North American Journal of Fisheries Management

ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1002/nafm.10544

ARTICLE

Atlantic Salmon Upstream Migration Delay in a Large Hydropower Reservoir

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Abstract
Spawning success of Atlantic Salmon *Salmo salar* is challenged when migratory routes to natal streams are obstructed by hydropower generation stations and reservoirs that lack directional cues, potentially causing migratory delay. This study used 74 acoustic-tagged adult Atlantic Salmon during their spawning migrations to quantify migratory success, rates, and delay through the Mactaquac Reservoir in the Saint John River, New Brunswick, during three migration seasons in 2014–2016. Tag loss or mortality was considerable, reducing the effective sample size to 34 successfully tracked adults. Of these, 41% experienced fallback over the dam, 12% were unsuccessful in exiting the reservoir, and 47% were successful in exiting the reservoir on the way to the spawning grounds. Migration rates were significantly slower in the reservoir (median $\pm$ SE = 9.3 $\pm$ 1.9 km/d) than upriver (39.0 $\pm$ 4.1 km/d), and the tagged Atlantic Salmon spent 31–53% of their time reversing direction and thus travelled longer distances (73 $\pm$ 58 km) than the minimum 37-km midline route through the reservoir. Traveling the distance of the reservoir at the upriver migration rate could have shortened their journey by a median of 3.8 d. Sensor tags indicated that individual Atlantic Salmon experienced temperatures of 10–20°C (median $\pm$ SE = 16.0 $\pm$ 0.03°C) and migrated at depths of 5–35 m (23.4 $\pm$ 0.1 m) within the reservoir. Given that some of the energy needed for reproductive development and activities was likely appropriated by migratory delay and that a moderate proportion (47%) of adults emigrated from the reservoir, volitional passage may not be a successful management strategy in the studied reservoir. However, a substantially reduced sample size negates conclusive remarks about which management strategy would maximize survival and spawning success, and further study is needed.

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Received April 10, 2020; accepted November 3, 2020

Adult salmonids often face barriers, both natural and anthropogenic, during their spawning migrations. Much effort has been placed on studying the challenge of passage past hydropower dams (Gregory et al. 2002; Bunt et al. 2012; Noonan et al. 2012), but reservoirs associated with dams may also be an additional obstacle to upstream migrations in cases where low water currents appear to alter directional cues (Andrew and Geen 1960; Geist et al. 2000). Flowing water is a natural directional cue for upstream migrants (Arnold 1974), and reduced currents within reservoirs can cause adult salmonids to travel greater distances than necessary while searching for the upstream exit from the reservoir toward their spawning grounds (Thorstad et al. 2008).

Spawning migrations of Atlantic Salmon *Salmo salar* within unregulated rivers typically begin by alternating active swimming with periods of rest, followed by an apparent search pattern moving both up- and downstream, and finally a holding phase until spawning activities begin in a synchronized fashion (Hawkins and Smith 1986; Thorstad et al. 2008). River systems with lakes are sometimes used as holding habitats for salmonids that enter the river much earlier than is necessary to reach the spawning grounds (Reed et al. 2017). In regulated rivers, salmonids are often found to actively migrate through low-flow reservoirs rather than use them as holding habitat but also display exploratory behaviors into tributaries without spawning (Karppinen et al. 2002; Kennedy and Allen 2016). Adult salmonids expend large amounts of energy without feeding as they migrate the long distance back to their natal stream to spawn (Fleming 1996; Hendry and Berg 1999; Mesa and Magie 2006). Migratory delay in regulated rivers can reduce energy reserves and delay their arrival to the spawning grounds, causing suboptimal or compromised egg production (Crossin et al. 2004; Mann et al. 2008). Within the Columbia River system, adult Chinook Salmon *Oncorhynchus tshawytscha* used 6–17% of their muscular energy density to migrate 510 km, with an additional 5–8% attributed to migratory delay (Mesa and Magie 2006).

Longer reservoir residence may expose coldwater salmonids migrating in spring and early summer to high water temperatures that could increase metabolic demands, affect sexual development, or lead to prespawning mortality (McCullough 1999; Crossin et al. 2008). The optimal temperature for salmonid spawning migrations is 18°C (Richter and Kolmes 2005). Atlantic Salmon upper thermal tolerance has been reported as 22–33°C (Jonsson and Jonsson 2009), although they have been shown to be adaptable by maintaining high aerobic capacity up to 23°C (Hvas et al. 2017). Higher water temperatures in reservoirs are particularly concerning for river systems that accommodate multiple dam and reservoir passages at which upstream migrants can accumulate migratory delay (Caudill et al. 2007).

The Outer Bay of Fundy population of Atlantic Salmon in this study are endangered (Saunders and Schom 1985; Committee on the Status of Endangered Wildlife in Canada 2011). This population has declined by 65% between 2000 and 2014 (Jones et al. 2014). Atlantic Salmon ascending the Saint John River encounter the first barrier that is impassable without human intervention at the Mactaquac Generating Station (MGS; river kilometer [rkm] 150, measuring from the mouth of the Saint John River). Here they are presumably attracted to fish collection facilities and transported to the Mactaquac Biodiversity Facility for inspection and measurement, then further transported to upstream locations (trap and haul). The Tobique River (confluence at rkm 314 of the Saint John River) is the largest habitat upstream of the MGS that is accessible and appropriate for salmonid spawning (Marshall et al. 2014). Early migrants (May–June) are transported approximately 3 km downstream of the confluence of the Tobique River because they are thought to be homing to headwater tributaries (i.e., Tobique or Aroostook rivers), whereas later migrants are transported to rkm 230 from which they can home to their respective natal streams (Clarke et al. 2014).

The MGS is currently undergoing an assessment for its future due to an alkali-aggregate reaction threatening its life span (Stantec Consulting 2015). The hydropower owner and operator (New Brunswick Power) was considering multiple options for the future of the MGS, including rebuilding the dam on the opposite side of the river, maintaining the reservoir for water control without generating power, removing the dam and allowing the Saint John River to flow freely in this reach, or attaining the intended lifetime of the dam via refurbishment (Stantec Consulting 2015). While the dam removal option would have resolved any dam and reservoir passage issues in their entirety at the MGS (Linnansaari et al. 2015), the other options may allow for the replacement of the current trap-and-haul strategy with volitional passage via a fish ladder or full height fish lift. However, before considering replacing the current trap-and-haul strategy with a volitional passage option, the migration behavior and success of adult salmonids through the MGS reservoir needed to be thoroughly assessed.

Previous studies examining adult Atlantic Salmon behavior within the MGS reservoir suggested that migratory success was low (22.3% of wild and 2.8% of hatchery adults; Marshall 1975). Based on Marshall (1975), the managers implemented a trap-and-haul strategy that bypasses a free swim through the MGS reservoir; however, that study utilized only external Carlin tags that do not allow for a detailed assessment of movements and behavior. Therefore, a reassessment of movement behavior using acoustic telemetry was desired to identify potential migration bottlenecks, as well as to describe the behavior, movement rates, and migratory success within the reservoir, such that management advice can be based on the best possible technologies. The overall purpose of this study was to explore the feasibility of reservoir transit of adult Atlantic Salmon if the current passage structures at the MGS were modified to allow volitional passage. With uncertainty about the reservoir transit impacts and the trap-and-haul strategy, our objectives were to assess the emigration success, behavior, and rates of movement of adult Atlantic Salmon during their spawning migration through the MGS hydropower reservoir.

