Received: 20 June 2019 | Revised: 10 November 2019 | Accepted: 29 November 2019

DOI: 10.1111/fwb.13467

Freshwater Biology WILEY

ORIGINAL ARTICLE

Survival and migration patterns of naturally and hatchery-reared Atlantic salmon (*Salmo salar*) smolts in a Lake Ontario tributary using acoustic telemetry

Sarah M. Larocque[1] | **Timothy B. Johnson**[2] | **Aaron T. Fisk**[1]

[1]Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON, Canada

[2]Glenora Fisheries Station, Ontario Ministry of Natural Resources and Forestry, ON, Canada

Correspondence
Sarah M. Larocque, Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON, Canada.
Email: slarocque9@gmail.com

Funding information
Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: Canada Graduate Scholarship and Strategic Partnership Grant

Abstract

1. Atlantic salmon (*Salmo salar*) smolts are often stocked into rivers to supplement natural reproduction, yet hatchery-reared fish have lower survival compared to wild conspecifics. However, few studies have assessed riverine migratory performance and survival differences in hatchery and wild smolts, or more specifically naturally reared smolts (hatchery fish released earlier as parr), particularly in rivers with weirs which may further reduce survival.
2. Using acoustic telemetry, including a subset of fish with novel transmitters that identify predation events, we assessed survival and migration patterns of hatchery- (2017: $n = 32$; 2018: $n = 30$) and naturally reared Atlantic salmon smolts (2017: $n = 8$; 2018: $n = 30$) in a Lake Ontario tributary with two weirs to better understand their ecology and assess the influence of environmental parameters on migration.
3. Naturally reared smolts were 13.9 times more likely to survive than hatchery-reared smolts and mark–recapture models indicated that weirs did not reduce survival for either group. Survival per km was lowest at the release site, indicating pre-migration mortality, and specifically high stocking-related mortality of hatchery-reared smolts. Speed and times of day fish migrated (i.e. migratory performance) did not vary by rearing group, suggesting that the high mortality of hatchery-reared smolts may be due to other factors related to hatchery and stocking operations. Overall mean (± *SD*) migration speed for smolts was 0.70 ± 0.39 km/hr and movements occurred significantly more frequently at night (18:00–06:00).
4. Smolts were detected in Lake Ontario after they left the river; however, the array in Lake Ontario was not conducive to providing much detail regarding movement patterns. There was no predation of the two predation tags detected in Lake Ontario, indicating that movements were made by smolts and not predators.
5. With ongoing restoration efforts of Atlantic salmon in Lake Ontario, it was important to understand the smolt migration patterns and success of the stocked fish. Our findings of similar migratory performance yet different relative survival of hatchery- and naturally reared smolts help inform management with regards to stocking strategies that could improve Atlantic salmon reintroduction success.

KEYWORDS

Cormack–Jolly–Seber model, great lakes, migration, stocking, weirs

1 | INTRODUCTION

It has become a common practice to stock hatchery-reared fish to supplement wild populations and enhance fisheries (Brown & Day, 2002; Minckley, 1995; Molony, Lenanton, Jackson, & Norriss, 2003). For instance, Atlantic salmon (*Salmo salar*) are commonly stocked as fry, parr, smolts, and adults in rivers to compensate for declining populations and supplement natural reproduction throughout the species' distribution range (Parrish, Behnke, Gephard, McCormick, & Reeves, 1998; Saltveit, 2006; Thorstad, Whoriskey, et al., 2012). However, hatchery-reared fish have lower fitness compared to their wild conspecifics (Araki, Berejikian, Ford, & Blouin, 2008; Araki, Cooper, & Blouin, 2007; Araki & Schmid, 2010; Brown & Day, 2002; Einum & Fleming, 2001). Studies are relatively limited examining fitness differences among hatchery fish stocked at differing life stages, and thus different rearing duration in the natural environment. Although fish stocked at later life stages (e.g. smolts) have increased survival while in the hatchery environment, they can avoid natural selection processes and later on have reduced fitness relative to similarly aged fish that were stocked at earlier life stages (e.g. fry or parr; Birnie-Gauvin, Larsen, Thomassen, & Aarestrup, 2018; Milot, Perrier, Papillon, Dodson, & Bernatchez, 2013; Thériault, Moyer, & Banks, 2010). For example, Coho salmon (*Oncorhynchus kisutch*) released as fry have been shown to exhibit more similar behaviour to wild fish than those released later as smolts (Thériault et al., 2010). Stocking fish earlier and being naturally reared may have increased fitness and better represent wild fish than if stocked later.

