Received: 16 December 2020 | Accepted: 26 April 2021

DOI: 10.1111/jfb.14768

REGULAR PAPER

JOURNAL OF FISH BIOLOGY fsbi

Overwintering and migration behaviour of post-spawned Atlantic salmon *Salmo salar* in a large hydropower-regulated river and reservoir

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Funding information
Atlantic Salmon Conservation Foundation (CA); Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: CRDPJ 462708-13; New Brunswick Power (CA); This research project is a part of Mactaquac Aquatic Ecosystem Study funded by New Brunswick Power, NSERC's Collaborative Research and Development programme (CRDPJ: 462708-13), and the Atlantic Salmon Conservation Foundation.

Abstract

Tracking 47 post-spawned adult Atlantic salmon *Salmo salar* L. in a hydropower-regulated river through autumn, winter and spring revealed that winter survival was 56% and 75% in two study years, respectively, with higher mortality of males than females (50% *vs.* 33% and 100% *vs.* 13%, respectively). Some kelts ($n = 7$) displayed nondirected movements that were interpreted as a reconditioning period for an average of 9–17 days prior to directed downstream movements indicating the initiation of migration. Survival after the initiation of migration in spring was 83% and 94% to the hydropower dam in the first and second study years, and decreased to 60 and 63%, respectively, after dam passage. There were no further losses in the downriver reach in the second year, with the first year having a cumulative survival estimate of 53% to the river mouth. Kelts approached the dam when the spillway gates were available as a passage option most of the time (64%–75%), but some kelts arrived at the dam or had not yet passed when spillways were closed ($n = 6$) and the only remaining passage option was restricted to the turbines. However, all but one kelt that must have passed *via* turbine were successful in reaching the river mouth. Migratory delay presumably due to searching behaviour caused by low water flow was estimated at approximately 6 days as migration rates were significantly slower in the reservoir (median ± S.E. 8.5 ± 2.5 km day^{-1}) than up- (29.7 ± 5.0 km day^{-1}) or downriver (22.1 ± 3.1 km day^{-1}). The proportion of time (median 30%) that kelts spent swimming upstream (searching behaviour) in the reservoir was a significant variable for migration success.

KEYWORDS
Atlantic salmon, hydropower, kelt, migration, telemetry, western Atlantic

1 | INTRODUCTION

There is a general paucity of data regarding adult Atlantic salmon *Salmo salar* behaviour and movements, especially in the freshwater environment (Bardonnet & Baglinière, 2000; Hubley *et al.*, 2008). Adult *S. salar* spawn in rivers in the autumn and due to their iteroparous life history strategy the surviving post-spawners (called kelts) either migrate back to the sea soon after spawning (Halttunen *et al.*, 2013; Lacroix, 2013) or more commonly overwinter in freshwater to brackish head-of-tide areas of the estuary and migrate to the sea in spring (Jonsson *et al.*, 1990; Ruggles, 1980). Some individuals begin downstream migrations soon after spawning, particularly if they

are in poor condition and therefore in need of reconditioning in the ocean, where food is more abundant than in the river (Gross, 1987; Halttunen *et al*., 2013). These can be females but are more commonly males and larger-bodied individuals who have expended substantial energy during spawning. While females invest approximately six times more energy into producing offspring than males, the injuries incurred by competing males significantly reduce their condition and chance of survival compared to females (Jonsson *et al*., 1991, 1997). Large-bodied individuals also expend more energy than their small-bodied counterparts during spawning and are therefore more likely to be in poor post-spawn condition (Jonsson *et al*., 1991, 1997).

Kelts can become repeat spawners in the population if they survive their outward migration, time at sea and return spawning migration. *S. salar* iteroparity could be a key factor in the recovery of declining populations (Niemelä *et al*., 2006; Saunders & Schom, 1985). Larger females produce fewer but larger eggs per unit body size, which can develop into larger-bodied juveniles than those from smaller eggs, providing a greater chance of survival (Beacham and Murray, 1993; Fleming, 1996). This strategy can contribute to the stability of a population by adding large-bodied individuals and thus increased fecundity to the spawning population, as well as contributing to genetic diversity (Halttunen, 2011; Jones, 1959). Genetic diversity is also increased by repeat spawners because they add multiple year-classes to the annual production of young (Niemelä *et al*., 2006; Saunders & Schom, 1985). Such diversity within a spawning population can create a portfolio effect that can help to stabilize a population and prevent extirpation (Schindler *et al*., 2010).

While iteroparity may be an aspect that helps *S. salar* populations remain healthy or recover from a depressed state, kelt survival presents a special challenge in regulated rivers with dams and reservoirs. Lawrence *et al*. (2016) predicted that the contribution of kelts to spawning events would lessen the probability of population decline in *S. salar* by 8%–27% depending on how many dams were obstructing downstream migration. During their downstream migration, salmon contend with reservoir and dam structures that can disrupt migratory cues and create migratory delay. Such delays have been observed for anadromous brown trout *Salmo trutta* L. (Östergren & Rivinoja, 2008; Wertheimer & Evans, 2005) and for post-spawned *S. salar* (Nyqvist *et al*., 2017). Kelts often travel near the surface of the water column (Hubley *et al*., 2008; Jonsson *et al*., 1990) and can pass surface spill bypass systems successfully (Arnekleiv *et al*., 2007; Nyqvist *et al*., 2016; Scruton *et al*., 2008). Passage *via* turbines makes them susceptible to injury and death due to their large body size (Nyqvist *et al*., 2016; Sigourney *et al*., 2015; Ruggles, 1980).

Many populations of *S. salar* are declining in Canada (Committee on the Status of Endangered Wildlife in Canada, 2011). *S. salar* returning to the Saint John River (New Brunswick, Canada) are part of the Outer Bay of Fundy population that has declined 64% over three generations (Committee on the Status of Endangered Wildlife in Canada, 2011), warranting potential consideration under the federal Species At Risk Act. Repeat spawners have been identified as a critical life stage for population recovery (Halttunen, 2011; Saunders & Schom, 1985). The objective of this study was to explore the overwinter and migratory behaviour of *S. salar* kelts in relation to a large hydropower generating station (the Mactaquac Generating Station) and its associated reservoir. Specifically, this study aimed to quantify (a) post-spawned adult survival over winter, (b) migration timing in relation to environmental conditions and hydropower operations, (c) migration rates through lotic and lentic reaches to estimate potential migratory delay in the reservoir, and (d) survival rates in the spring as they navigated the reservoir and dam on their way to the river mouth.

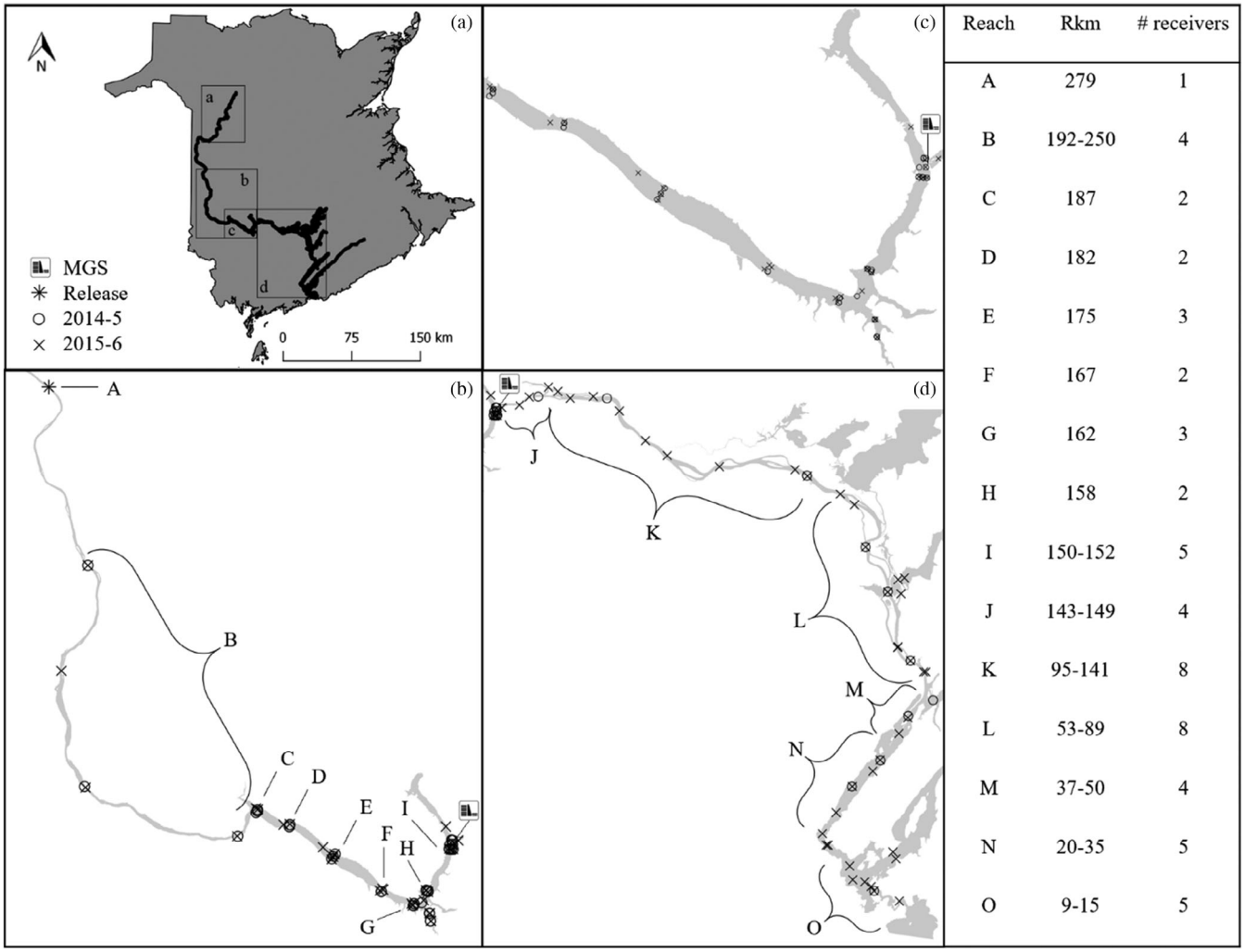
2 | MATERIALS AND METHODS

2.1 | Study area

The Saint John River (SJR) is the largest river in New Brunswick, Canada, and the largest between the St Lawrence and Mississippi rivers. It has a drainage area of 55,000 km^2, being 700 km long with an average width of 750 m (Kidd *et al*., 2011). Mean annual discharge of the SJR is 1100 $m^3\ s^{-1}$ (Cunjak & Newbury, 2005), ranging from 280 $m^3\ s^{-1}$ in the summer to 10,000 $m^3\ s^{-1}$ during the spring freshet (Stantec Consulting Ltd, 2015). The river downstream of the MGS was ice-covered for 104 and 39 days from 30 December 2014 to 12 April 2015, and from 14 January to 21 February 2016, respectively (C. Côté, Environment Canada, personal communication).