METHODS

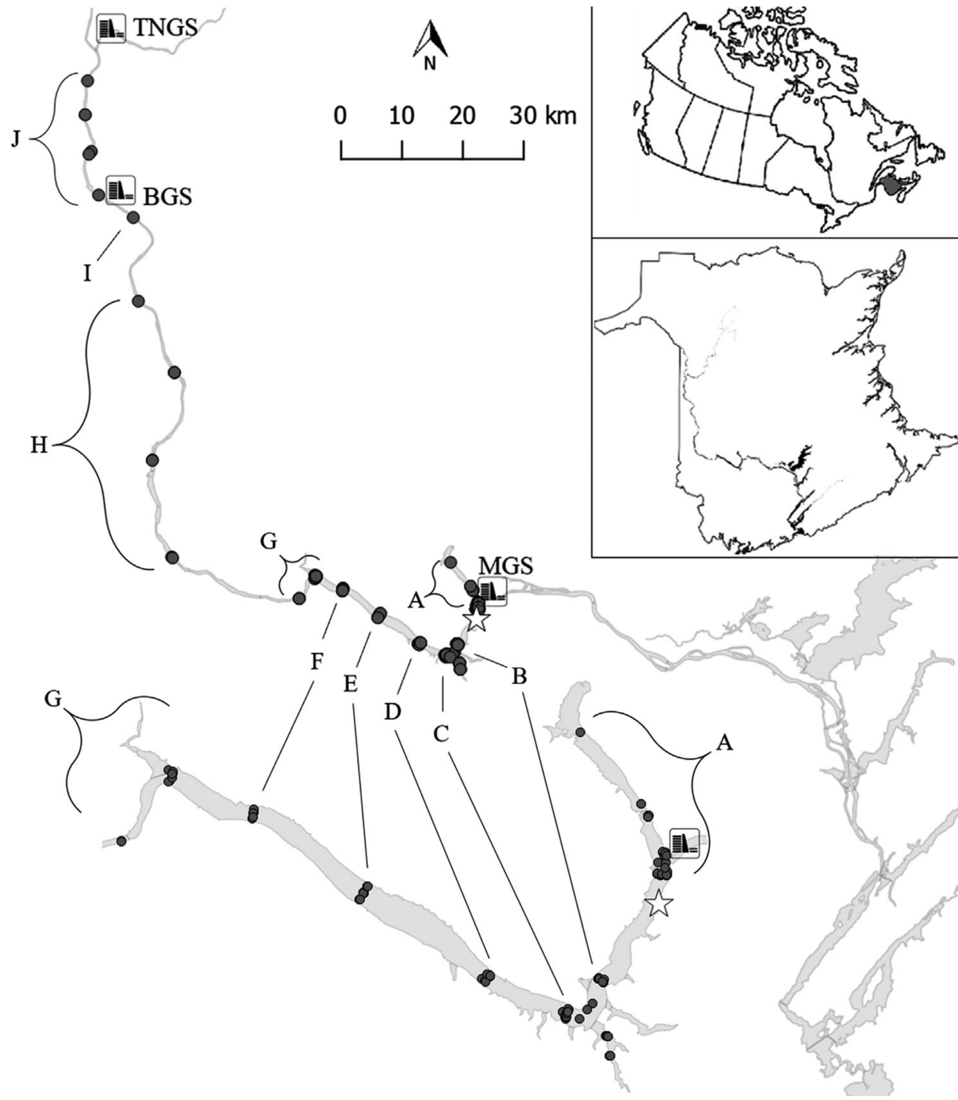
Study site.— The Saint John River is 700 km long, with an average width of 750 m and an average depth of 2 m (Kidd et al. 2011). Discharge ranges from 280 m^3/s in the summer to 10,000 m^3/s during the spring freshet (Kidd et al. 2011). The MGS was built in 1968 and is the first hydropower facility encountered by adult salmonids (rkm 150; Figure 1), followed by the Beechwood Generating Station (BGS; rkm 285; Figure 1) on the main stem and the Tobique Narrows Generating Station (rkm 315; Figure 1) near the mouth of the Tobique River tributary, which contains the majority of Atlantic Salmon spawning habitat upstream of the MGS (Marshall et al. 2014). The MGS affects water flow for 100 km upstream, but it is the first 37 km (i.e., from the MGS to the town of Nackawic [the "reservoir proper"; MGS to reach G]; Figure 1) that has had the most drastic decline in water flow from an average of 0.52 m/s before impoundment to 0.06 m/s after dam construction (Stantec Consulting 2015). The river upstream of this location (reach G) changes angle and narrows substantially in both width (750–300 m) and depth (40–18 m), becoming more lotic (0.04–0.14 m/s; M. Ndong, unpublished data; Figure 2). Therefore, this study considered reaches A–G (Figure 1) to be the "reservoir" and reaches H–I to be "upriver" (Figure 1).

Fish tagging and tracking.— Two sources of adult Atlantic Salmon were used in this study; wild Atlantic Salmon adults were acoustic-tagged for the in situ tracking study, whereas captive-reared fish (i.e., Atlantic Salmon that had been grown to adulthood from wild presmolts or smolts in a hatchery environment) were used as dummy-tagged control groups (in 2014 and 2016; Table 1) to assess tag retention and other tagging-related effects. The wild Atlantic Salmon were captured from the fish collection facilities of the MGS and then transported approximately 7 km to the Mactaquac Biodiversity Facility for assessment and tagging (Table 1). Although these fish were considered wild, they were likely to have experienced captivity at some point in their lives because only small proportions of returns to the MGS are sea-run adults (7% in 2014; R. Jones, Fisheries and Oceans Canada, personal communication). The captive-reared Atlantic Salmon had been raised at the Mactaquac Biodiversity Facility and were kept there for monitoring after dummy tagging.

Acoustic (69-kHz) V13 transmitters (hereafter called tags; Vemco, Halifax, Nova Scotia) were used in this study (13 mm in diameter, 36 mm in length, 11 g in air, 6 g in water). In 2015, $n = 10$ acoustic tags were equipped with additional temperature and pressure (as a proxy of depth) sensors (48 mm in length, 13 g in air, 6.5 g in water). The dummy tags on the control groups matched the specifications of the live tags described above but did not emit an acoustic signal. In 2014 and 2016, the tags were programmed to ping every 30–90 s on average, with the battery life estimated to last 362 d. In 2015, the tags were programmed to ping every 60–180 s, extending battery life to 653 d for nonsensor tags, whereas the sensor tags were expected to last 277 d. The tags averaged 0.34% (SE = 0.65%) of body weights over the study.

Due to the vulnerable population status of Atlantic Salmon in the Saint John River, two different acoustic tagging methods were employed in this study. Specifically, gastric tagging (in 2014) and external tagging (in 2015–2016) were used to avoid any potential impact of tagging on spawning success. Tagging was performed using 40 ppm clove oil anesthetic (eugenol as active ingredient; ethanol in 1:10 ratio used as carrier; exposure time = 291 ± 103 s [mean $\pm$ SD]) and took a total of 178 ± 66 s, except for in 2016 when flow-through water was used instead of anesthetic and the tagging process was quicker (135 ± 43 s).

In 2014, adult Atlantic Salmon were gastric-tagged with either dummy tags ($n = 12$) or live tags ($n = 20$). For gastric tagging, the V13 tags were modified by fixing a rubber O-ring to the middle of the tag using fusion tape to decrease the chances of regurgitation (Rivinoja et al. 2006). The control fish were tagged first to ensure that the gastric tagging process resulted in reliable tag insertion and retention without complications; these fish were fasted for 24 h prior to tagging. A long vinyl tube lubricated with glycerin was used to gently place the tag 32% (18.8 ± 1.3 cm [median $\pm$ SE]) into the body, and a thin wooden dowel was used to expel the tag from the tube and into the stomach. The tagged control fish were then observed on days 1, 2, and 7 after tagging. As no tag expulsion, complications, or mortality was observed, we proceeded to tag the wild sea-run Atlantic Salmon using the same methods. The wild Atlantic Salmon were allowed to recover at the Mactaquac Biodiversity Facility for 48 h posttagging, where they were treated with a salt bath to physically remove loose parasites and bacteria and reduce stress before transportation (2% salinity for 1 h; Warren 1991). Tagged Atlantic Salmon were then transported and released 3 km upstream of the MGS (Figure 1); 10 fish were released on July 30, 9 on July 31, and 1 on August 1



Reach	Rkm	Number of receivers
A	150-152	6
B	158	2
C	162	3
D	167	2
E	175	3
F	182	3
G	187-192	4
H	215-264	4
I	280	1
J	287-317	4

FIGURE 1. A map of the Saint John River, New Brunswick, Canada, highlighting the locations of VR2W receivers (circles) and river-reach groupings (labeled with letters), with a zoomed-in reservoir section (A–G). The location of fish release is indicated by a star, and the main-stem generating stations (Mactaquac Generating Station [MGS], Beechwood Generating Station [BGS], and Tobique Narrows Generating Station [TNGS]) are indicated by dam icons.

(Table 1). The monitoring of the control fish continued at the Mactaquac Biodiversity Facility, with one tag being found to be expelled after 17 d and an additional two tags being found to be expelled 23 d after tagging (total = 25%), but no mortalities occurred among the control fish.

In 2015, the tagging method was changed to external tagging due to presumed low tag retention with the gastric method in the in situ fieldwork during the 2014 field season (see Results). The external-tagging procedure involved preparation of the cylindrical acoustic tags by wrapping monofilament line over the tag casing and then covering the monofilament wraps in epoxy such that approximately 10 cm of line remained at either end of the tag for external attachment (see the Supplement in the online version of this article). No controls were used in 2015, and only wild sea-run Atlantic Salmon were tagged ($n = 24$, including $n = 10$ tags with sensors). During tagging, the fish were anesthetized and then placed upright on a V-trough, where large-gauge hypodermic needles were inserted through the fish's dorsal musculature, monofilament lines were fed through the hollow needles, and a soft rubber barrier was inserted between the skin and the monofilament, which was knotted to secure the tag. External Carlin tags were also placed into the dorsal musculature to allow for identification at upstream dam passages and to assess the loss of acoustic tags when fish were resighted. All tagged fish

