 3–4 days sooner than was observed. The downriver migration rates were comparable with the 12–24 km·day^{-1} observed from smolts of the Nashwaak River located ~20 rkm downstream of the MGS (Nashwaak Watershed Association Inc. 2004).

When passing multiple dams in the Columbia River system, steelhead (*Oncorhynchus mykiss*) juveniles were found to have better survival probabilities during high-flow years than low-flow years (Williams et al. 2005). When both low- and free-flowing reaches have been compared within the same study, low-flow water bodies have been reported to cause juvenile salmonids to migrate 33%–50% slower than through free-flowing waters (Raymond 1968; Thorpe and Morgan 1978; Raymond 1979). This study found similar values, with smolts moving 32%–57% slower in the reservoir than the up- and downriver reaches, which had a more lotic character. These reductions are hypothesized to be related to the reduced water currents within the reservoir, lacking the directional cues juvenile salmon use to find their way to the ocean. However, our analyses did not detect a direct association between individual downstream movements between receivers and concurrent water velocities. When only downstream movements between receivers were considered, there was no effect of reach. This indicates that the rates of downstream movements between receivers were not different within each reach, but rather it was the back-and-forth movements that led to decreased migration rates within the reservoir as a whole.

Smolt migration is typically unidirectional and relatively fast (Svendsen et al. 2007; Davidsen et al. 2009). However, Honkanen et al. (2018) tracked Atlantic salmon smolts through Loch Lomond in Scotland and found they had to swim actively in the lake, and they repeatedly observed instances of swimming away from the outflowing river, considerably increasing migration time. In the MGS reservoir, smolts were actively swimming (fish migration rate > water velocity) for 93% of movements between receivers and for 68% of movements in the upriver reach.

Modeling of hydrodynamic conditions within a large reservoir in China showed that flow velocities did not meet migratory fish requirements (>17 km·day^{-1}) for orientation cues in over half of the areas studied (Xu et al. 2017). When directional cues are lacking, out-migrating smolts need to actively search for the downstream exit, contributing to migratory delay. Migratory delay has been estimated to increase mortality probabilities by 13% over dam passage alone (Marschall et al. 2011) and decrease smolt-to-adult survival by 16.5% (Zabel 2002). Aarestrup et al. (1999) observed upstream-directed movements by Atlantic salmon smolts in a reservoir that took 16% of their migration time and was associated with strong winds. The hydrodynamic model used in this study incorporated wind speeds and direction in the outputs of water speed and direction, but these variables did not appear to be related to fish direction. However, it was observed that up to half of the total migration time upstream of the MGS was spent traveling upstream rather than downstream, covering tens or hundreds of extra rkm in comparison with swimming downstream in the most direct route. Upstream movements between receivers was more common in the reservoir than upriver (35% versus 3%). These movements included searching in dead-end tributaries such as the Longs Creek and the Mactaquac Arm. The latter tributary could only be accessed through large culverts at a causeway and contains ideal, shallow, vegetated habitat for predators such as the smallmouth bass (*Micropterus dolomieu*) and the recently introduced largemouth bass (*Micropterus salmoides*; M. Gautreau, University of New Brunswick, unpublished data).

Predation may be increased within reservoirs due to high water transparency as compared with river reaches (Pelicice et al. 2014), along with increasing water temperatures and increasing smolt disorientation and searching behaviour (Beamesderfer et al. 1990; Smith et al. 2003). Areas where predators congregate, such as tailrace areas of hydropower dams, may introduce bottlenecks to the survival of smolts during their migration (Blackwell and Juanes 1998; Naughton et al. 2004). Previous studies examining the predation of Atlantic salmon smolts downstream of the MGS have concluded that the predation threat is negligible downstream of the MGS in spring (Curry et al. 2007; Andrews et al. 2018), although Babin et al. (A.B. Babin, S. Peake, R. Jones, R.A. Curry, and T. Linnansaari, unpublished data) hypothesized potential predation in late autumn. However, predation of Atlantic salmon smolts has not been thoroughly examined in the lower parts of the SJR during their migration. In this study, it was estimated that 12%–46% of mortalities of the tagged fish actively migrating downstream of the MGS could be attributed to predation. Predation was inferred from detections where smolts were showing unidirectional and consistent mainstem migration towards the sea, until a migration reversal and entry into nontypical smolt habitat, such as Grand Lake, Washademoak Lake, Belleisle Bay, and Kennebecasis River in the lower reaches of the SJR, which appeared to be a substantial migration bottleneck in the spring. Inference of predation events was more difficult in the reservoir due to frequent migratory reversal behaviour and smolt entry to dead-end tributaries. However, predators such as smallmouth bass, chain pickerel (*Esox niger*), and muskellunge (*Esox masquinongy*) are known to reside in the reservoir (Ritter 2002; Clarke et al. 2014).