The Mactaquac Generating Station (MGS; Figure 1) was completed in 1968. It is the largest dam in New Brunswick (1100 m wide, 55 m high with 34.1 m forebay to tailrace head differential) with a capacity to generate 672 MW with six Kaplan turbines (maximum discharge 2294 $m^3\ s^{-1}$) and is the lowermost dam on the SJR situated at 150 river km (rkm; Chateauvert *et al*., 2018). There are no specific downstream fish passage structures. *S. salar* kelts had three alternative routes for dam passage at the MGS, consisting of two spillway routes, that is, either the diversion sluiceway directly from the reservoir (diversion sluiceway, DS; Figure 2) or the spillway within the forebay (Chateauvert *et al*., 2018; spillway, SW; Figure 2) which are bottom spill at 17 m opening upwards or through one of the six Kaplan turbines (112 MW/112.5 rpm each) which have their intake at 8–23 m depth in the generating station (GS; Figure 2). There are trash racks with 16.5 cm spacing between bars. The MGS affects water levels up to 97 rkm upstream (average depth 26 m, maximum depth 51 m, volume 1.36 km^3), but a drastic decrease in width and depth at 187 rkm delineated the 37 rkm 'reservoir' from 'upriver' reach in this study (transition from reach C to B; Figure 1). Average water velocity in this 37 rkm lake-like reach upstream of the MGS (reaches I to C; Figure 1) was historically 52 cm s^{-1}, but was reduced to 6 cm s^{-1} due to impoundment (Stantec Consulting Ltd, 2015). Downstream of the MGS was labelled as the 'downriver' reach in this study.

While the SJR has a total of 11 hydropower installations, there are two additional hydropower dams [the Beechwood Generating Station at rkm 285 (BGS) and the Tobique-Narrows Generating Station at



Reach	Rkm	# receivers
A	279	1
B	192-250	4
C	187	2
D	182	2
E	175	3
F	167	2
G	162	3
H	158	2
I	150-152	5
J	143-149	4
K	95-141	8
L	53-89	8
M	37-50	4
N	20-35	5
O	9-15	5

FIGURE 1 A map of New Brunswick, Canada, highlighting the studied area of the Saint John River and its tributary, the Tobique River (a), and the subsequent tracking areas of acoustically tagged post-spawned *Salmo salar*. Inserts identify the locations of individual acoustic VR2W receivers upstream of the Mactaquac Generating Station (MGS; b), within the MGS reservoir (c), and downstream of the MGS (d) in 2014–2015 (o; $n = 27$) and 2015–2016 (x; $n = 65$). These receivers were combined into 15 reaches (A–O, with corresponding river kilometres and the number of receivers in each reach) for the purposes of the Cormack–Jolly–Seber (CJS) estimation of survival and encounter probabilities; all but the locations adjacent to the release site (a) consisted of multiple receivers that were treated as one spatial entity in the CJS models. The release site of tagged *S. salar* in reach A is also marked (*). (▪) MGS; (✳) release; (○) 2014–5; (×) 2015–6

rkm 315] along the main salmon migration route to the Tobique River, which is the main *S. salar* nursery and spawning habitat in the upper SJR (Marshall *et al*., 2014).

The Mactaquac Biodiversity Facility just downstream of the MGS is operated by Fisheries and Oceans Canada to supplement *S. salar* production within the river (Jones *et al*., 2004). The Mactaquac Biodiversity Facility currently focuses on circumventing the marine life stage by employing smolt-to-adult supplementation (Fraser, 2016; also referred to as captive-rearing to mature adults, henceforth CR), whereby juveniles (approximately 1000–3000 annually) are captured from the Tobique River or the BGS gatewells on their seaward migration, captively reared to maturity and released back to the wild as adults (387–1450; Jones *et al*., 2014) to spawn naturally.

2.2 | Tagging and tracking

Post-spawned *S. salar* adults were acoustic-tagged (Table 1) and tracked to determine overwintering behaviour, spring migration speed (rates) and success. Fish were sourced from the wild *via* rotary screw traps operated by Fisheries and Oceans Canada located at Three Brooks (rkm 346) or by angling in pools at the Forks of Tobique River (rkm 415) or the Barrier Pool (rkm 416) just downstream of the spawning grounds. Despite being captured in the wild, these kelts were likely to have been captive-reared fish that were released in the river to spawn naturally because small proportions of returns to the MGS are sea-run adults (7% in 2014; R. Jones, Fisheries and Oceans Canada, personal communication), and therefore these fish are termed wild-caught, captive-reared (WC-CR). The number of kelts tagged was

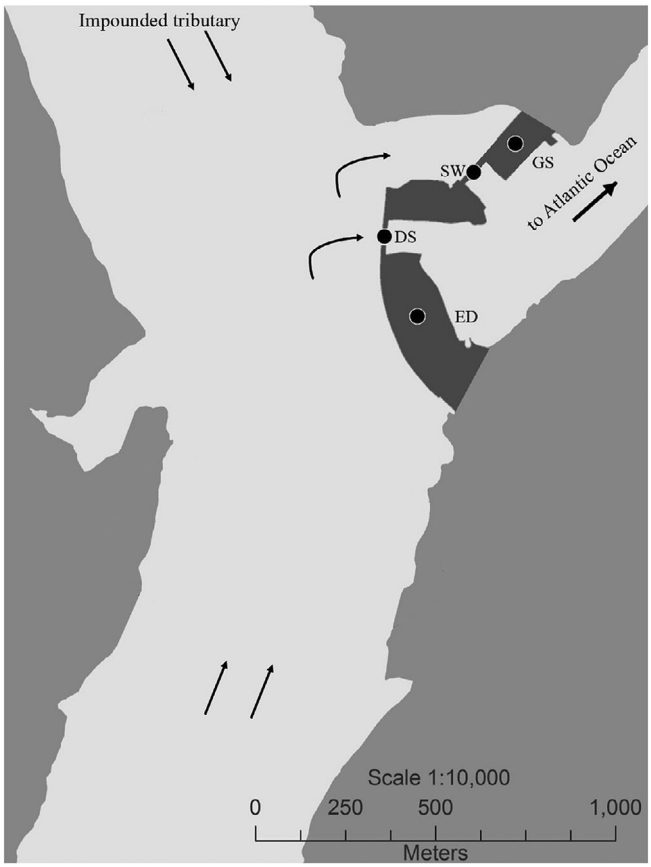


FIGURE 2 Structures of the Mactaquac Generating Station (MGS): GS, generating station; SW, spillway; DS, diversion sluiceway; ED, earthen dam. The arrows show the direction of main flow

also supplemented by kelts that were spawned at the Mactaquac Biodiversity Facility as part of a broodstock programme, and these fish are termed CR-broodstock. Captive-reared fish may not have experience at sea and were therefore classified by size (≤63 cm = small, >63 cm = large) rather than the number of sea-winters. In comparison to sea-run adults, the small salmon would be roughly comparable to 1-sea-winter fish whereas large salmon would be comparable to -multi-sea-winter fish.

All tagged fish in both years were released in the downstream vicinity of the BGS at rkm 280 to avoid any mortality potentially inflicted by either of the upstream dams to focus on the effects of the MGS and its reservoir. While transporting and releasing of the tagged fish away from their capture sites in the Tobique River could have potentially affected behaviour patterns compared to the natural free-swimming population, it ensured that limited sample sizes would not be further restricted, and served as a proxy to those post-spawners that would naturally descend to the main stem of the SJR from tributaries downstream of the BGS (*e.g.*, Shikatehawk Stream, Becaguimec River, Meduxnekeag River).

In 2014, 14 WC-CR post-spawned adults were captured in the Tobique River (Figure 1) and tagged (Table 1). Two of these salmon were captured in a rotary screw trap on 10 and 12 November 2014, tagged on site (see below) and transported in a 1000 l oxygenated tank for 1 h 15 min to the release site 6.5 rkm downstream of the BGS (rkm 280; Figure 1). Twelve were captured by angling; seven were captured on 14 November 2014, transported for 1 h 25 min to a heated shed at Three Brooks for tagging and then transported further to the release site. The remaining five fish were captured, tagged on site and transported to the release site on 17 November 2014. Eleven

TABLE 1 Fork length (cm), weight (kg) and condition (mean ± S.E.) of acoustic tagged adult *Salmo salar* in 2014 and 2015

Year	Origin	Sex	*N* tagged	Fork length (cm)	Weight (kg)	Condition
2014	WCS	F	1	78.4	4.95	1.03
	WCS	M	1	56.8	2.05	1.12
	CR-Br	F	4	63.7 ± 2.1	2.56 ± 0.29	0.98 ± 0.02
	CR-Br	M	7	66.1 ± 1.4	2.76 ± 0.19	0.94 ± 0.01
	CR-Br	All	11	65.2 ± 1.2	2.69 ± 0.16	0.96 ± 0.01
	WC-CR	F	10	56.8 ± 5.2	1.75 ± 0.43	1.30 ± 0.17
	WC-CR	M	2	44.9 ± 1.7	1.45	1.80
	WC-CR	Unknown	2	59.9 ± 3.9	3.31 ± 0.49	1.63 ± 0.54
	WC-CR	All	14	56.3 ± 3.9	2.10 ± 0.38	1.45 ± 0.16
2015	CR-Br	M	2	65.0 ± 5.0	3.45 ± 1.09	1.21 ± 0.12
	WC-CR	F	15	64.6 ± 2.4	3.08 ± 0.29	1.05 ± 0.02
	WC-CR	M	1	60.0[b]	1.41	0.65
	WC-CR	Unknown	2	62.9 ± 2.9	2.11 ± 0.75	0.82 ± 0.19
	WC-CR	All	18	64.4 ± 2.0	2.87 ± 0.27	1.04 ± 0.03

Note. The tagged *S. salar* included wild-caught captive-reared (WC-CR) and captive-reared broodstock[a] (CR-Br) post-spawned adults, and wild-caught sea-run adults that were tagged in the summer (WCS) during the upstream migration prior to spawning.

[a]Captive-rearing refers to a strategy used in the Saint John River where wild pre-smolts or smolts are collected during their downstream migration, raised to maturity in captivity, and released back to their river of origin to spawn (Jones *et al*., 2004).

[b]Total length.

CR-broodstock adults were also tagged on 24 November 2014 at the Mactaquac Biodiversity Facility (Table 1). After tagging, the fish were treated in a 1:300 formaldehyde bath for 45 min then held at the Mactaquac Biodiversity Facility for 2 days before being transported for 1.5 h and released at the same site.