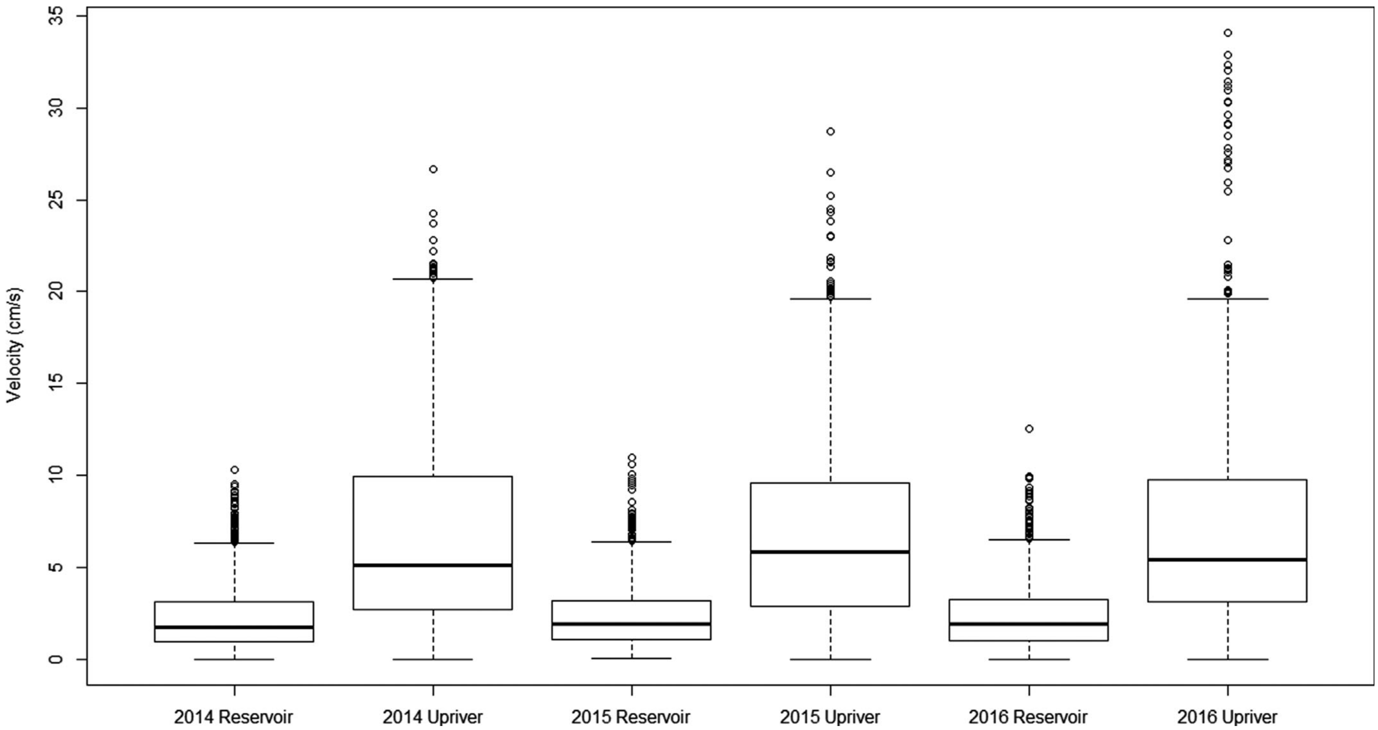


FIGURE 2. Box plots of velocity (cm/s) output from the hydrodynamic model Delft3D-FLOW 4.01.00 within the Mactaquac Reservoir (reach A; Figure 1) and upriver section (reach H; Figure 1) of the Saint John River for the study years (2014–2016) from the tagging date to November 15. The horizontal line in each box indicates the median, the box dimensions represent the 25th to 75th percentile ranges, the error bars represent 1.5 times the interquartile range, and the dots show outliers.

TABLE 1. Mean ± SE weight (kg) and fork length (FL; cm) of wild (released in reservoir) and captive-reared (CR; controls kept at Mactaquac Biodiversity Facility) Atlantic Salmon adults tagged in 2014–2016. The number (*N*) of tagged wild adult Atlantic Salmon is split into small (≤63 cm) and large (>63 cm) females (A and B, respectively) and small and large males (C and D, respectively).

Origin	Year	Tagging date	Tagging method	*N* (A, B, C, D)	Weight (kg)	FL (cm)
CR	2014	Jul 21	Gastric	12 (no females, 10, 2)	2.8 ± 0.2	59.3 ± 1.5
CR	2016	Jun 27	External	8 (no females, 5, 3)	2.7 ± 0.4	59.1 ± 2.3
Wild	2014	Jul 28–Aug 1	Gastric	20 (0, 5, 15, 0)	2.7 ± 0.3	62.5 ± 2.1
Wild	2015	Jul 9–10	External	24 (1, 10, 11, 3)	3.6 ± 0.4	66.9 ± 2.4
Wild	2016	Jun 28–Jul 7	External	30 (1, 11, 18, 0)	3.2 ± 0.3	63.4 ± 1.8

were released on July 9 after a minimum recovery period of 1 h (maximum of 7 h; salt bath administered), with the exception of one fish that was tagged and released after 30 min on July 10 (Table 1).

In 2016, external tagging was performed on $n = 8$ captive-reared control adult Atlantic Salmon and $n = 30$ wild fish using the same methods as in 2015. The wild fish were released to the same location as previous years after 24 h recovery ($n = 7$ on June 28, $n = 15$ on July 4, and $n = 8$ on July 7; Table 1). The control group was monitored daily for 16 d, during which time one tag broke off, five tags were slightly loose, and two were in perfect condition, with no mortalities.

Adults were passively tracked through the Mactaquac Reservoir and Saint John River upriver area using $n = 46$ Vemco VR2W receivers in 2014, $n = 44$ in 2015, and $n = 26$ in 2016 (Figure 1). The fish were also actively tracked using a Vemco VR100 receiver and an omnidirectional hydrophone, with a total effort of 77.8 h. Active tracking was restricted to daylight hours and wind speeds below 25 km/h.

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 modeling 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/s; angle from downstream) every 2 h during the study period at the same locations as the acoustic receivers (Haralampides et al. 2018; Ndong, 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 rkm 167 (reach F; Figure 1) and rkm 233 (reach B; Figure 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 ($r^2 > 0.99$; Ndong, unpublished data).

Definitions and statistical analyses.— 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 (range testing = 537 ± 53 m [median ± SE] near the MGS, 897 ± 227 m upriver; Babin et al. 2019) that was found to produce excellent encounter probabilities (>99%), ensuring that movements could be inferred from the presence or absence of detections. Four categories were defined: (1) tag loss or mortality, (2) fallbacks, (3) unsuccessful migrants, and (4) reservoir emigrants. Tag loss or mortality (category 1) were adult Atlantic Salmon that were presumed to have either lost their tag or to have died when detections were near continuous at a single receiver line for the duration of the battery life of the tag or when detections ceased abruptly, indicating that the tag or fish had been lost in an area outside the detection range of any receivers. This determination was further confirmed for fish carrying sensor tags when detections indicated that the tag was resting on the bottom. Tag loss or mortality could be attributed to natural causes, tagging effects, dam- or reservoir-related impacts (i.e., physical abrasion, increasing temperatures), or potential predation (i.e., avian predators). In many cases, detections indicated active fish movements for a period of time before presumed tag loss. When appropriate, these data were included in the analyses. Fallbacks (category 2) were adult Atlantic Salmon that were known to have fallen back over the MGS when their acoustic tags were detected by receiver(s) downstream of the dam or when a fish entered the fish lift operations and were identified by a Carlin tag. Individuals were also presumed to have fallen back over the MGS when detections ceased abruptly within the vicinity of the MGS (<3 km). Unsuccessful migrants (category 3) were adult Atlantic Salmon that were considered to have been unsuccessful in migrating upstream of the reservoir when the last detection came from a receiver in or downstream of Nackawic (rkm 187; reach G; Figure 1). Reservoir emigrants (category 4) were individuals that were categorized as successfully exiting the reservoir when they were detected by receivers upstream of the reservoir and/or further upstream of the BGS toward the spawning grounds.

Cormack–Jolly–Seber modeling was attempted but was hindered by high tag losses and/or mortality. Time-to-event analysis with a Cox proportional hazards model was used to identify variables impacting the fish's success as a reservoir emigrant (Castro-Santos and Haro 2003; Caudill et al. 2007), including sex, size (≤63 cm = small, >63 cm = large), and study year. The duration was between the first detection after release and the last detection in the reservoir. Fish that had experienced tag loss/mortality or fallback or were unsuccessful in exiting the reservoir were censored at the time of these respective events.

Linear mixed-effects models (LMEMs) 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 model compared overall migration rates (km/d) within the reservoir and upriver reaches. These rates were calculated as follows: reservoir = from the first detection upon release to the first detection at the exit of the reservoir (reach G; Figure 1), and upriver = from the last detection at the Nackawic (reach G; Figure 1) receivers to the first detection at the last receiver they were observed at upriver. Migration rates were further examined by only considering upstream movements between receivers within the reservoir and upriver reaches, then relating these movements to concurrent water temperatures and velocities, as well as the fish's sex and size, through a second LMEM. The variables included were selected by using the model with the lowest Akaike information criterion (AIC) value (Hurvich and Tsai 1993; Burnham and Anderson

2002). Water temperature values were taken from sensor tag detections, when available, or from temperature loggers deployed at midcolumn alongside the receivers. A small proportion (5%) 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.