Another source of migratory delay occurred after fish encountered the MGS but continued to search for a downstream exit through the dam. At the MGS, smolts left and returned to the forebay area up to seven times and waited up to 43 days before being detected downriver. To aid smolts in identifying the direction of the downstream exit, Flow Velocity Enhancement Systems have been installed in other hydropower systems to induce water currents toward the direction of migration (Coutant 2001) and could be tried at the MGS to expedite smolt migration. Contrary to the prevailing literature (Brege and Absolon 1996; Aarestrup et al. 1999; Beeman et al. 2013), dam passage occurred mostly during daylight hours (76%). Successful passage of the MGS itself took ~5 h (i.e., the time differential between the last detection in the forebay and the first detection in the vicinity of the tailrace). Part of the delay inherent in dam passage is the time spent travelling through the dam structures, such as gatewells. In this study, there was an effort to track smolts of wild origin in the spring of 2015 that were sourced from the gatewells of the BGS by using a specifically designed net that could be lowered into the structure. Although 20 wild smolts were tagged, only one reached the MGS reservoir and did not make it as far as the MGS. These tagged fish were removed from all analyses due to potential tagging-related bias. It is important to note that smolts sourced in the spring had most likely already undergone one dam passage at the TNGS and were in the process of passing the BGS and thus may not have been able to persist after the additional stressors associated with capture, tagging, and transport. Owing to the physiologically taxing nature of smoltification, the smolt life stage is more sensitive than the presmolt life stage and can be at higher risk of mortality

when subjected to the stress of being in a tagging study (Carey and McCormick 1998). Therefore, researchers should attempt to target the presmolt population wherever possible to allow for acclimatization over winter and avoid adding to the cumulative stress of spring smolts migrating in hydropower-regulated systems.

Following many other hydropower systems, a fish hatchery (Mactaquac Biodiversity Facility) was tasked with producing and releasing Atlantic salmon with the goal of mitigating losses due to hydropower effects (Young 2013; Maynard and Trial 2014). The current management practice in the SJR includes both captive rearing of wild juveniles from the Tobique River into mature adults that are then released to spawn naturally or are used as a brood stock in a traditional juvenile (age-0 fall parr) hatchery stocking program with releases back into the tributary of origin (Jones et al. 2014). Along with suppressed water currents and dam operations, rearing conditions can also affect migration timing, rates, and success of juvenile salmonids (Monzyk et al. 2009). Hatchery-raised fish are less adapted to the natural environment; therefore, they often travel at slower rates and experience higher mortality probabilities during the spring migration than their wild counterparts (Jonsson et al. 1991; Chittenden et al. 2008). However, no clear pattern of this result emerged from the two tagging groups of spring smolts that spent their entire lives in captivity and were used to supplement the wild presmolts and smolts in our study. The current study was not designed as a comparative study between the success of wild and hatchery smolts, and the hatchery fish were only used to supplement the tagging numbers, and as such, our study had no analytical capacity to analyze differences by origin. However, it should be noted that even fish considered part of the wild population are very likely to have genetic components from hatchery fish in their ancestry due to decades of hatchery releases mixing with the spawning population (Jones et al. 2014).

This study has some limitations, including restricted sample sizes of wild fish from this endangered population, requiring supplementation of hatchery fish. While relatively low sample sizes (especially compared with Pacific salmonid studies) and heterogeneity in the release locations could affect statistical analyses, the observations of smolts moving throughout the river are helpful for informing managers of this Atlantic salmon population and hydropower managers operating within the SJR.

The Cormack–Jolly–Seber model was restricted to active migrants in the spring because of the period of transmission inactivity to conserve battery life, which overestimates overall survival probabilities; therefore, the reader is cautioned to take into account the overwinter losses observed from confounding factors such as natural mortality, predation, tagging, and transport effects. For example, the trap-and-haul group was estimated to have 100% survival for the first three reaches in which they were tracked, but if sample sizes were higher there would likely be some risk of mortality observed. Also, the river was sectioned into spatial units according to the level of interest for each reach, with the BGS reservoir, the free-flowing river downstream of the BGS, and some downriver reaches being larger spatial units and the MGS reservoir being sectioned into smaller spatial units. The detections from within the reaches would therefore span differing periods of time. Each of these detections were considered "instantaneous" within the context of the biological phenomenon of the smolt migration. It was of interest to understand whether mortality occurred within the larger reaches, but not of great interest whether that mortality occurred at the beginning or the middle of the reach. However, this variable sectioning could introduce bias into the encounter estimates and survival probabilities.

The main objective of this study was to quantify juvenile Atlantic salmon migration rates within the MGS reservoir in comparison with lotic portions of the SJR and to relate fish movements to dam operations to inform practices affecting survival probabilities. Migration rates were found to be suppressed by 32%–57% within the reservoir compared with the river reaches, and delays of 3–4 days were incurred by low water flow, reversed swimming direction, and dam passage. Migration success and rates were not detected to be influenced by specific hydrodynamic conditions influenced by hydropower operations at the MGS; therefore, changes to management practices with the goal of increasing water flows, and therefore directional cues to smolts, is not directly supported by this study. Currently, dam operations at the MGS are not managed to allow for downstream passage of smolts via spill or bypass, which could produce higher survival probabilities than through turbines. Migration success could be aided by providing spill passage further into the smolt migration window but could potentially be cost-prohibitive. However, construction of a functional bypass system that would allow volitional passage at all times could minimize the expenditure in water lost for power generation but may offer a safe route through the MGS for migrating Atlantic salmon smolts.

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