Two sea-run adult *S. salar* that had been gastric-tagged as part of a study examining the upstream migration of wild adults through the MGS reservoir were also tracked (Babin *et al*., 2020). These two adult *S. salar* were captured at the MGS fishlift during their summer spawning migration (Table 1; WCS), tagged on 28 July 2014 and held for 2 days before being released 3 rkm upstream of the MGS. These fish produced detections during their downstream migration after they had presumably spawned just downstream of the BGS and therefore were also included in this dataset.

In 2015, 18 WC-CR post-spawners were captured in the Tobique River and tagged (Table 1). Scale samples were examined to determine the years spent in fresh and salt waters. This analysis followed standard procedures of collecting multiple scales from the left side of the fish above the lateral line and having an experienced person (C. Fitzgerald, Fisheries and Oceans Canada) examine the scales microscopically for the distance between circuli to distinguish freshwater from seawater growth patterns (Shearer, 1992; Table 2). All tagged fish were then transported for 2 h to the release site. Two CR-broodstock fish were also tagged on 27 November 2015, treated in a

TABLE 2 Location (reach, rkm) and timing of initiation of *Salmo salar* kelt spring migration, and timing of the first encounter and passage of the Mactaquac Generating Station with availability for fish passage *via* spillway gates upon the date of last encounter

Year	Tag[a]	Origin	Reach (rkm)	Initiation	MGS encounter	MGS Passage	Spillway
2015	12,395/96	WC-CR	C (187)	19 April	23 April	23 April	Open
	12,381/82	WC-CR	C (187)	20 April	22 April		Open
	12,387/88	WC-CR	C (187)	20 April	27 April		Open
	12,391/92	CR-Br.	C (187)	23 April	27 April	27 April	Open
	22,746	CR-Br.	C (187)	23 April	27 April	27 April	Open
	12,383/84	WC-CR	C (187)	24 April	29 April		Open
	22,752	CR-Br.	E (175)	26 April	28 April		Open
	17,154	WCS	G-H (160)	1 May	2 May	2 May	Open
	22,757	WC-CR	C (187)	4 May	8 May	9 May	Open
	22,750	CR-Br.	B (216)	7 May	14 May	15 May	Closed
	12,377/78[b]	WC-CR	B (216)	20 May	22 May	26 May	Closed
	12,379/80[b]	WC-CR	B (216)	20 May	22 May	22 May	Closed
	22,743[b]	CR-Br.	B (216)	2 June	22 June	22 June	Closed
2016	2134/35	WC-CR	B (192)	21 March	9 April	9 April	Open
	39,354[b]	WC-CR	B (216)	23 March	9 April	9 April	Open[c]
	39,352[d]	WC-CR	B (216)	29 March	8 April	8 April	Open
	2130/31[b]	WC-CR	B (216)	1 April	8 April	8 April	Open
	2124/25	WC-CR	B (216)	2 April	18 April	18 April	Open
	2128/29[d]	WC-CR	B (216)	2 April	22 April	22 April	Open
	39,356	WC-CR	B (216)	4 April	14 April	14 April	Open
	39,350[d]	WC-CR	B (216)	8 April	24 April	24 April	Open
	2132/33[bd]	WC-CR	D (182)	8 April	16 April	17 April	Open[c]
	2126/27[b]	WC-CR	I (150)	8 April	8 April	8 April	Open
	2138/39[d]	WC-CR	B (216)	9 April	15 April	15 April	Open[c]
	39,355	WC-CR	B (216)	15 April	24 April	26 April	Open
	39,351	WC-CR	E (175)	16 April	18 April		Open
	39,349[d]	WC-CR	B (216)	25 April	3 May	3 May	Closed[c]
	39,357	WC-CR	B (233)	5 May	17 May	20 May	Closed

Note. MGS, Mactaquac Generating Station WC-CR, wild-caught, captive-reared; CR-Br, captive-reared, broodstock; WCS, wild-caught, summer. The reaches are indicated using the lettering corresponding to Figure 1.

[a]Tags with two ID codes indicate transmitters with temperature/depth sensors.

[b]Individuals which were observed to have a reconditioning period.

[c]Presumed dam passage mortality.

[d]Scale analysis indicates at-sea experience (sea age 2–4 years).

formaldehyde bath and were allowed to recover for 10 h prior to being transported 1.5 h to the release site.

Acoustic (69 kHz) V13 tags (Vemco, Halifax, NS, Canada) were used (13 mm diameter, 36 mm long, 11 g in air, 6 g in water). Ten tags each year had temperature and depth sensors (45 mm long, 12 g in air, 6 g in water). In 2014, tags were programmed to transmit on average every 300 s for the first 30 days, every 600 s for the next 100 days (over the winter period) and every 60 s during the spring migration period. Battery life was estimated to last 1078 days for nonsensor tags and 770 days for sensor tags. In 2015, tags transmitted at an average of 60 s for the duration of the study. Battery life was estimated as 362 days for the nonsensor tags and 277 days for the sensor tags. The tag/body weight ratio averaged 0.51% (S.E. = 0.05%). Tagging was performed using 40–80 ppm clove oil anaesthetic (eugenol as active ingredient; ethanol in 1:10 ratio used as carrier) for 402 ± 122 s, with surgery lasting 288 ± 106 s when acoustic tags were surgically inserted into the peritoneal cavity and closed using two monofilament sutures (Monosof 6–0, ce-2 needle). The fish recovered in either a 1000 l tank (wild-caught) or a 72 m^3 hatchery pool with 60 cm depth.

Kelts were passively tracked downstream through the SJR and Mactaquac reservoir using 37 VR2W receivers in 2014–2015 and 65 receivers in 2015–2016 (Figure 1). The reservoir was the focus of the study and had a wider channel, therefore lines of two or three receivers were spaced approximately 5 km apart in this area, whereas the upriver and downriver sections had more narrow channels that allowed for one receiver in most locations except for the lowermost locations where receivers were again set in a line or placed closer together. A data partnership with the Ocean Tracking Network also provided detections from these tagged kelts as they exited the SJR and travelled the Bay of Fundy, Gulf of Maine and the Atlantic side of Nova Scotia. Range-testing of the V13 tag using VR2W receivers was performed over 26 trials within the reservoir at two locations. Detection range was defined as the distance whereby 50% of transmissions were reliably detected. Average detection ranges were 537–897 m (Babin *et al*., 2019).

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 licences were granted by Fisheries and Oceans Canada (Licence 325,657).

2.3 | Hydrodynamic model and water temperature

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 s^{-1}, current angle from downstream) every 2 h during the study period at the same locations as the acoustic receivers (Haralampides *et al*., 2018; Ndong *et al*., unpublished). 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; Figure 1) and 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 *et al*., unpublished).

Water temperature was recorded every 2 h using HOBO loggers attached to most receivers throughout the SJR. Loggers were placed at mid-depth in the reservoir and near the riverbed in the up- and downriver reaches where water depth was much shallower.

2.4 | Statistical analyses and definitions

Mann–Whitney U tests were used to compare the duration between release and first detections (the initiation period) of fish of different origin (WC-CR *vs*. CR-broodstock) and sex as a proxy to determine whether tagging may have had differing effects on initial movements between groups.

The last detection of each tag was assumed to represent the area of mortality, although this may not be a fair assumption for some reaches in the first study year that did not have reliable detection probabilities. Overwintering mortality location was inferred from the last detection of tags without detections indicating the initiation of spring movement. Presumed mortality could be due to natural overwinter stressors or due to tagging and handling stress, and may encompass tag loss due to expulsion of the tag or early tag failure (Kennedy *et al*., 2018). Fisher's exact tests were used to compare proportions of winter survival between years, sexes and sizes.

The initiation of spring migration was defined as the time at which fish began directed downstream movements. There was a period of pre-migration movement apparent from some tagged individuals when activity was observed, but the direction of movement was not primarily downstream or upstream. Rather, this pre-migration period was characterized by back-and-forth movements.

Linear mixed effects models (LMEMs) were used to identify the variables (see below) 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.

Migration rates (km day^{-1}) were examined by comparing overall values within the upriver (defined as reach B; Figure 1), reservoir (C–I; Figure 1) and downriver (J–O; Figure 1) reaches for both study years in the first LMEM, with *post hoc* Tukey contrasts. These rates were calculated as: upriver – from the first detection indicating the initiation of migration (directed downstream movements) to the first detection as they entered the reservoir (reach C; Figure 1); reservoir – from the last detection as they first entered the reservoir (reach C; Figure 1) to the first detection near the MGS (reach I; Figure 1); and downriver – from the last detection as they were first detected downstream of the MGS (reach J; Figure 1) to the first detection at the last receiver they were observed at downriver. To examine the relationship between kelt movements and water movements, migration rates were further examined on a fine spatial scale by only considering downstream movements between receivers within the upriver and reservoir reaches, and relating these to concurrent water temperature and velocity from the hydrodynamic model through a second LMEM. Missing water temperature values were interpolated based on the closest spatial and temporal locations.

To test the prediction that the reservoir could cause directional confusion, the proportions of time that fish spent travelling upstream during winter, the pre-migration movement period, during active spring migration within the reservoir and downriver were compared using a Kruskal–Wallis test with a *post hoc* Dunn test. Fish direction (upstream or downstream) between receivers was examined in relation to the associated maximum water angle from downstream from the hydrodynamic model in the upriver and reservoir reaches using a LME logistic regression model.

An ordinal regression model (ORM) was used to identify the variables affecting migration success, including the fixed effects of tide (ebb or flood during the last detection or none if not detected in the lower SJR >20 rkm), average water temperature throughout the migration, average water velocities within the reservoir from the hydrodynamic model, and the fish's migration rate (velocity) and proportion of time swimming in the reverse direction within the reservoir. Candidate variables were assessed for multicollinearity prior to analysis and continuous variables were scaled using *z*-scores to account for differences in units. Migration success was coded as an index as follows: 0 = no dam passage at MGS (movements observed down to reach I but no further; Figure 1), 1 = dam passage at MGS but no further migration (J; Figure 1), 2 = movement downstream of the MGS (K; Figure 1), 3 = halfway downriver (L; Figure 1), 4 = top of estuary (N; Figure 1), 5 = lower SJR (O; Figure 1), 6 = outside of SJR.