The proportion of time that tagged adults spent traveling in the reversed direction to their upstream spawning migration, and the minimum extra kilometers that they travelled as a consequence, was calculated and compared to a situation where the movement would have been unidirectional (i.e., tagged fish moved only in the upstream direction). Fish direction (upstream or downstream) between receivers was examined in relation to the direction of surface waters in the reservoir and upriver reaches using a linear mixed-effects (LME) logistic regression model. For each time interval over which the fish's direction was determined, the maximum water angle that deviated from the upstream centerline over that time interval and in that spatial range was also determined for comparison in the model. For example, if a fish moved from reach D to E (Figure 1), their direction would be determined to be upstream. During the time range that these movements took place, the hydrodynamic model between reach D and E was consulted to determine the water directions (as angles from the upstream centerline) at that time and place. The angle that deviated most from the upstream centerline was included in the model rather than a mean value that could represent a false composite water direction. The dependence of fish direction on their sex and size was also examined, but the variables ultimately included were selected by using the model with the lowest AIC value (Burnham and Anderson 2002; Hurvich and Tsai 1993).

Migratory delay was quantified by comparing the expected duration to traverse the reservoir (37 km) based on each individual fish's upriver migration rates to the observed durations. This method assumes that the tagged Atlantic Salmon would have migrated the reservoir section using the rate that was observed in the upriver section in the hypothetical case that the reservoir was absent (i.e., no-dam scenario).

Water temperatures and depths of individual fish with sensor tags were visualized with box plots and kernel density plots (violin plots), without any data after presumed tag loss or mortality (i.e., after a tag was observed to reside at the bottom of the reservoir or river without any further movements detected throughout the study). Two fish with sensor tags that travelled upriver were explored further by plotting their sensor tag temperatures along with logger temperatures at representative locations within the reservoir and upriver. Water temperatures in the transition area between the reservoir and upriver as fish were emigrating were examined for differences that could explain the reversals in this area. A separate analysis examined the relationship between concurrent temperature measures by sensor tag and by logger through linear regressions.

Analyses were done in R Studio (version 1.3.1093, 2009–2020; RStudio; packages car, lme4, lmerTest, survival). Normality plots were analyzed where appropriate, and statistical significance was assumed when P was less than or equal to 0.05.

RESULTS

Reservoir Emigration Success

Although controls for both tagging methods were largely successful with few tag losses and no mortalities, releasing wild fish in the reservoir produced lower than expected proportions of tagged fish successfully retaining the tags throughout the study (46%). Among the tagged fish, 57% of females and 50% of males experienced such loss at various times after release (Table 2).

In 2015, 10 fish had temperature and pressure tags from which tag loss or mortality could be confirmed when depths suddenly reached and remained near the bottom. These determinations are included in the number of tag losses or mortalities tallied in Table 2. From active movements of the fish with sensor tags before tag loss, 75% of adult detections were within 13 and 29 m in the reservoir with temperatures of 12–18.5°C (mean 16°C; Figure 3). Comparing the water temperatures recorded by the sensor tags to concurrent water temperatures recorded by loggers in the same location and at the closest depth to the fish with sensor tags, we found that their agreement differed

TABLE 2. The number of adult Atlantic Salmon in each fate categorization within each study year. See Methods for definitions of fate categories.

Fate and total	2014	2015	2016	Total
Tag loss/mortality				40
Immediate (<3 d)	6	8	5	
Within a week (4–7 d)		2	4	
Within 2 weeks (8–14 d)	1	2	1	
Within a month (15–30 d)	1		2	
Over a month (>30 d)	1	5	2	
Fallback				14
Immediate (<3 d)	2		5	
Within a week (4–7 d)	1	2	2	
Within 2 weeks (8–14 d)		1	1	
Unsuccessful migrants	3	1	0	4
Reservoir emigrants	5	3	8	16
Total	20	24	30	74

by location. Locations within the reservoir had r^2 values that ranged from 0.01 at reach E (Figure 1) to 0.80 at reach F (Figure 1). All reaches within the reservoir had positive relationships between these two temperature records, with slopes ranging from 0.03 at reach E (Figure 1) to 1.32 at reach F (Figure 1), except near the MGS where the relationship was negative (slope = –0.18, $r^2 =$ 0.18). Too few data points were available to determine these relationships at upriver locations.

The total number of fish that were determined to have each of the assigned fates for each study year are given in Table 2. Many ($n = 14$; 41%) tagged adult Atlantic Salmon experienced fallback over the MGS. The majority of fallbacks were small males (79%). There were also many instances where a tagged fish had likely fallen back and experienced tag loss or mortality based on abruptly ceased detections within the vicinity of the MGS (but no detections by downriver receivers). Four tagged adults (12%) were determined to have been unsuccessful migrants (2014: $n = 3$, 2015: $n = 1$; Table 2), and all of these were small males.

Sixteen tagged adults (47%; equally split between the sexes) emigrated out of the reservoir (2014: $n = 5$, 2015: $n = 3$, 2016: $n = 8$; Table 2) during mean ± SD water temperatures of 19.7 ± 3.1°C (Figure 4), with half of the reservoir emigrants being last detected at the first receiver within reach H (Figure 1) and two detected downstream of the BGS (reach I; Figure 1) in 2014, the only year when that particular receiver was successfully retrieved. Both of these latter fish continued to be tracked after 20 and 30 d in the area as they moved downstream as kelts in a concurrent study (A. B. Babin, unpublished data). The median time to emigrate from the reservoir was 7.8 d for those that were successful. The duration of time it took for the adults to exit the reservoir was not significantly impacted by fish sex, size, or study year (Cox proportional hazards model: $P > 0.229$).

When water temperature data from loggers were available both within the reservoir (midcolumn) and upriver during emigration from the reservoir (Figure 5), 8 out of 12 fish emigrated when it was cooler upriver (by 0.2–2.7°C) and four fish in 2016 emigrated when it was warmer upriver (by 0.8–2.1°C). Only two fish with sensor tags migrated upriver. These fish remained within the surface 8 m, with temperature ranges of 20°C to 23°C reflecting the general habitat conditions in the upriver reach (Figures 3 and 4). Both of these fish reversed direction at the exit of the reservoir once before deciding to return and move upriver (Figure 4). There was no discernable temperature difference between locations as recorded by the first sensor tag (Figure 4A), but the second fish (Figure 4B) experienced temperatures of up to 21.7°C before turning back into the reservoir with temperatures of 18.2–20.9°C. This fish then remained within that temperature range until moving upriver, where temperatures increased to 22.9°C.

Six tagged adults (also equally split between the sexes) were successful in finding upstream passage over the BGS (2014: $n = 2$, 2015: $n = 1$, 2016: $n = 3$). Only one fish with a Carlin tag was observed by operators at the BGS, which was on a female tagged in 2014 and was actively tracked at rkm 374, which could be the fish's spawning grounds. The single migrant that reached upstream of the BGS in 2015 was a female with a sensor tag that indicated it was traveling within the surface 1 m of water, where water temperature was near 20°C.

Migration Rate and Delay

Migration rates in the reservoir were significantly suppressed when compared to rates in the upriver reach (LMEM: $P < 0.001$; Table 3, model A) but did not differ by sex or size (LMEM: $P > 0.337$; Table 3, model A). Overall, pooled median ± SE migration rates were 9.3 ± 1.9 km/d in the reservoir and 39.0 ± 4.1 km/d upriver, reaching 65.2 ± 12.5 km/d upstream of the BGS (2016 only). When considering the movements from release to the BGS, pooled migration rates were 10.2 ± 2.7 km/d. Individual fish accounted for 38.6% of the variance between migration rates. All but two tagged fish (both in 2014) traveled 2–17 times faster in the upriver reach than in the reservoir.

Migration rates between each receiver line only as the fish were moving upstream were tested to determine dependence on concurrent water velocities. The best model according to AIC comparisons (Table 4) indicated that individual fish accounted for 8.3% of the variance between upstream migration rates. When only upstream movements between receivers were considered, there was no effect of reach (LMEM: $P = 0.130$; Table 3, model B), indicating that the rate of movements between receiver lines was not different within each reach but rather the back-and-forth movements or reversals (see below) led to decreased migration rates within the reservoir as a whole. There were also no relationships found between upstream migration rates and sex or size (LMEM: $P > 0.976$; Table 3, model B), as well as concurrent water velocities (LMEM: $P = 0.731$; Table 3, model B) or average water temperatures (LMEM: $P = 0.266$; Table 3, model B). The median delay within the reservoir (37 km) in comparison to migrating that distance at the upriver rate was 3.8 d (range = 11 h to 19 d; Table 5).