A Cormack–Jolly–Seber (CJS) model (Bowerman and Budy, 2012; Lebreton *et al*., 1992) was used to estimate survival (Φ) and encounter (p) probabilities during the spring migration toward the ocean. CJS uses the number of unique tags detected on receivers and the detection efficiency of the receivers to estimate survival for each reach (Bowerman and Budy, 2012; Lebreton *et al*., 1992). The model assumed that (a) tagged individuals alive in spring were representative of the population, (b) survival rates in spring (*i.e*., >3 months post-tagging) did not differ between tagged and untagged individuals, (c) each tagged individual had an equal but independent probability of survival and detection during spring migration, (d) no tags were lost or failed in the spring and sampling was instantaneous, and (e) movement during spring was generally unidirectional (*i.e*., downstream with an *a priori* motivation of exiting the river). To avoid overdispersion from attempting to model survival and encounter probabilities for up to 65 receivers, detections from receivers were pooled into 14 reaches for which Φ and p estimates were calculated (Figure 1). The pooling of receivers was necessary to avoid overdispersion of the Φ and p estimates that would have necessarily resulted given the number of tracked individuals *versus* the number of individual receivers (*i.e*., spatial locations available for parameterization). Survival within a reach was estimated as $k = \Phi^d$ where k is the survival rate of a reach, Φ is the survival estimate per rkm and d is the distance (rkm) between the upstream limits of each reach. The outputs of survival and encounter probabilities were compared to the raw data showing positive detections, missed detections and the location of presumed tag loss or mortality, and the associated hand-calculations of survival and encounter probabilities. Fisher's exact tests were used wherever proportions were compared for significance, including survival estimates of multiple reaches between study years.

Analyses were done in R (Version 1.1.423 2009–2018 RStudio, Inc. Packages car, FSA, lme4, lmerTest, multcomp, ordinal), with the exception of CJS analyses done in Program MARK (Version 8.2; White & Burnham, 1999). Normality plots were analysed where appropriate, and statistical significance was assumed when P was less than or equal to 0.05.

3 | RESULTS

In total, 45 tagged post-spawned adult *S. salar* were successfully tracked through the winter. Two tagged fish were never detected downstream of the release site in 2014 and were potentially mortalities related to tagging and associated stress. In the spring, 28 tagged fish were tracked through to the lower reservoir, whereas 23 were detected downriver.

3.1 | Winter movements and survival, and pre-migration movement period

The duration of time it took a tagged post-spawned adult to travel the first approximately 30 rkm from the release site downstream of the BGS (280 rkm, reach A; Figure 1) to the next receiver downstream (250 rkm, reach B; Figure 1) was considered the initiation period. The length of the initiation period was 7.9 days (median; 25th, 75th percentiles: 2.6 days, 14.7 days; $n = 17$; 2014) and 20.2 ± 5.9 days (25th, 75th percentiles: 8.6 days, 31.0 days; $n = 16$; 2015), with WC-CR fish taking significantly longer (median 11.5 days; 25th, 75th percentiles: 7.0 days, 33.5 days) than CR-broodstock fish (7.9 days; 25th, 75th

percentiles: 2.4 days, 18.0 days; $P = 0.016$), but did not differ between the sexes (female median 5.1 days; 25th, 75th percentiles: 16.0 days, 28.5 days; male median 5.0 days; 25th, 75th percentiles: 8.3 days, 18.2 days; $P = 0.246$).

Winter survival including potential mortality related to tagging was 56% and 75% for 2014 and 2015, respectively ($P = 0.35$). The majority ($n = 7/11$, 64%) of overwintering mortality occurred upriver (reach B; Figure 1) in 2014 and in the lower reaches of the reservoir in 2015 ($n = 4/5$, 80%, reaches H–I; Figure 1). Winter survival was generally higher for females than males in both years (2014 67% *vs*. 50%, $P = 0.442$; 2015 88% *vs*. 0%, $P = 0.04$) and for small than large salmon in both years (2014 47% *vs*. 30%, $P = 0.679$; 2015 44% *vs*. 9%, $P = 0.127$).

Kelts exhibited nondirected movements prior to directed downstream movements indicating the initiation of migration in the spring. This behaviour could only be documented for kelts which had been overwintering in areas sufficiently near to receivers ($n = 3$ in 2015, $n = 4$ in 2016) representing 23% and 27% of the tagged kelt population that initiated migrations each spring, respectively. In 2015, the latest migrants were observed to have undertaken nondirected movements (Table 2) from 7 to 20 May (mean ± S.E. 9 ± 1 day) with water temperatures of 9–15°C, whereas in 2016 pre-migration movements were observed by some of the earliest migrants as well as later migrants (Table 2) from 21 February to 8 April (17 ± 6 days) in waters just above freezing. In both years, all individuals displayed this behaviour over an approximately 30 rkm reach spanning from upriver into the reservoir (B–C; Figure 1), with the exception of one kelt in 2016 that had pre-migration movements and initiated migration from near the MGS.

3.2 | Spring migration timing

Most kelts initiated their spring migration from upriver or the top of the reservoir, indicating their respective overwintering locations (reaches B–C; Figure 1). In 2015, earlier migrants (19 April–4 May; Table 2) initiated their migration from the top of the reservoir (reach C; Figure 1), with later migrants (7 May–2 June; Table 2) beginning their migration from upriver (reach B; Figure 1). Five kelts initiated their migration while the spring freshet was increasing, with the timing being associated with peaks in discharge (Figure 3). The remaining eight kelts initiated migration as the freshet was decreasing; however, four of these migrations were still initiated during short-term increases in flow (Figure 3). There were only three males in the first study year that initiated migration,

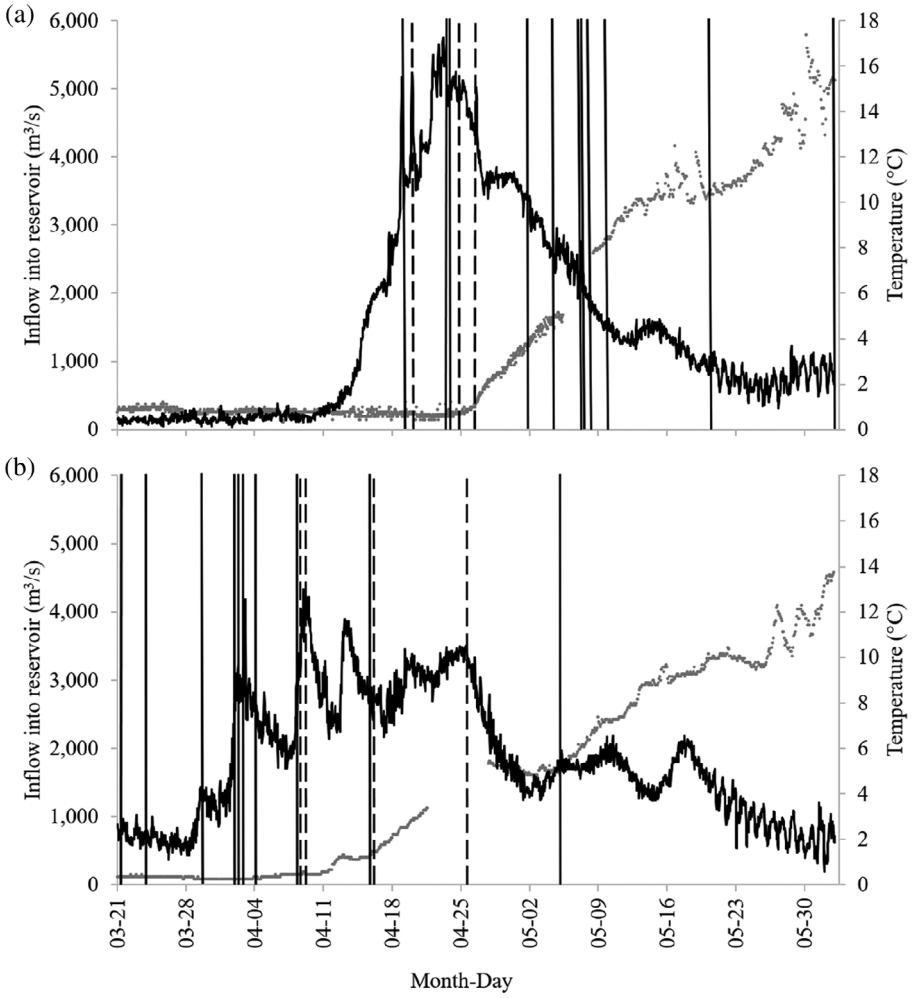


FIGURE 3 Initiation of *Salmo salar* kelt spring migration (vertical lines) in (a) 2015 and (b) 2016, and associated inflow ($m^3\ s^{-1}$, black line) into the Mactaquac Generating Station (MGS) reservoir and mid-water column water temperature (°C; grey circles) recorded near the MGS. Solid vertical lines indicate tagged kelts that were detected in the lower Saint John River (SJR; *i.e.*, successful migration) and dashed vertical lines represent those that were not detected in the lower SJR (*i.e.*, unsuccessful migration)

with the first being on 24 April 2015 and the last on 2 June 2015 being the latest initiation of all tagged kelts (Table 2). The majority of kelt migrations started when water temperature was still below 2°C and thus the initiation of migration did not seem to be in response to increasing water temperature.

In 2016, all kelts initiated spring migration by 5 May, with upriver reaches being the most common starting point (reach B; Figure 1 and Table 2). Two kelts initiated migration before the onset of the spring freshet. There was a strong association of the initiation of migration with peak discharges (Figure 3). The remaining four kelts initiated migration after the peak freshet (Figure 3). Similarly to 2015, water temperature did not appear to be a direct trigger of kelt migration. Overall, cumulative degree day rates were slower in 2015 than 2016.

All of the tagged kelts that approached the MGS experienced some amount of delay between their first and last detections in the forebay area before being either unsuccessful or successful in passing through the dam. The forebay area was only approximately 1 rkm, but individuals often left the forebay area and swam back upstream before returning to attempt dam passage. In 2015, 58% were delayed for over an hour (median 1.2 h, $n = 12$), and in 2016, 69% were delayed for over an hour (median 2.9 h, $n = 13$). MGS passage occurred during both day (54%) and night (46%) in 2015, approximately 6 days after the initiation of spring migration (Table 2). In 2016, MGS passage primarily occurred at night (73% *vs*. 27%), approximately 11 days after migration initiation (Table 2). The median duration between the last detection upstream and the first detection downstream of the MGS was 81 min ($n = 11$).

Most turbine gates were open for passage during the active spring migration period of tagged kelts; however, spillway gates were closed after 15 May 2015 and 3 May 2016 when four and two migrating kelts were still upstream of the MGS in 2015 and 2016, respectively. In 2015, 69% of kelts ($n = 9$) last encountered the MGS when spillway gates were open, 44% of which were unsuccessful in finding passage (Table 2) and 56% of which were successful in reaching the lower SJR (Table 2). Four kelts attempted passage when spillway gates were closed with all being successful in reaching the lower SJR (Table 2). In 2016, 87% of kelts ($n = 13$) last encountered the MGS when spillway gates were open, 7.7% of which were unsuccessful in finding passage (Table 2) and 25% of which presumably experienced delayed mortality because their last detections occurred within 4 rkm of the MGS (reach J; Figure 1 and Table 2). Two kelts last encountered the MGS when spillway gates were closed, one of which presumably experienced delayed mortality (reach J; Figure 1 and Table 2) while the other reached the lower SJR (Table 2). Overall, 28 of the kelts actively migrating in the spring reached the MGS, 85% were able to pass the MGS, but four of those (17%) were not detected downstream of reach J (Figure 1).

3.3 | Spring migration rates, and temperature and depth of migration

Migration rates were significantly slower in the reservoir (mean ± S.E. 8.5 ± 2.5 km day^{-1}) than up- (29.7 ± 5.0 km day^{-1}) or downriver (22.1 ± 3.1 km day^{-1}; LMEM, $P < 0.01$; Table 3a and Figure 4), with 11.7% of the observed variation in overall migration rates attributable to individual fish. If kelts had the ability to travel through the reservoir at the river rates (*i.e*., reservoir in its natural river state prior to MGS

TABLE 3 Model type, formula, sample size and coefficient estimates, standard errors (S.E.), *z* (ordinal regression model; ORM) or *t* values [linear mixed effects models (LMEMs) and linear mixed effects (LME) logistic regression model] and *P* values

Coefficient	Estimate	S.E.	*z*/*t*	*P*
(a) LMEM; fish_km_d ~ stretch + (1|fish_id), $n = 62$ from 28 fish				
stretch	12.527	2.798	4.478	<0.0001
(b) LMEM; fish_km_d ~ stretch * temperature_avg * water_velocity_avg + (1|fish_id)[a], $n = 221$ from 21 fish				
Stretch	−1.685	6.255	−0.269	0.7879
Temperature_avg	12.882	6.174	2.087	0.0393
Water_velocity_avg	−11.694	5.727	−2.042	0.0423
(c) ORM; success index ~ tides + temperature_avg + water_velocity_avg *fish_km_d * proportion_upstream[a], $n = 28$				
Tides ebb *vs*. flood	0.1302	0.6514	0.200	0.8416
Tides overall	−10.8781	5.8090	−1.873	0.0611
Temperature_avg	3.0541	1.4320	2.133	0.0329
Water_velocity_avg	−2.2702	1.8478	−1.229	0.2192
Fish_km_d	−0.7135	1.6060	−0.444	0.6568
Proportion_upstream	−3.7164	1.8624	−1.996	0.0460
(d) LME logistic regression model; fish_direction ~ stretch * water_angle + (1|fish_id)[a], $n = 465$ from 24 fish				
Stretch	0.12080	0.25537	0.473	0.636
Water_angle	0.02912	0.38302	0.076	0.939

[a]Interactions (not shown) were nonsignificant.

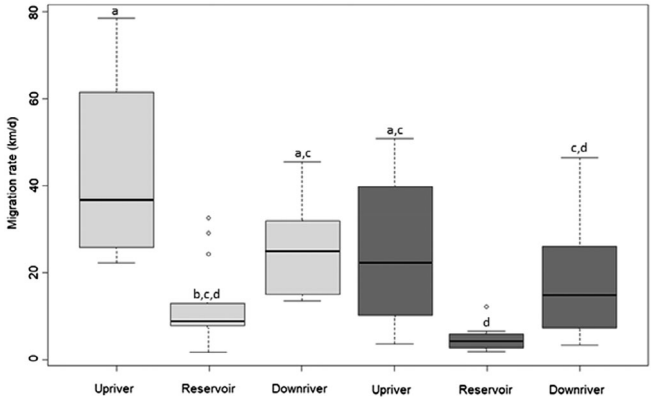


FIGURE 4 Migration rate (km day^{-1}) of *Salmo salar* kelts migrating through the upriver, reservoir of the Mactaquac Generating Station and downriver reaches of the Saint John River in 2015 (light grey) and 2016 (dark grey). Letters represent significant differences

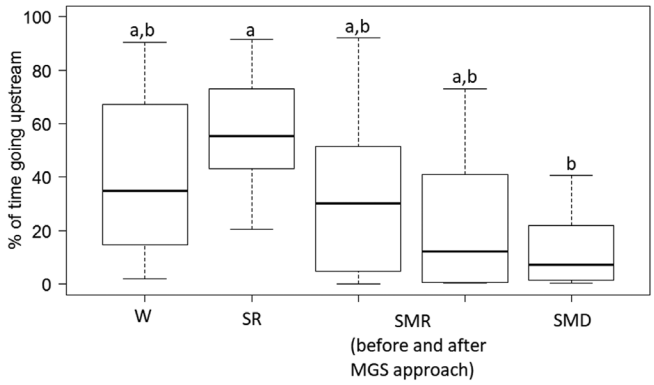


FIGURE 5 Percentage of time tagged *Salmo salar* kelts spent moving upstream, in reverse of the main migration direction, during winter (W), spring reconditioning (SR), spring migration in the reservoir (SMR) and spring migration downriver (SMD) of the Mactaquac Generating Station in the Saint John River. Letters represent significant differences

construction), they could have covered this distance approximately 5–6 days sooner than was observed (median; 25th, 75th percentiles: upriver migration rate 5.4 days, 4.0 days, 12.6 days; downriver migration rate 6.2 days, 2.5 days, 11.2 days).

Downstream-directed, fine-scale migration rates did not differ by reach (*i.e.*, upriver, reservoir, downriver; LMEM, $P = 0.79$; Table 3b); however, greater water temperatures were found to be associated with higher downstream migration rates between receivers (LMEM, $P = 0.04$; Table 3b) and concurrent water velocity was negatively related to downstream migration rates between receivers (LMEM, $P = 0.04$; Table 3b).

After initiating their directed spring migration, tagged kelts were often observed swimming in the reverse direction to the main migratory direction (Figure 5). Overall, kelts covered a minimum of an additional 57–61 (± 20–23) extra rkm due to the reversals as compared to travelling the centerline distance of 37 rkm. In both studied years, the majority of migrating kelts spent a considerable amount of their time swimming in the reverse direction; the behaviour was especially prevalent in the reservoir where 68% of the tagged kelts spent a median of 30% of their time prior to reaching the MGS swimming upstream during the spring migration (Figure 5). The proportion of time spent in reverse direction in the reservoir was lower (pooled median 12%; Figure 5) after the fish had approached the MGS at least once, and the reversals were relatively rare once fish had passed through the MGS (pooled median 7%; Figure 5; Kruskal–Wallis test, $\chi^2 = 13.26$, $df = 4$, $P = 0.01$). The magnitude of detections indicating reversed movements was highest in the bends located at the upper reservoir (reach C; Figures 1 and 6), the middle of the reservoir (reaches G–I; Figures 1 and 6), within the reservoir in proximity to the MGS (Figure 6) and in the estuarine part of the river that is under the influence of high tidal action (reach O; Figures 1 and 6). The higher the proportion of time that fish spent travelling upstream, the lower their overall migration success (ORM, $P = 0.05$; Table 3c) and water temperature was positively correlated with migration success (ORM, $P = 0.03$; Table 3c). Tides (ORM, $P = 0.06$; Table 3c), water velocity (ORM, $P = 0.22$; Table 3c) and individual migration rates (ORM, $P = 0.66$; Table 3c) did not influence migration success. Fish direction (upstream or downstream) between receivers was not detectably affected by whether they were upriver or within the reservoir (LMEM, $P = 0.64$; Table 3d) or by the maximum angle of the water from downstream (LMEM, $P = 0.94$; Table 3d).

The distance that kelts travelled during their spring migration was equally distributed between the day and night (2015 50% day, 2016 52% day). The percentage of distance travelled during the day was similar between movements in the reservoir before encountering the MGS and downriver (2015 66% and 66%, 2016 55% and 56%), but there was a slight shift toward night-time movements in the reservoir after the kelts had encountered the MGS, especially in the second study year (2015 64% day, 2016 36% day).

Median temperatures recorded by the sensor tags prior to the initiation of spring migration were <2°C in both years ($n = 20$; Figure 7a). Temperature experienced by the tagged kelts was different during the pre-migration movement period between the 2 years, with median temperatures of 10–11°C experienced by the late pre-migration period in 2015 compared to <1°C experienced by those displaying nondirected movements over a wider time frame in 2016. During the spring migration period, median temperatures experienced in the reservoir ranged from just above 0 to 11°C in 2015, increasing to 1–14°C downriver, whereas in 2016 the temperature differential between upstream and downstream of the MGS was more pronounced with medians of <2°C in the reservoir compared to 2–10.5°C downriver.

Kelts with sensor tags remained near the surface (<5 m; Figure 7b) 96% (25th, 7th percentiles: 86%, 99%) of the time (including the winter, pre-migratory and migratory periods), with the exception of one tagged kelt in the second study year that spent 60% of the time between 30 and 40 m overwintering near the MGS. It moved between 23 and 34 m (99% of activity) during its pre-migration movement period and was never observed above 10 m. This fish survived