Many fish (36% of all adults tagged) spent time within Longs Creek, a dead-end tributary located at a large bend of the MGS reservoir (between reaches B and C; Figure 1). Time spent in Longs Creek had an important contribution to their overall delay within the reservoir, with tagged Atlantic Salmon spending a median of 5.2 h, but up to 4.7 d, in the creek over multiple visits ($n = 15$

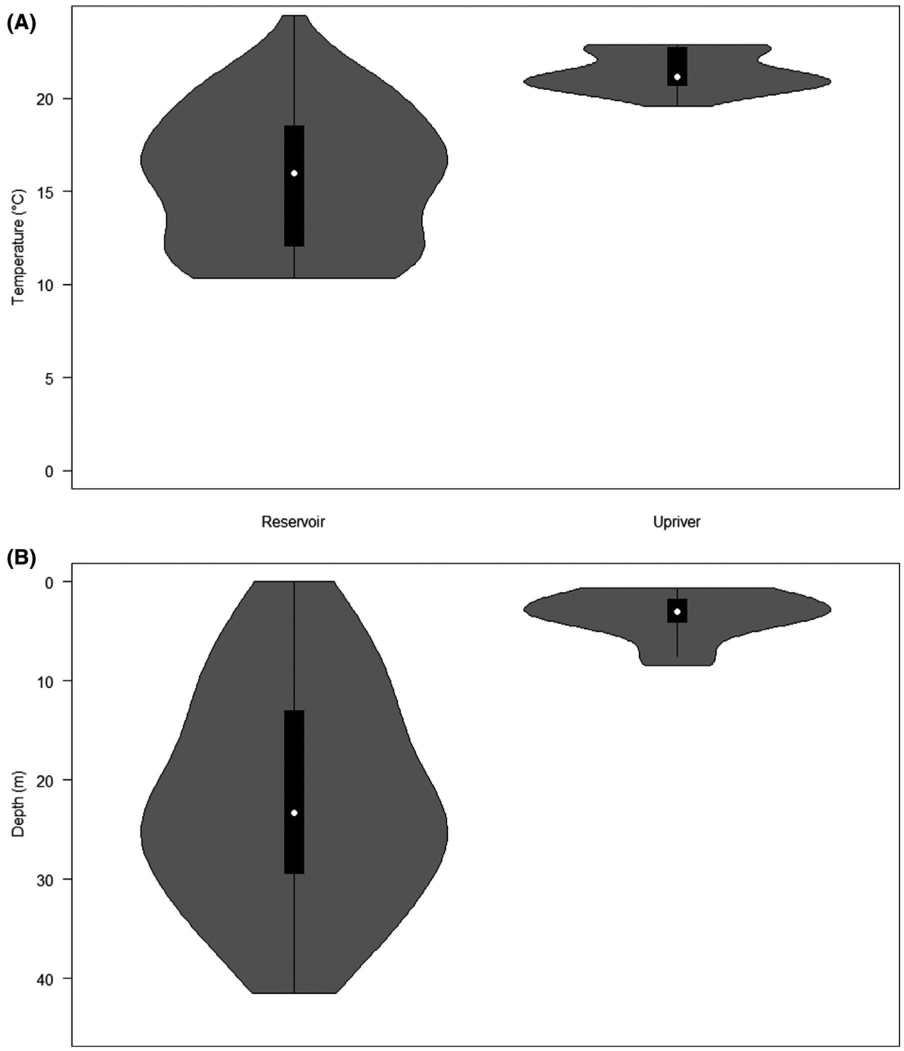


FIGURE 3. Violin plot of **(A)** water temperature (°C) and **(B)** depth (m) of adult Atlantic Salmon with temperature or pressure sensor tags within the Mactaquac Reservoir and upriver section of the Saint John River. The black bars are box plots with the white dot representing the median, the black bars representing the first and third quartiles, and the black lines representing the minimum and maximum. The gray areas are kernel density plots. Data after presumed tag loss or mortality are not included.

females, $n = 12$ males; Table 6). Water temperatures in Longs Creek from available data in 2015 averaged 20–21°C (temperature loggers during fish visits = 20.1 ± 0.2°C [mean ± SE], sensor tags = 21.1 ± 0.1°C). Five tagged adults (two females, three males) also entered the Mactaquac Arm (reach A; Figure 1), a dead-end tributary northwest of the MGS. Four of these fish visited the arm only once, spending 0.5–2.6 d, whereas one individual visited three times for a total duration of 4.3 d. Temperature data was taken in the Mactaquac Arm in 2016, while three fish visited the area, showing a mean temperature of 15.3 ± 0.1°C.

Slow water currents in the reservoir (Figure 2) removed directional cues, and this was evidenced by the large proportion of time adults spent reversing direction, thus swimming downstream rather than making progress upstream. The majority of tagged adult Atlantic Salmon each year exhibited the reversal behavior (2014: 20/20, 2015: 21/24, 2016: 29/30) and spent a median of 31–53% of their active movement time in the reservoir reversing direction. Fish direction was best explained by a model only including whether the fish was in the reservoir or upriver, but we wanted to also include the dependence of fish direction on water direction. Therefore, the second-best model is reported (Table 3, model C). Fish direction was not detectably affected by the maximum angle of the water from downstream (LME logistic regression model: $P = 0.158$; Table 3, model C) but was more common in the reservoir than upriver (LME logistic regression model: $P < 0.001$; Table 3, model C). Compared to the

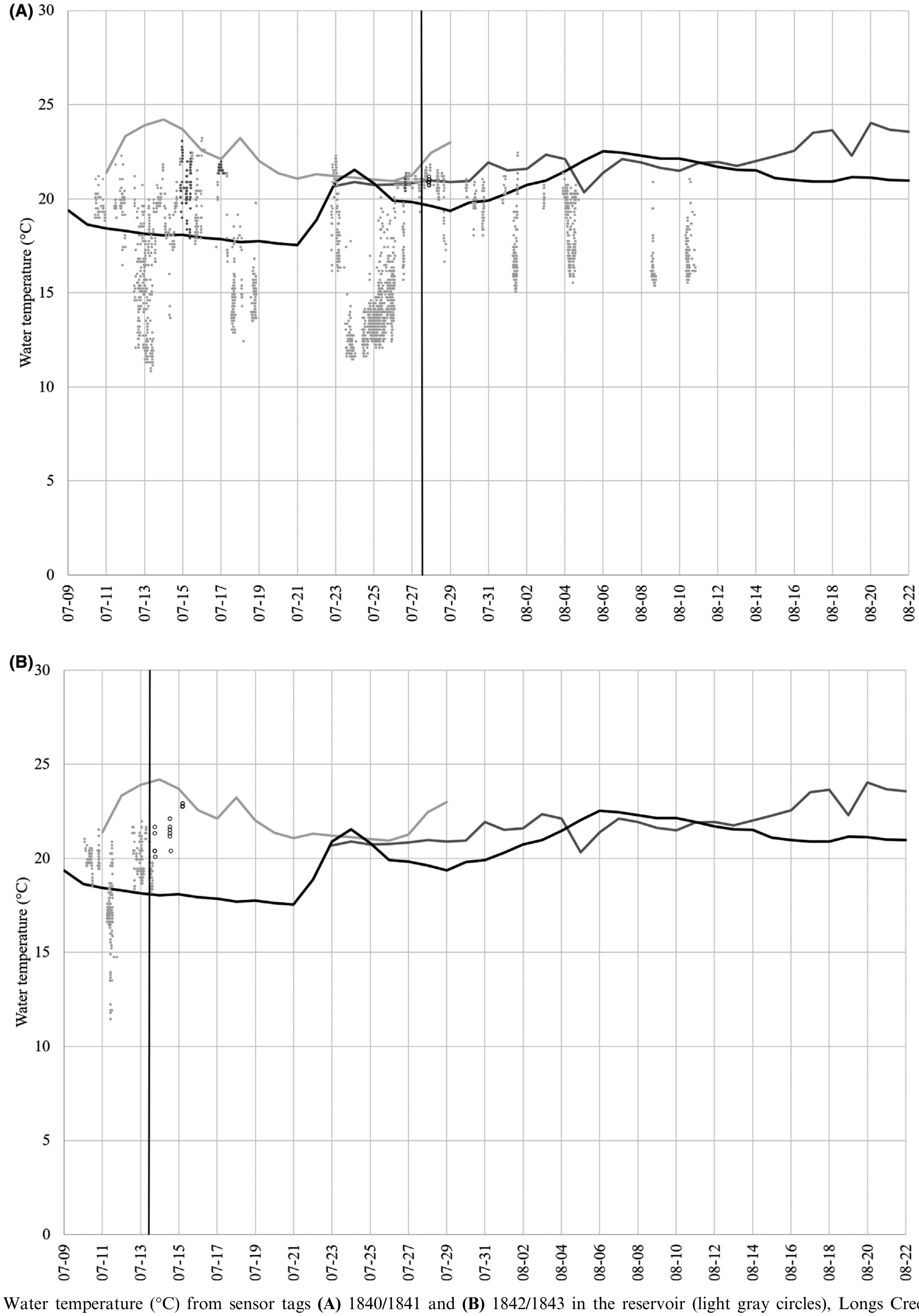


FIGURE 4. Water temperature (°C) from sensor tags **(A)** 1840/1841 and **(B)** 1842/1843 in the reservoir (light gray circles), Longs Creek (dark gray circles), and upriver (open circles) and from water temperature loggers in the reservoir (light gray line = 3 m, dark gray line = 11 m; reach B; Figure 1) and upriver (black line = 18 m; reach H; Figure 1). Vertical black lines represent times when the adult Atlantic Salmon reversed direction at the reservoir exit.