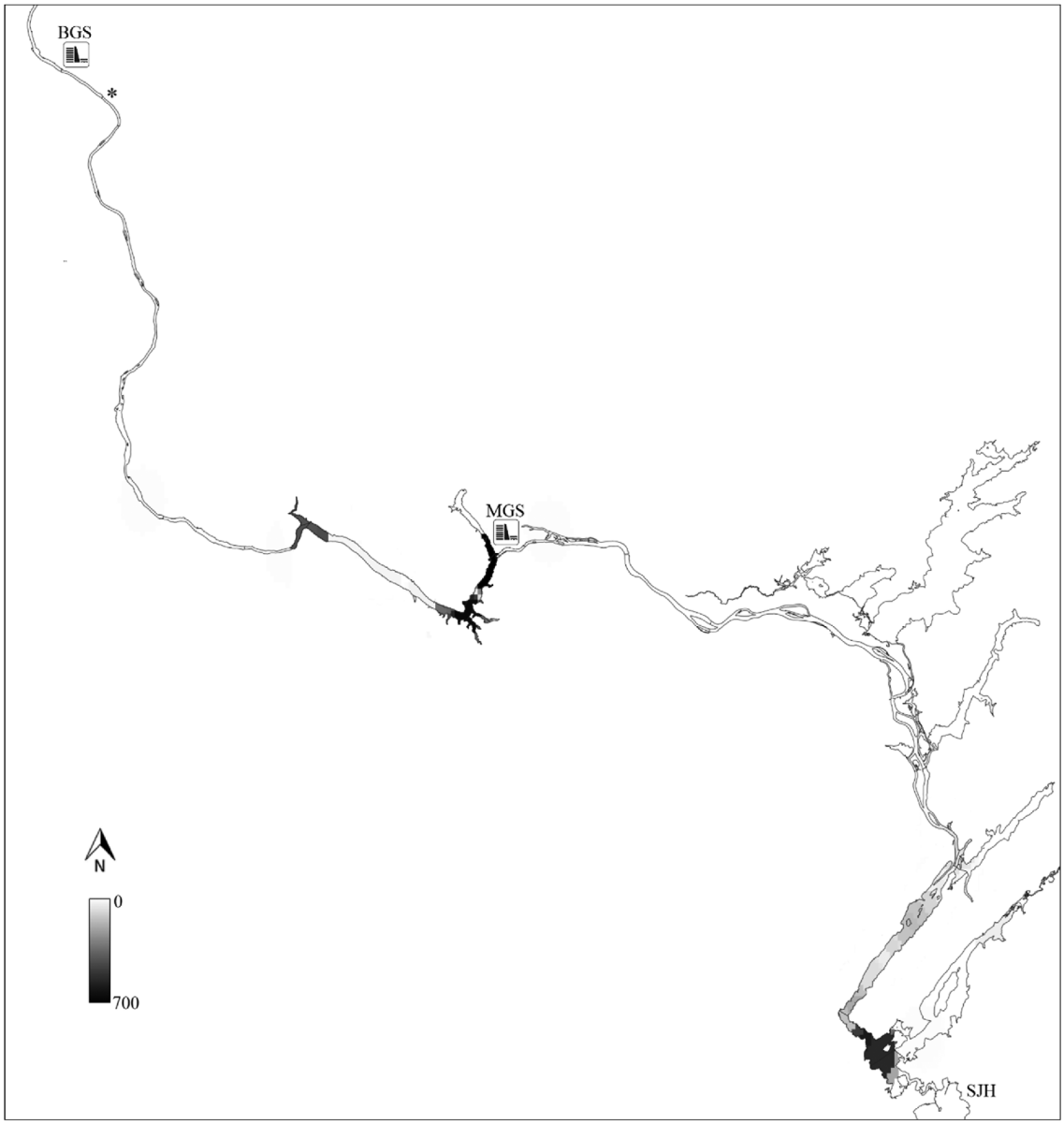


FIGURE 6 Heatmap of the number of movement reversals by *Salmo salar* kelts in the Saint John River. Locations of release (*), the Beechwood Generating Station (BGS), the Mactaquac Generating Station (MGS) and the Saint John Harbour (SJH) are shown

and exited the river, where it was subsequently detected in the Gulf of Maine (Figure 8). Besides this individual, there was only one other tagged fish that dove greater than 5 m near the MGS for a short period of time. All other dives greater than 5 m tended to take place near the reservoir–upriver transition area.

3.4 | Spring survival

The CJS model included spatial variability in encounter (p) and survival (Φ) estimates between the 14 reaches (Figure 1). Encounter estimates were greater than 75% in the second study year (Figure 9) which was deemed sufficient for reliable detection; however, there were some reaches in the first study year that had encounter estimates <50% (C–D 33%, E–F 30%, F–G 38%, J–K 33%, M–N 38%; Figure 9) which could impact survival estimates. Therefore, model outputs were compared to hand-calculations of the raw data and agreement was found for both encounter (mean difference 2015 0.9%, 2016 0.5%) and survival estimates (mean difference 2015 0.4%, 2016 1.0%). Cumulative survival estimates in all reaches upstream of the MGS were generally high (94% in 2015 and 83% in 2016; Figure 9; reaches A–I; Figure 1) and similar between study years ($P = 0.298$). The greatest declines in cumulative survival occurred during and shortly after the kelts passed the MGS in both years (32% in 2015, 23% in 2016; Figure 9; reach I–J; Figure 1). The tagged kelts that survived passage at the MGS and were found to be actively swimming had generally high survival for the rest of the migration downriver (7% decrease in 2015, no losses in 2016; Figure 9; reaches L–O; Figure 1).

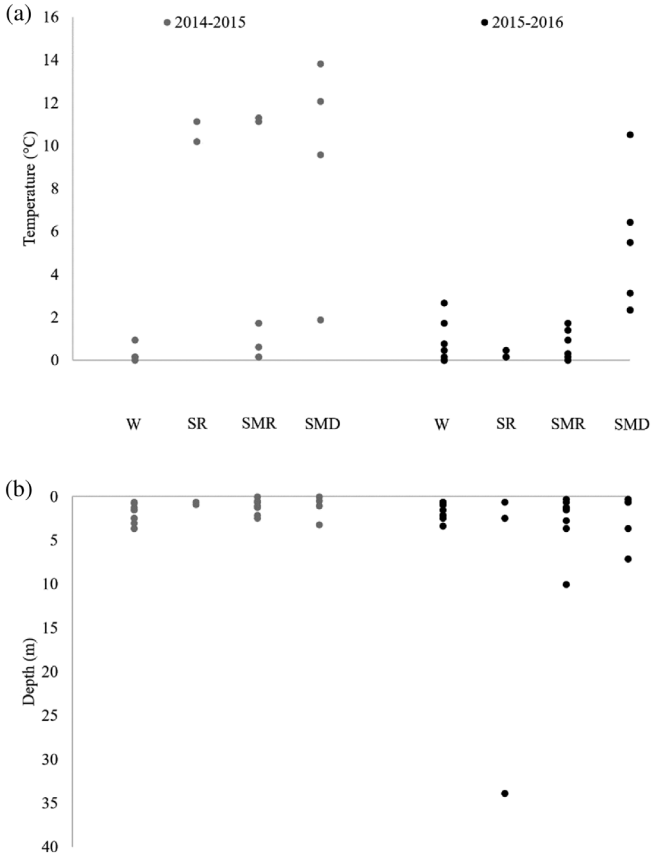


FIGURE 7 Medians of (a) water temperature (°C) and (b) depth (m) as experienced by individual *Salmo salar* kelts tagged with temperature/pressure sensor tags in 2014–2015 (grey) and 2015–2016 (black) during winter (W), spring reconditioning (SR), spring migration in the reservoir (SMR) and spring migration downriver (SMD) of the Mactaquac Generating Station in the Saint John River

On reaching the lower SJR (reach O; Figure 1), cumulative survival estimates were 53% in 2015 and 63% in 2016, which are not significantly different ($P = 0.765$). Survival was similar between the sexes (2015 60% males, 50% females; 2016 no males remaining, 57% females; pooled $P = 0.290$) and between small and large kelts (2015 37% small, 57% large; 2016 80% small, 40% large; pooled $P = 0.226$). Six kelts were found to have at-sea experience through scale analysis, half of which were last detected in reach J and the other half were last detected at the lowermost receiver (Table 2).

Five kelts were detected after leaving the SJR (Ocean Tracking Network; Figure 8). In 2015, four kelts were detected by receivers on the Halifax Line. On average, it took 16 days (range 13–20 days) for the kelts to travel from the SJR to the Halifax Line, where they were detected over a 2 week window on seven receivers between 31 May and 13 June. All of the detections took place at night, with the kelts remaining in the receivers' range for 23 min (range 14–32 min). Most kelts were detected by one or multiple receivers nearby one another; however, one kelt was detected on multiple receivers over 86 km apart. Two fish were equipped with sensor tags indicating that the migration temperatures were 7.2 and 10.2°C, and that both kelts were migrating at the surface (<1 m). In 2016, a single kelt took 69 days to travel to the Gulf of Maine, where it was detected by one receiver for 41 min at night, travelling from 0 to 22 m depth and experiencing temperatures of 10.4–11.1°C.

4 | DISCUSSION

This study tracked *S. salar* post-spawners/kelts from upstream of and in a large hydropower reservoir, and then downstream of a hydropower generating station. We observed that (a) the reservoir appeared not to be a preferred overwintering area but was potentially used for reconditioning in the spring by some kelts, (b) migration rates were slower in the reservoir with frequent migration reversals leading to migratory delay and (c) dam passage was apparently associated with declines in survival.

Winter survival of tagged post-spawned *S. salar* in the current study was relatively high (56–75%) given the common view that winter is a physiologically and physically challenging period and is often considered to be a bottleneck for survival for many life stages of *S. salar* (Huusko *et al*., 2007). However, there was likely post-spawning mortality in the population before the fish tagged in this study were captured. Overwinter survival rates reported in the literature are similar to or lower than survival rates observed in the current study: 54–70% in a Nova Scotian river (Ruggles, 1980), 57% in the Penobscot River (Maine, USA; Maynard *et al*., 2018), 20–37% in a Norwegian river (Halttunen, 2011) and 49% in a Swedish river (Nyqvist *et al*., 2016). Female kelts are thought to be more likely to survive, emigrate and become repeat spawners since males lose more somatic energy and can incur injuries during spawning (Jones, 1959; Jonsson *et al*., 1990). This aligns with the current study where females generally had higher winter survival rates than males (females 2014–2015 67%, 2015–2016 88%; males 2014–2015 50, 2015–2016 0%), and compared to other systems where females had higher survival rates than males (60–74% *vs*. 38–62%; Halttunen *et al*., 2013; Niemelä *et al*., 2000; Nyqvist *et al*., 2016). It is important to note that inherent in the winter survival estimate in this study is the potential effects that may have been caused by any tagging-induced mortality and potential tag loss or failure. Therefore, winter survival in the non-tagged population may be higher than reported here. Within 35 days after release, 20% of the tagged fish in 2014 and 15% of the tagged fish in 2015 produced their last detections. Apart from some initial tagging-related effects on survival, the effects of handling and internal tagging on the swimming performance of *S. salar* kelts was assumed to be minimal since the tag burden averaged less than 0.5% of fish weight and thus was well below ratios considered to cause tagging effects (Thorsteinsson, 2002) and kelts are tolerant of handling (Brobbel *et al*., 1996). Importantly, the subsequent CJS analysis on spring migration success is considered to be unaffected by tagging-induced mortality because spring migration (and the related survival analysis) occurred greater than 115 days post-tagging.