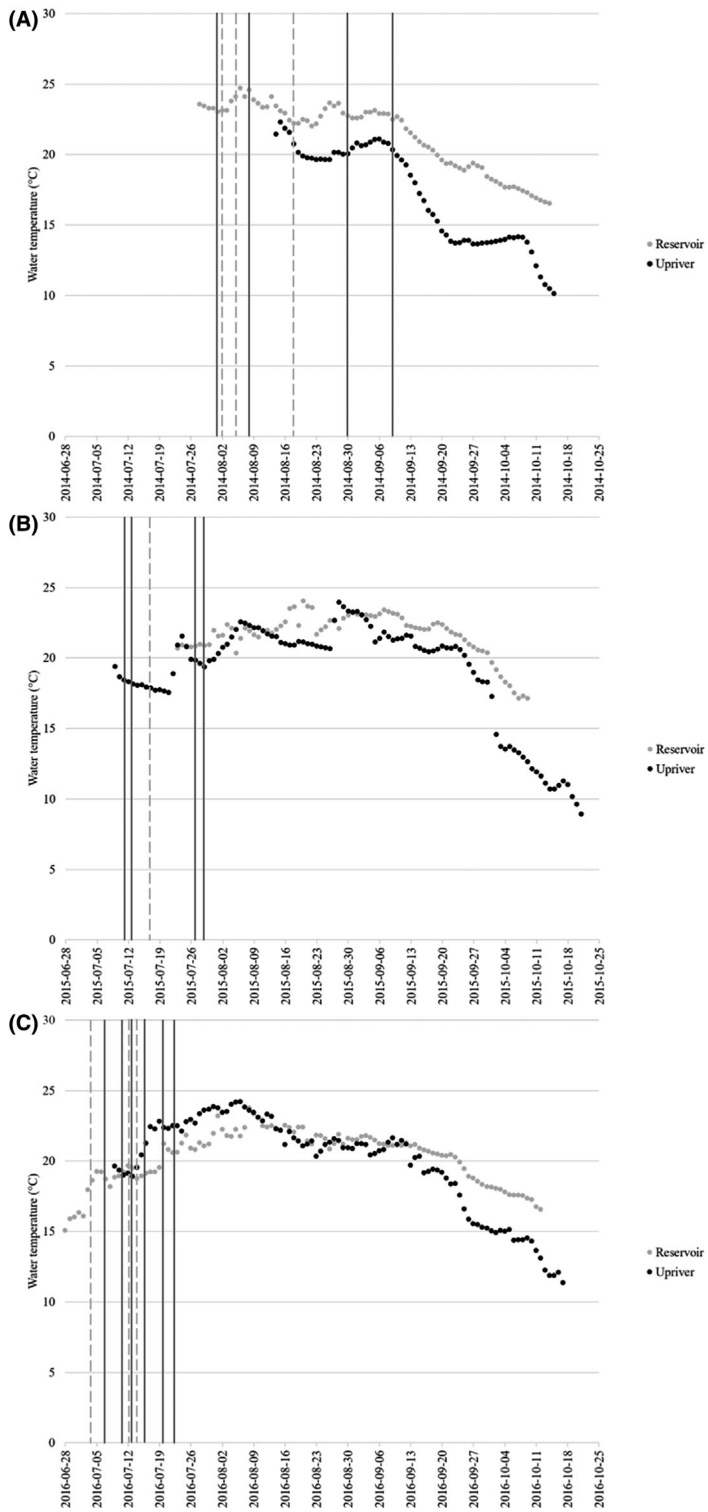


FIGURE 5. Average daily water temperature (°C) in **(A)** 2014, **(B)** 2015, and **(C)** 2016 within the Mactaquac Reservoir (gray dots; reach B; Figure 1) and the upriver section (black dots; 2014: reach J, 2015–2016: reach H; Figure 1) of the Saint John River. Dates when adult Atlantic Salmon left the reservoir and returned are shown by dashed vertical lines, and dates when they moved upriver without returning are shown by solid vertical lines. The depths of the water temperature loggers were at 12 m in the reservoir and 20 m in the upriver section for 2014, at 12 m in the reservoir and 18 m upriver for 2015, and at 16 m in the reservoir and 8 m upriver for 2016.

TABLE 3. Model type (linear mixed-effects model [LMEM] or linear mixed-effects [LME] logistic regression model), formula, sample size, and coefficient estimates, standard errors (SEs), *t*-values, and *P*-values for models testing the dependence of Atlantic Salmon migration rates (overall km/d is the migration rate from first to last detection in the reservoir, whereas upstream km/d is the migration rate between receivers when moving in the upstream direction) and direction on environmental variables, such as their presence in the reservoir (reach = reservoir or upriver), water temperature, water velocity, water angle (direction from downstream = 0°), and fish direction (upstream or downstream).

Coefficient	Estimate	SE	*t*	*P*
Model A = LMEM: overall_km_d ~ reach × sex × size + (1|fish_id)[a], *n* = 37 from 21 fish				
Reach	–12.615	1.639	–7.695	<0.0001
Sex	–3.585	5.192	–0.690	0.498
Size	5.159	5.238	0.985	0.337
Model B = LMEM: upstream_km_d ~ reach × temperature_avg × water_velocity_avg × sex × size + (1|fish_id)[a], *n* = 664 from 36 fish				
Reach	12.0547	7.9612	1.514	0.130
Temperature_avg	10.1139	9.0767	1.114	0.266
Water_velocity_avg	1.4924	4.3400	0.344	0.731
Sex	2.3379	76.6397	0.031	0.976
Size	–1.8989	76.7499	–0.025	0.980
Model C = LME logistic regression model: fish_direction ~ reach + water_angle + (1|fish_id), *n* = 1102 from 36 fish				
Reach	0.0196	0.0034	5.837	<0.0001
Water_angle	0.0021	0.0015	1.414	0.158

[a]Interactions (not shown) were not significant ($P > 0.066$).

minimum distance the fish would need to travel to exit the reservoir (37 km), reversed-direction swimming added a median ± SE of 73 ± 58 km. Once the fish exited the reservoir, no time was spent swimming downstream by fish tagged in 2015 and 2016, and two tagged fish that were both males reversed direction in 2014 (with 3.7% and 24.3% of time upriver spent swimming in the reverse direction). This behavior is highlighted using an example acoustic track of a reservoir emigrant (Figure 6), demonstrating typical but extensive reservoir reversal movements, adding a minimum of 760 km to traverse the reservoir.

Reservoir emigrants never remained in a single area of the reservoir for longer than 1.1 d, whereas the unsuccessful migrants tended to have greater holding durations ranging from 1.1 to 25.5 d. Reservoir emigrants did not immediately enter upriver after they were first detected in the reservoir exit area but continued reversal behavior before migrating upstream. This delay in exiting the reservoir took a median ± SE of 1.1 ± 5.5 d (range = 27 min to 88 d).

DISCUSSION

Reservoirs associated with hydropower generating stations are an obstacle in their own right to upstream salmonid migrations, having low water currents that remove directional cues (Andrew and Geen 1960; Geist et al. 2000). Such reduced currents can potentially cause salmonids to be unable to reach the spawning grounds or be exposed to high water temperatures that could lead to prespawning mortality (McCullough 1999). To aid upstream migration of adult salmonids, fisheries managers may opt to deploy strategies that bypass the potentially problematic reservoir reaches by capturing the migrating adults at a hydropower facility's fish passage or attraction structures and subsequently transporting them upstream of one or multiple reservoirs and hydropower dams. Such a strategy is referred to as trap and haul and is practiced in many hydropower-regulated rivers with success when transport is short and waters are cold (see Lusardi and Moyle 2017 for a recent review). While the trap-and-haul strategy may bypass the potential negative effects caused by reservoir passage, it may introduce uncertainty regarding the correct upstream release locations for migrating adult salmonids homing to each of their natal streams. A trap-and-haul management strategy can have other drawbacks as well, including potential delay during transportation, introduction of stressors from handling and transport which can affect swimming ability, or outright mortality (Lusardi and Moyle 2017). Also, the water temperatures found in the upriver reach (up to 23°C) are likely not cold enough to support the trap-and-haul strategy in full success. Still, this strategy has been shown to increase the chances of Atlantic Salmon successfully migrating upstream in comparison to volitional passage through reservoirs (Sigourney et al. 2015).

The owner and operator of the MGS is currently considering options for improving fish passage, including the possibility of allowing volitional upstream passage to

Atlantic Salmon adults during their spawning migration. The current trap-and-haul strategy removes the obstacle of reservoir passage, whereas volitional passage through the MGS would include navigation of the associated reservoir. This would be a new management strategy, and therefore the emigration success, migration rates, and behavior of adult Atlantic Salmon in the MGS reservoir needed to be assessed to inform the decision. The study was hampered by a large proportion (54%) of tag loss or mortality; however, of the fish successfully tracked, 47% were successful in finding the upstream exit and traveling upriver toward the spawning grounds and 12% were unsuccessful in exiting the reservoir.