Migratory timing can depend on biological as well as environmental conditions. In the current study, the two years differed in their

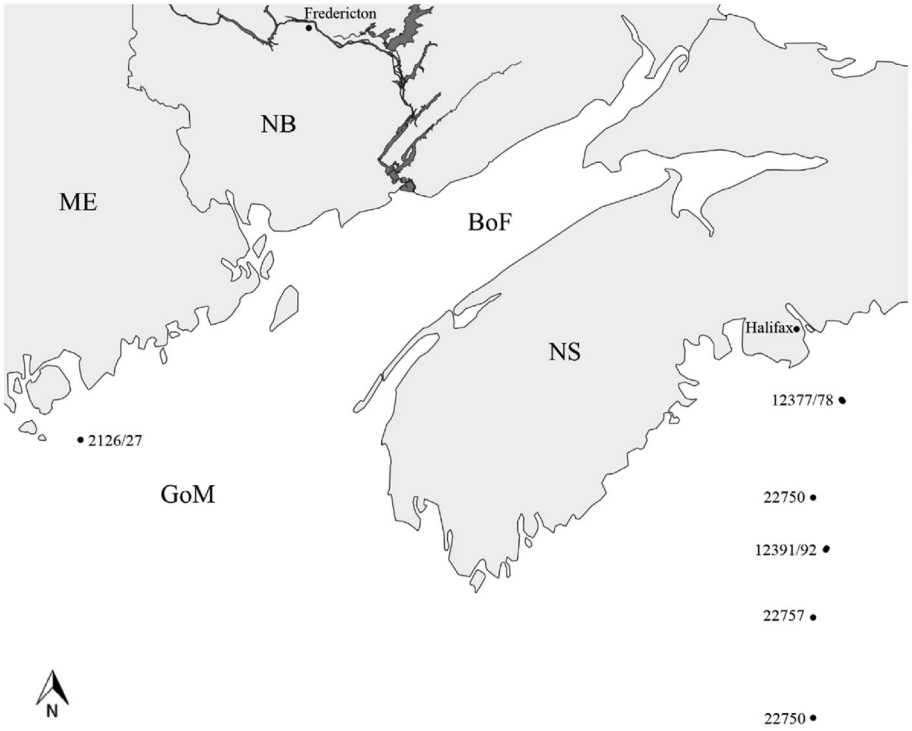


FIGURE 8 Locations of tagged *Salmo salar* kelt detections outside of the Saint John River in New Brunswick (NB), Canada, as they travelled through the Bay of Fundy (BoF), the Gulf of Maine (GoM) off Maine (ME) and the Atlantic Ocean near Halifax, Nova Scotia (NS). Tags with two ID codes indicate transmitters with temperature/depth sensors. Detections are from data sharing with the Ocean Tracking Network

timing of ice cover, water temperature increases and discharge patterns during the spring freshet. Just downstream of the MGS was ice-covered for a longer period of time in 2014–2015 (30 December to 12 April) than in 2016 (14 January to 21 February; C. Côté, Environment and Climate Change Canada, personal communication). Jonsson *et al.* (1990) reported that post-spawned *S. salar* activity is low when water temperatures are <2°C and migration initiation is often reported when water temperature exceeds 4–6°C (Östergren & Rivinoja, 2008). At the MGS, water temperatures began rising from near zero earlier in 2016 (12 April) than in 2015 (25 April), driving faster cumulative degree day rates. Water temperature was not strongly associated with the onset of migration, but higher average water temperatures during migration were found to be associated with greater overall migration success. Discharge also began increasing earlier in 2016 (28 March) than in 2015 (14 April), and peaks were associated with kelts initiating their migrations. However, in unregulated rivers kelts tend to reach the tidal limit before increases in discharge during the spring freshet (Hubley *et al*., 2008), indicating that the kelts in the regulated SJR may be experiencing migratory delay.

Male kelts tend to migrate downstream before females because they are often in poorer condition after spawning (Fleming, 1996; Jonsson *et al*., 1990; Niemelä *et al*., 2000). A study that transported kelts downstream to the SJR estuary in the autumn found that they moved upstream and remained in the river until the spring (Huntsman, 1931). In the current study, there was little evidence of kelts attempting to pass the MGS in the autumn and sex differences were not seen; however, this study had a low number of tagged males. The first male initiated spring migration 2 weeks after the first female (2 May 2015, condition 1.12 *vs*. 19 April 2015, condition 1.28) and the kelt which migrated latest in either season was also a male (2 June 2015, condition 0.94).

There is evidence of kelts beginning to recondition by feeding in the spring while emigrating to the ocean (Penney & Moffitt, 2014). Kelts from Hammond River in the lower SJR were found to spend 10–27 days in the estuary feeding and reconditioning before entering the ocean (Lacroix, 2013). Food items can include smolts, other small fish and invertebrates (Penney & Moffitt, 2014). In the current study, some kelts displayed nondirected movements for 10–33 days before the initiation of spring migration. We hypothesize that this is a reconditioning period but further study of their condition and potential diets is required. Harnish *et al*. (2014) found that body condition was the best predictor of *O. mykiss* kelt survival through Snake River dams. Only initial body condition during tagging was known in the current study, with males having lower condition than females on average, but this did not translate into significant differences in survival between the sexes. The fish could be increasing muscular functioning by obtaining nutrition before undertaking a long migration; however, unlike other salmon rivers, there are no smelt (*Osmeridae* sp.) or alewife (*Alosa* sp.) available at this time of year for kelts upstream of the MGS.

Throughout their migration, kelts positioned themselves within the top 5 m of the water column with only a few exceptions, indicating a surface-oriented passage route would likely have a higher efficacy than the current bottom-draw available at the MGS for spillway and turbine passage (Harnish *et al*., 2014). The kelts also travelled roughly equal distances during the day and night, indicating that a passage route that is open at all times, such as a surface bypass, would be more advantageous than routes such as spillway gates that are only open during the spring freshet, or turbines that take in differing

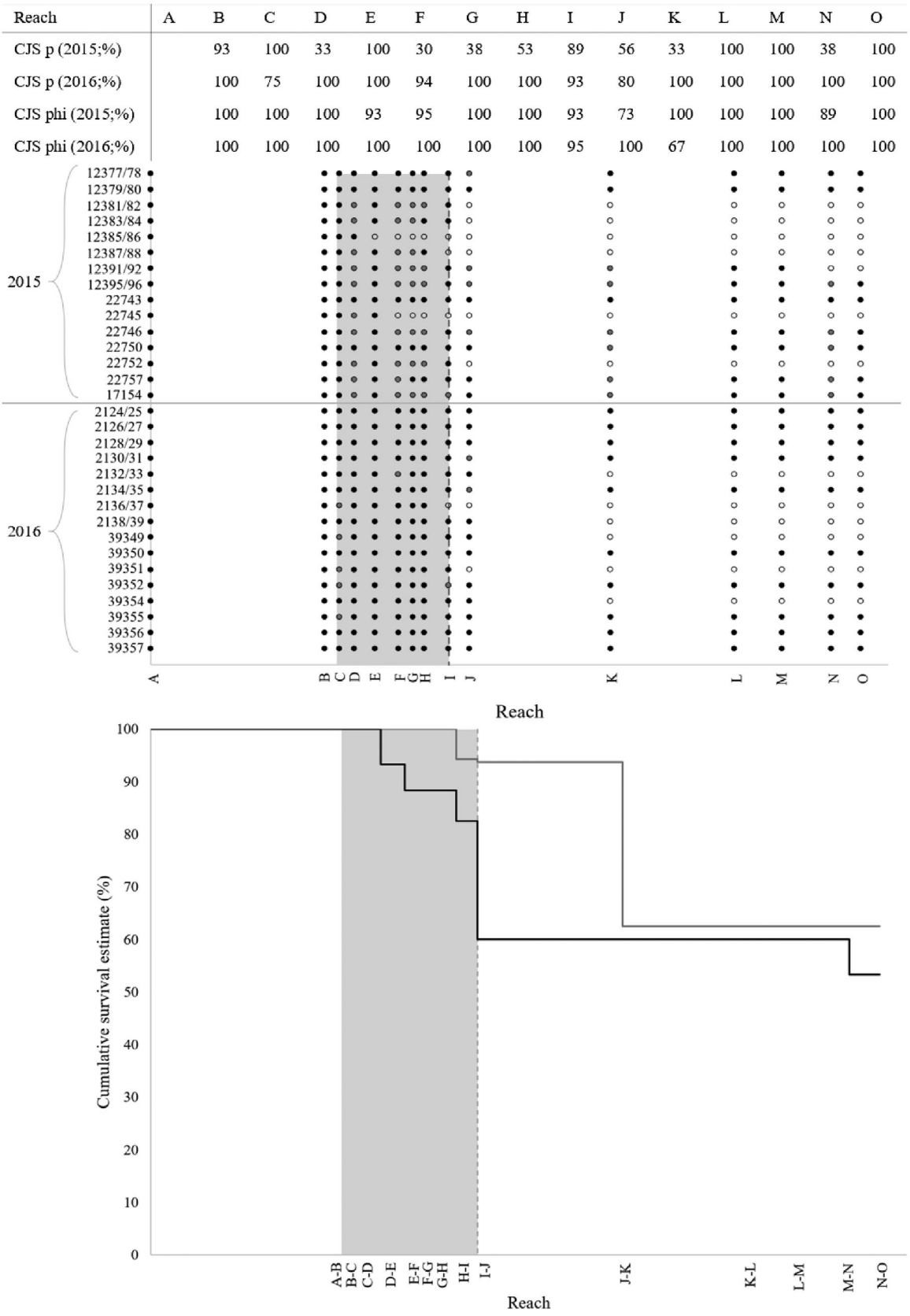


FIGURE 9 (a) Raw survival data (black dots = detection, grey dots = missed detection, unfilled dots = presumed mortality) and (b) modelled cumulative apparent survival from Cormack–Jolly–Seber φ estimates (%) during the spring migration of tagged (2015 black line, 2016 grey line) *Salmo salar* kelts in 14 river reaches (see Figure 1) in the Saint John River. Shaded areas represent the Mactaquac reservoir and the dashed vertical lines represents the location of the Mactaquac Generating Station. Reach-specific *p* (encounter probability, 2015 and 2016; %) and φ (survival probability, 2015 and 2016; %) estimates are given

amounts of water throughout the day or night based on demand for power generation.

Migration rates were significantly suppressed within the reservoir when compared to movements up- and downriver (upriver 29.7 ± 5.0 km day^{-1}, reservoir 8.5 ± 2.5 km day^{-1}, downriver 22.1 ± 3.1 km day^{-1}). This was interpreted to result in an approximate 6 days delay due to low water velocities. It took a median of 6.8 days for kelts to travel the 150 rkm of the downriver reach, whereas it took a similar amount of time (6.3 days) for them to navigate the 37 rkm of the reservoir. Such a delay could be detrimental for kelts attempting to navigate their way to the ocean, where opportunities for accelerated growth and reconditioning exist (Gross *et al*., 1988); otherwise, the exacerbated depletion in energy reserves could decrease the likelihood of a kelt becoming a repeat spawner (Fleming, 1996; Wertheimer & Evans, 2005).

Migratory delay in the reservoir could be attributed to three separate aspects: (a) low water currents leading to reversed direction swimming during searching behaviour; (b) time spent in dead-end tributaries; and (c) dam passage. Presumably due to low water currents, kelts were delayed by approximately 5–6 days in the reservoir in comparison to the up- and downriver reaches. Water currents were modelled to be weak, especially at the bend in the reservoir (*i.e*., between reaches G and H) where fish sometimes made quick movements, apparently driving the negatively correlation with water velocity. The directional cue of water flow could potentially be reintroduced through the use of a large-scale implementation of a flow velocity enhancement system (Coutant, 2001). Using a hydraulic system to induce water currents toward the direction of migration has been attempted in other regulated systems for juvenile salmonids (Darland *et al*., 2001) but could be applied to other downstream migrants such as kelts.