The assessment of reservoir emigration success was hampered by presumed tag losses or fish mortalities (54% of all adults tagged). However, because no mortalities were observed among control fish and because one of the fallbacks was recaptured in the MGS fish lift without their acoustic transmitter but were identifiable through an external (Carlin) tag, we suspect that tag loss was a more likely fate than mortality. This is an abnormal occurrence among externally tagged salmonids in other studies (<20% losses; Jepsen et al. 2015). Greater water temperatures at the reservoir surface (up to 23.7°C) could have been a factor upon release since the Mactaquac Biodiversity Facility used cooler water drawn at depth from the reservoir when holding fish. For those fish that were determined to have either experienced tag loss or mortality later into the tracking period (i.e., >1 month), migratory delay within the reservoir (discussed below) could have caused depleted energy stores leading to actual mortality rather than having lost their tag.

Many (41%) tagged adults were known to have fallen back over the MGS based on subsequent detections downstream of the dam, and most (79%) of these were small males. This proportion of fallbacks was observed despite careful timing of release in coordination with dam operators to avoid entrainment. A substantial proportion (27.5%) of adults determined to have experienced tag loss or mortality could potentially be attributed to fallback over the MGS based on abruptly ceased detections within the vicinity of the MGS. These results contrast with an earlier Carlin tag study that placed 289 (1972) and 350 (1973) wild adult salmonids less than 1 km upstream from the MGS and only observed fallback rates of 5.8% and 6.6%, respectively (Marshall 1975). However, the same study observed much larger fallback rates of 54.2% and 12.5% for the 11 hatchery fish released in 1972 and the 144 released in 1973, respectively (Marshall 1975). For Chinook Salmon and steelhead *Oncorhynchus mykiss* in the Columbia River system, fallback has been reported to occur to 15–22% of fish (Boggs et al. 2004), with a high proportion among males (67%; Keefer et al. 2006). While the cause is unknown, it has been discussed that rivers altered by hydropower may remove homing cues and fish altered by the hatchery environment may also lack homing abilities (Keefer et al. 2006). In the Saint John River, water temperatures just downstream of the MGS over the time frame that fish were captured in 2016 averaged 18.5°C, which is generally warmer than they would have experienced in the reservoir (mean 16°C) and could have been a stressor immediately preceding and during capture, with latent effects such as fallback. Temperatures of 19.5–23.7°C during release could have also been prohibitively high despite all fish swimming away freely. The timing of descending downstream over the MGS most commonly occurred in the first week but extended up to a month after release, with the adults not attempting to travel very far upstream in search of the reservoir exit; therefore, one motivation for fallback could be a case of mistaken homing locations by fish that had intended to enter tributaries just downstream of the MGS (i.e., Nashwaak River, located approximately 20 km downstream of the MGS) rather than spawning grounds upstream of the MGS (Marshall et al. 2000). Another possibility is that the stark contrast between free-flowing water downstream of the MGS and the low-flow reservoir prompted fish to return downstream in search of more preferred conditions as was reported by Thorstad et al. (2008). Fallbacks can incur injuries, especially when the fallback route is via turbines (Dauble and Mueller 2000). Fallback via turbine would be the only route available to adults at the MGS in the summer (spillways are typically only available during the spring freshet). This high rate of fallback with the potential risk of mortality in the absence of a bypass leads to the suggestion that volitional passage may not be advisable unless a safe downstream route (e.g., a surface bypass with prevention of adult entry to turbines) for fallback salmonids is installed and its efficiency is further proven.

Only four tagged adults were determined to have been unsuccessful in navigating the reservoir as determined by continued movements in the reservoir throughout the autumn spawning migration season. All but one of these fish entered a dead-end tributary (Longs Creek), visiting one to seven times for a total duration of 3.5–19.4 h, adding to their migratory delay that could have contributed to their unsuccessful migration. Caudill et al. (2007) observed Chinook Salmon and steelhead during their spawning migration in the Columbia River and found that the fish that were unsuccessful in reaching the spawning grounds were delayed at nearly all of the eight dams and reservoirs in comparison to those fish that were successful in reaching the spawning grounds. Movement of Atlantic Salmon into tributaries without spawning was also seen in a low-flow lake in northern Ireland (Kennedy and Allen 2016). Temporary movements into tributaries within reservoirs was attributed to seeking coldwater refugia for

TABLE 4. Model selection using Akaike information criterion (AIC) for linear mixed-effects models (LMEMs) and linear mixed-effects (LME) logistic regression models (see Table 3 for model details) for testing the dependence of Atlantic Salmon migration rates and direction on environmental variables, such as their presence in the reservoir (reach = reservoir or upriver), water temperature, water velocity, water angle (direction from downstream = 0°), and fish direction (upstream or downstream).

Model	AIC
Model B (LMEM)	
Upstream_km_d ~ reach × temperature_avg × water_velocity_avg × sex × size + (1|fish_id)	7,089
Upstream_km_d ~ reach × temperature_avg × water_velocity_avg × sex + size + (1|fish_id)	7,139
Upstream_km_d ~ reach × temperature_avg × water_velocity_avg × sex	7,145
Model C (LME logistic regression)	
Fish_direction ~ reach + (1|fish_id)	1,551
Fish_direction ~ reach + water_angle + (1|fish_id)	1,557
Fish_direction ~ reach + sex + (1|fish_id)	1,559

TABLE 5. Observed duration (d; mean ± SE) that adult groups spent traversing the Mactaquac Generating Station reservoir (37 km) versus the expected duration based on individual upriver migration rates (km/d).

Tagging group	Observed (d)	Expected (d)	Delay (d)
2014	4.5 ± 1.0	3.1 ± 1.6	1.4 ± 1.0
2015	2.4 ± 0.6	0.8 ± 0.1	1.6 ± 0.5
2016	8.1 ± 2.1	0.9 ± 0.1	7.2 ± 2.1

TABLE 6. Number of Atlantic Salmon adults that skipped or entered Longs Creek, the number that entered upon their first encounter, and the median ± SE duration of time spent in the tributary.

Tagging group	*N* skipped	*N* entered	*N* first encounter	Duration
2014	3	7	3	5.2 ± 2.2 h
2015	2	7	4	17.2 ± 6.8 d
2016	3	13	1	1.3 ± 10.8 d

Chinook Salmon and steelhead during their spawning migration in the Columbia River (Keefer et al. 2008). The water temperatures from sensor tags when fish entered Longs Creek were higher on average (20°C) than the main stem of the reservoir (16°C) but were lower within the Mactaquac Arm (15°C), indicating that the latter may have been used as coldwater refugia. The negative relationship found between temperatures recorded by loggers versus sensor tags near the MGS may also indicate that those fish were seeking cooler temperatures than were recorded by the loggers at a 3-m depth.

For the endangered Outer Bay of Fundy Atlantic Salmon population, every adult's contribution (especially females) to recruitment is critical to work toward population recovery (O'Connell et al. 1997). The previous Carlin tag study done in the 1970s on 1,355 adults released in the MGS reservoir resulted in low proportions of fish reaching the BGS (22.3% wild fish, 2.8% captive-reared fish; Marshall 1975). Stemming from this, managers employed a trap-and-haul strategy to aid their survival along the migratory route to their spawning grounds, although the efficacy of this strategy has not been formally tested in this river system. In the Penobscot River, less than 200 km south of the Saint John River, Sigourney et al. (2015) directly compared the trap-and-haul strategy of Atlantic Salmon adults with volitional passage starting at the reservoir of the lowermost dam and found that transporting the adults resulted in a higher percentage of fish (78.6–82.4%) reaching upstream dams in a shorter period of time (5–7 d) than those fish that travelled under their own power (22.4–41.3%, 23–25 d). In the Saint John River, managers acknowledge that transport likely causes some stress and disorientation but assume that mortality is minimal (R. Jones, Fisheries and Oceans Canada, personal communication). The current strategy is for adult Atlantic Salmon that return to the MGS to be released upstream of the MGS reservoir, with the majority being released at rkm 230 (Clarke et al. 2014). Migration success of the adults through the reservoir (47%) and to the BGS (29%) in the current study appears to have resulted in greater rates than reported by Marshall (1975), although the small sample sizes due to tag loss could increase our uncertainty to levels that would negate direct comparison. If the total number of fish are retained despite tag loss, the proportion of successful reservoir emigrants (21.6%) closely matches the Marshall (1975) study of wild adult Atlantic Salmon (22.3%). The results of the current study and the previous Marshall (1975) study are more closely aligned with the results of the volitional passage in the Sigourney et al. (2015) study than their trap-and-haul results.

Atlantic Salmon cease feeding during their spawning migration; as a consequence, their energy reserves can be greatly impacted by reduced migration rates influencing their efficiency in reaching the spawning grounds (Salinger and Anderson 2006). Migration rates tend to be faster earlier in the migration and slow as they reach the spawning grounds (Thorstad et al. 2008). In this study, median migration rates were significantly lower early in the migration within the reservoir (9.3 km/d) and were faster as they moved upriver (39.0 km/d) and upstream of the BGS (65.2 km/d). The slower migration rate in the reservoir was assessed to result in a moderate migratory delay of 3.8 d and may be associated with the lack of water current. Reported rates of salmonids moving through free-flowing rivers are variable (0.7 km/d in Gowans et al. 1999; 65 km/d in Salinger and Anderson 2006). Upstream movements of adult Atlantic Salmon through small (<10 km) reservoirs in Scotland were found to range from 0.7 to 32 km/d (Gowans et al. 1999, 2003) and through a large reservoir (50 km) in Russia ranged from 17 to 52 km/d (Karppinen et al. 2002). Chinook Salmon and steelhead have been reported to move through multiple reservoirs in the Pacific Northwest fairly quickly (22–77 km/d), with faster movements associated with greater water temperatures (Keefer et al. 2004). Compared to other studies, the migration rates found within the MGS reservoir appear to be exceptionally slow. However, previous studies in the Saint John River have found adult migration rates to range from 5.5 to 6.2 km/d from the MGS to the BGS, with slower rates when released closer to the BGS (2.9 km/d; Marshall 1975). The current study found a median migration rate between the MGS and the BGS of 10.2 km/d, which is slightly faster than the previous study. It is possible that water temperatures were higher during the current study years than during the comparable works done in 1972–1973, driving faster migration rates, but this cannot be discussed without comparative data within Marshall (1975).

While up- and downstream movements are typically seen as adult Atlantic Salmon search for appropriate spawning grounds (Thorstad et al. 2008), this does not explain the reversals observed within the MGS reservoir since the impoundment is a minimum of 285 km downstream from their assumed spawning habitat. Instead, these reversals could be influenced by handling (Bernard et al. 1999) or by fish searching for the upstream exit of the reservoir with minimal directional cues from flowing water, or the adults may have been maturing their gametes in a preferable temperature range. In the reservoir, 95% of the adults spent 31–53% of their time swimming downstream rather than upstream, covering distances much greater than was needed to reach the upstream exit. Even the migrant that ascended furthest toward the spawning grounds in the Tobique River exhibited extensive movements to presumably search for the exit of the

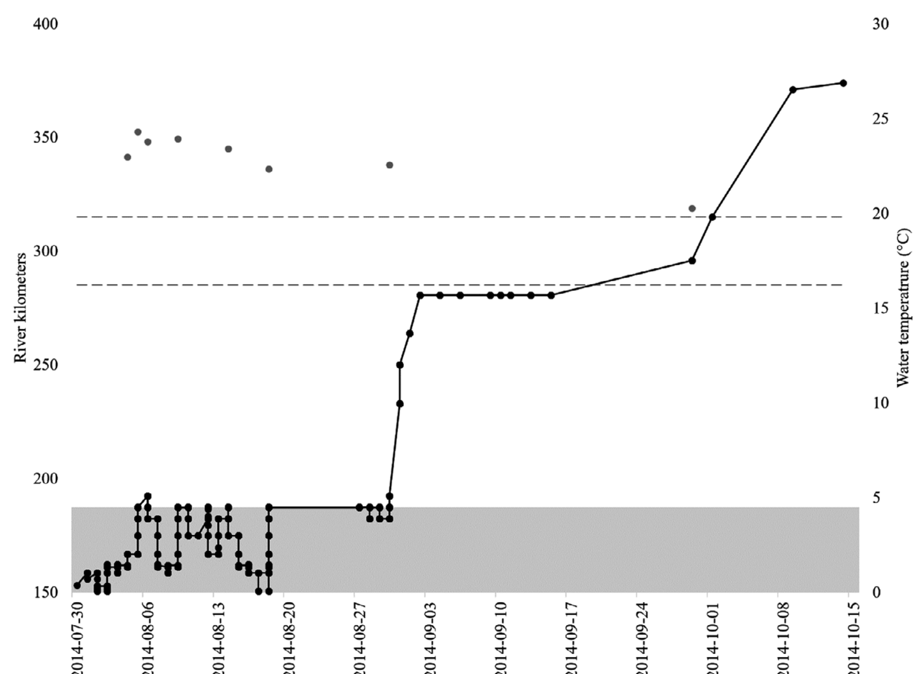


FIGURE 6. Location (river kilometer [rkm]; black line) of detections from an acoustic-tagged adult Atlantic Salmon released 3 km upstream of the Mactaquac Generating Station (rkm 150). The example acoustic track demonstrates the extensive reversals often observed within the Mactaquac Reservoir (light gray shading) before successfully exiting the reservoir and ceasing reversals in the upriver reaches as it passed the Beechwood Generating Station (rkm 285; lower dashed line) and Tobique Narrows Generating Station (rkm 315; upper dashed line) on the way to the spawning grounds. Associated water temperatures (°C; gray dots) are given on the secondary axis.

MGS reservoir, visiting Longs Creek 22 times, approaching the exit eight times, and spending approximately 30% of the time within the reservoir swimming downstream covering a minimum of 760 extra kilometers. Migratory delay accumulated between slower migration rates, entering dead-end tributaries for up to 4.7 d (median 5.2 h) over multiple visits, and continued reversal behavior for a considerable period of time ranging from 12 h to 13 d after the fish were detected at the upstream exit before continuing their migration upriver.

Water temperature is a controlling factor for poikilotherms, impacting their swimming speed and sexual development. Although Atlantic Salmon are adaptable and can maintain high aerobic capacity up to 23°C, their critical swimming speed peaks at 18°C (Hvas et al. 2017), but at this same temperature, survival of adult female Sockeye Salmon *Oncorhynchus nerka* was significantly lower than for those exposed to a lower temperature of 10°C, potentially due to their greater investment in egg development (Crossin et al. 2008). Salinger and Anderson (2006) found that upstream-migrating Chinook Salmon had a maximum swimming speed and minimal delay at 16°C. In the current study, Atlantic Salmon with sensor tags spent three-quarters of their time between 13 and 29 m, with associated water temperatures of 12–18.5°C.

Increased temperatures as salmonids move from one water body to another may delay their upstream migration, as has been seen for Chinook Salmon moving from the Columbia River to the Snake River (Dauble and Mueller 2000) and has been consistently observed among salmonids within the temperature range of 19–23°C (McCullough et al. 2001). As the adult Atlantic Salmon in this study reached the reservoir exit, one fish with a sensor tag reversed direction and then returned to move upriver with no discernable temperature difference between locations but a second fish with a sensor tag was observed to take similar movements reporting temperatures up to 21.7°C at the reservoir exit, potentially prompting the fish's reversal back into the reservoir with temperatures of 18.2–20.9°C before returning to move upriver with temperatures up to 22.9°C. Based on the temperature logger data, most fish ($n = 8$) emigrated when daily average temperatures were cooler upriver than in the reservoir, but there were others ($n = 4$) that moved out of the reservoir while it was warmer upriver than in the reservoir.

Overall, these sources of delay added approximately 4–30 d to their migration to the spawning grounds. Delay within the lentic MGS reservoir could result in reduced energy stores typically reserved for spawning activities, as has been seen among Chinook Salmon adults that had 5–8% of muscular energy density reduction attributed to migratory delay within the regulated Columbia River (Mesa and Magie 2006). Such energetic losses are expected to be exasperated as salmonids experience climatic-driven water temperature increases (Keefer et al. 2019).

This study examined the migratory movements of adult Atlantic Salmon within the large MGS reservoir to determine whether the option of volitional passage upstream of the MGS would be viable. The ability to draw conclusive results suffered from a high proportion of tag loss and fallbacks, but from the successfully tracked fish, only 47% successfully navigated the reservoir. This suggests that volitional passage may expose a large proportion of adult Atlantic Salmon to risks that may increase adult mortality and energy expenditure during the reversal behavior exhibited in the reservoir in comparison with the current trap-and-haul management strategy. However, trap and haul has also not been sufficiently studied in this system to decipher whether the potential negative effects from handling and transport impact fish during their spawning migration. To better understand whether volitional passage or trap and haul would result in higher survival and spawning success of migrating adult Atlantic Salmon, future research should include a direct comparison of these management strategies along with an increased focus of tracking on the spawning grounds; however, such a study would be challenging in this river system given the low numbers in the spawning runs of this endangered population.

ACKNOWLEDGMENTS

Funding for this project was received from New Brunswick Power, Natural Sciences and Engineering Research Council of Canada's Collaborative Research and Development program (CRDPJ: 462708-13), and the Atlantic Salmon Conservation Foundation. Fisheries and Oceans Canada personnel (in particular Leroy Anderson) are thanked for their assistance with fish capture and tagging. Mona Crewdson is thanked for providing access to her property for fish release. We also thank Mark Gautreau, Ben Wallace, Samuel Andrews, Daniel Arluison, and Kaleb Zelman for extensive efforts during receiver installation and retrieval. Samantha Pettey and Caitlin Tarr are thanked for their extensive active tracking commitments. Finally, we would like to recognize the help we have received from Fisheries and Oceans Canada personnel at Mactaquac Biodiversity Facility (John Whitelaw and Becky Graham) with regard to the husbandry of the control fish. There is no conflict of interest declared in this article.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.