Searching behaviour was displayed as up- and downstream movements within the reservoir. Such upstream movements were also observed for the first month after kelts were released in the Penobscot River (Maynard *et al*., 2018), and for *S. trutta* kelts but only after the fish had approached a dam and to a much lesser extent than observed in this study (Arnekleiv *et al*., 2007). Reverse direction swimming was displayed by two-thirds of the kelts in this study, taking up approximately one-third of their time in the reservoir during the spring migration. This ratio was similar to that seen during winter movements, but multidirectional movements are to be expected when the kelts are not motivated to migrate in a predisposed direction. The highest proportion of reversals was observed during the presumed reconditioning period, which is inherent to its definition. During the spring migration, the majority of reversals took place between Longs Creek (*i.e*., a dead-end tributary between reaches G and H) and the MGS (*i.e*., transition between reaches B and C), with the bend at the top of the reservoir being a secondary area of concern. From the hydrodynamic model, surface water direction was highly variable near the MGS and velocity was low (data not shown). Fish movements could have been influenced both by this backwater effect, as well as the confusion associated with the obstacle. Once the kelts passed the MGS, movements were largely unidirectional until they reached the lower (and heavily tidal) sections of the river. Although the waters are tidal nearly as far upstream as the MGS due to the extreme tides of the Bay of Fundy (>8 m vertical difference at the SJR mouth), it is only in the first approximately 45 rkm from the river mouth that the tidal effect would be strong enough to produce backwater effects that could influence fish movements; it was in this area that reversals were observed to reoccur.

If *S. salar* are to become repeat spawners, they must survive their first spawning, overwintering and kelt spring migration, which may include passage of one or multiple dams such as in the current study. This study represents the first published data on kelt survival and spring migration success from upstream of the MGS in the SJR. During the migration in spring, *S. salar* kelts had relatively high survival in the MGS reservoir (82%–95%), comparable to the high survival rates seen among *S. salar* kelts in an unregulated river of Nova Scotia (90%; Hubley *et al*., 2008). *S. salar* kelts had three alternative routes for dam passage at the MGS, consisting of two spillway routes (*i.e*., either the diversion sluiceway directly from the reservoir or the spillway within the forebay; Chateauvert *et al*., 2018) or egress through the turbines. In hydropower installations elsewhere, higher discharge through spillways has been found to improve survival and decrease migratory delay for kelts (Colotelo *et al*., 2014; Harnish *et al*., 2014; Nyqvist, 2016; Wertheimer & Evans, 2005), indicating that unless specific bypass is available, passage through spillway may be preferred in comparison to turbine passage. Turbine passage is typically associated with greater mortality rates than spillway passage (Jones & Flanagan, 2007; Muir *et al*., 2001), especially for larger-bodied fish (Harnish *et al*., 2014; Nyqvist *et al*., 2016; Sigourney *et al*., 2015; Ruggles, 1980), although spillway passage is not free of risks (*e.g*., gas bubble disease; Brown *et al*., 2014). Surface-oriented steelhead (*Oncorhynchus mykiss*) kelts at Snake River dams tended to pass *via* spillways over turbines (Harnish *et al*., 2014). While it was unknown in this study which route the fish chose, the majority (64%–75%) of attempts to pass the MGS occurred when spillway gates were open as a passage option. The four later migrants (after 15 May 2015 and 3 May 2016) would have been forced to pass *via* the turbines since the two alternative spillway options were closed. Turbine passage has been reported to cause death in 62%–67% of *S. salar* kelts (Nyqvist, 2016; Nyqvist *et al*., 2016). In our study, dam passage was associated with declines in survival estimates (23%–32%), including four kelts that presumably experienced delayed dam passage mortality as evidenced by those fish being observed by the first receiver downstream of the MGS but not by any further receivers. It is possible that kelts had passed the dam and experienced natural or dam-related mortality before being detected by the closest receivers downstream of the MGS, especially in first study year when the closest receiver was 4 km downstream of the MGS as opposed to only 1 km in the second study year. Dam passage at the MGS occurred mostly during the night, which is consistent with other studies (Nyqvist, 2016; Scruton *et al*., 2007).

Survival in the downriver reaches was high, with cumulative survival rates to the lower SJR being 53%–63%. These estimates are higher than the minimum survival rate of 23% as kelts exited the hydropower-regulated Penobscot River (Maynard *et al*., 2018), but could be slightly lower in comparison to the high rates found for

S. salar in unregulated rivers (63%–80%, Halttunen, 2011; 90%, Hubley *et al*., 2008).

S. salar are known to employ two alternative life history strategies to recondition at sea before beginning another spawning migration. They may return as either consecutive spawners (*i.e*., return in the autumn of the same year as the spring kelt migration) or as alternate spawners (*i.e*., spend a full winter in the ocean before returning; Marshall and MacPhail, 1987; Ritter, 1989). In acoustic tagging studies that track post-spawners or kelts, the battery life of the transmitters would ideally allow for tracking kelts further into their next life stage as a repeat spawner. The programmed transmission rate of the V13 tags used in this study would have generally allowed redetection of the tagged kelts should they have returned to the SJR as consecutive spawners, but detection of alternate spawners would not have been possible due to expiry of the battery. Of the 18 acoustic-tagged kelts that were known to enter the Bay of Fundy during the 2 years of study, four were detected on the Ocean Tracking Network's Halifax Line in 2015, implying that they were likely heading to western Greenland to feed (Ritter, 1989) and may have only returned as alternate spawners in 2017 after the expected expiry of the acoustic tags. One kelt was detected approximately 14 km offshore in the Gulf of Maine in the summer of 2016, indicating that it may have returned as a consecutive spawner in 2017 should it have survived the reconditioning at sea. However, none of the acoustic-tagged kelts were detected re-entering the SJR as repeat spawners. While post-spawner survival may be relatively high elsewhere (Chaput *et al*., 2016; Halttunen, 2011) and the repeat spawners have become an increasingly large component of total returns in some *S. salar* populations (*e.g*., Chaput *et al*., 2016), the opposite is true in many other populations where repeat spawners make up less than 10% of returning salmon and/or the mortality rate of repeat spawners is increasing (Fleming and Reynolds, 2004; Hubley and Gibson, 2011; Jones *et al*., 2014; Maynard *et al*., 2018; Mills, 1989). In the light of the *S. salar* population dynamics in the SJR, it was not surprising that none of the tagged kelts were detected as repeat spawners. For example, 15 years of scale analysis showed that only 1.8% (760 of 43,109 salmon) of the wild adults returning to tributaries upstream of the MGS were repeat spawners (Gibson *et al*., 2009), indicating that survival to repeat spawning in the SJR is generally very low. A multitude of research points to the variability in ocean climate and consequent ecosystem shifts being major drivers in the natural mortality of *S. salar* in the marine environment (Benoît and Swain, 2008; Chaput and Jones, 2006; Hubley and Gibson, 2011; Lacroix, 2013; Kelly *et al*., 2018).

There are limitations to the current study that should be noted as potentially affecting some of the reported metrics. One theoretical possibility is that tag failure before the estimated battery life had expired would have affected survival rates. The tag manufacturer, however, has a proven track record of providing technologically sound tags and widespread tag failure rate in V13 tags has never been reported, so any bias due to premature tag failure is likely negligible. Some reaches had encounter estimates <50% in the first study year, which may have affected survival estimates. The receiver network was improved in the second study year such that all reaches had encounter estimates >75%. Small sample sizes may have also resulted in poor precision of survival estimates. Given that captive-reared fish have had a genetic influence on this population and the fish within this study, one may ask whether their motivation to migrate to sea might have been impacted; however, six kelts were confirmed to have at-sea experience using scale analysis.

Hydropower managers should ensure that safe and efficient downstream migration routes are available for migrating *S. salar* kelts. While providing access for spillway passage for the duration of the kelt migration maximizes survival rates during dam passage in some hydropower-regulated river systems (Maynard *et al*., 2018), this may not be a sufficient method along at the MGS to ensure maximal survival. Although spillway passage was an option that was available for the majority of tagged kelts migrating at the MGS, the passage through the MGS still presented a decline in survival in the SJR, and the spilling period did not cover the whole duration of the migration. Also recognizing that any additional spilling may be economically unfeasible, a better and more sustainable option would be to construct a surface bypass for downstream migrating kelts with associated bar racks or louvers preventing their migration or entrainment through turbines (Linnansaari *et al*., 2015). While such structures would potentially incur a high one-time construction cost, it would potentially lead to future savings by reducing the provision of water toward spilling for the purpose of fish passage, and a bypass would ensure that a nonturbine egress route would be available throughout the whole kelt migration period. Although ensuring survival of all of the descending kelts through the entire hydropower system is unlikely to lead to population recovery in the SJR without also improving smolt production and at-sea mortality (Gibson *et al*., 2009), recognizing the unique value of kelts to the stability of the population *via* the portfolio effect (Schindler *et al*., 2010) and then subsequently improving their survival would be a necessary first step contributing to recovery of the Atlantic salmon population in the SJR.

ACKNOWLEDGEMENTS

This research project is a part of Mactaquac Aquatic Ecosystem Study funded by New Brunswick Power, NSERC's Collaborative Research and Development programme (CRDPJ: 462708-13) and the Atlantic Salmon Conservation Foundation. We thank Mark Gautreau, Ben Wallace, Gordon Yamazaki, Sam Andrews, Daniel Arluison, Kaleb Zelman, Ben Andrews, Adam Archibald, Colin De Coste and Cody Brooks for extensive efforts during receiver installation and retrieval. We also thank Peter Cronin, Bruce Beaton, Austin Paul, Philip Lee, Chris Blair, Allison Ferguson, Mark Gautreau, Ben Wallace and Theoren Ellis for participating in capturing the post-spawned salmon for tagging, and Brian Polchies for help with fish tagging. Thank you to two anonymous reviewers whose work improved this manuscript. This research project is a part of Mactaquac Aquatic Ecosystem Study funded by New Brunswick Power, NSERC's Collaborative Research and Development programme (CRDPJ: 462708-13), and the Atlantic Salmon Conservation Foundation.

AUTHOR CONTRIBUTIONS

A.B.B. performed the majority of the fieldwork, including fish collection, tagging, active tracking, data management and analysis, and

wrote the article. T.L. designed the study, supervised the fieldwork and was the primary editor. M.N. created the hydrodynamic model under the supervision of K.H. S.P. provided input on fieldwork and data analysis and contributed to editing the article. R.J. supervised the use of captive-reared kelts, provided input on fieldwork and data analysis, and contributed to editing the article. R.A.C. helped to design the study, provided input on fieldwork and data analysis, and contributed to editing the article.

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How to cite this article: Babin, A. B., Ndong, M., Haralampides, K., Peake, S., Jones, R., Curry, R. A., & Linnansaari, T. (2021). Overwintering and migration behaviour of post-spawned Atlantic salmon *Salmo salar* in a large hydropower-regulated river and reservoir. *Journal of Fish Biology*, 1–19. https://doi.org/10.1111/jfb.14768