Smolting, the transition from rivers to oceans (or lakes), can be a period of high natural mortality in Atlantic salmon (Klemetsen et al., 2003; Thorstad, Whoriskey, Rikardsen, & Aarestrup, 2011). Studies indicate that hatchery-reared salmonid smolts have poorer survival once in the marine environment relative to wild smolts (Beamish et al., 2012; Jonsson, Jonsson, & Hansen, 1991; Saloniemi, Jokikokko, Kallio-Nyberg, Jutila, & Psanen, 2004) or to naturally reared smolts (i.e. released earlier as parr and reared in rivers; Jokikokko, Kallio-Nyberg, Saloniemi, & Jutila, 2006). Similarly, hatchery Atlantic salmon released as parr have greater smolt migration survival than when released as either fry or smolts (Birnie-Gauvin et al., 2018). However, few studies have assessed riverine migratory performance differences in hatchery-reared and wild smolts (Thorstad, Whoriskey, et al., 2012; Urke, Kristensen, Ulvund, & Alfredsen, 2013) and none to our knowledge have assessed these differences with hatchery- and naturally reared smolts. There is some indication that hatchery-reared Atlantic salmon smolts have similar migratory performance (e.g. speed, times of day, effects of environmental parameters on migration initiation) yet lower overall survival than wild smolts (Thorstad, Whoriskey, et al., 2012; Urke et al., 2013). Thus, presumably, naturally reared smolts would have migratory performances similar to wild and hatchery-reared smolts.

Migratory performance and survival of smolts may potentially be reduced in rivers with migratory barriers such as dams (Holbrook, Kinnison, & Zydlewski, 2011; Huusko et al., 2018; Saltveit, 2006; Stich, Bailey, Holbrook, Kinnison, & Zydlewski, 2015). Hydroelectric and water regulatory dams with turbines and/or augmented flow rates can cause immediate mortality, injury, migratory delays, and/or impassable barriers, which further reduce overall smolt survival and migratory success (Aarestrup & Koed, 2003; Holbrook et al., 2011). Even weirs (e.g. mill dams or fish farming weirs) can reduce flows or increase presence of fish predators that can reduce survival of downstream migrating smolts (Aarestrup & Koed, 2003). Thus, hatchery-reared Atlantic salmon smolts may have reduced survival relative to naturally reared smolts which may be further compounded with the presence of weirs.

The Ontario Ministry of Natural Resources and Forestry (OMNRF) has been reintroducing Atlantic salmon to Lake Ontario since the 1990s by stocking different life stages of hatchery-reared fish in select tributaries in which there is no known natural reproduction (OMNRF, 2017). Fish stocked as parr (<1 year old) reside in the river for approximately 1–2 years until the appropriate size to smolt (e.g. naturally reared smolts), while fish stocked as smolts will leave the river the same season upon stocking (e.g. hatchery-reared smolts). Using a rotary screw trap, OMNRF has observed both naturally and hatchery-reared smolts moving through the Credit River system, a key tributary for Atlantic salmon stocking (OMNRF, 2016, 2017). However, the overall survival and movement strategies (e.g. speed, times of day, effects of environmental parameters on migration) for naturally and hatchery-reared smolts to complete the migration to Lake Ontario are unknown. Furthermore, the presence of two weirs on the Credit River, which are common in the tributaries of Lake Ontario, may further reduce survival of smolts.

With the use of acoustic telemetry and availability of smaller transmitters (herein called tags), we can remotely detect an animals' movement and behaviour and better evaluate survival, timing (in association with environmental parameters), and performance of Atlantic salmon smolts during the river migration (Halfyard, Gibson, Stokesbury, Ruzzante, & Whoriskey, 2013; Holbrook et al., 2011; Urke et al., 2013). Therefore, using acoustic telemetry, we aimed to determine naturally and hatchery-reared Atlantic salmon smolt survival and migration patterns in a tributary with weirs in order to improve our understanding of the smolt migration of a landlocked population and contribute to stocking strategies and reintroduction success. With no known natural reproduction in the system, naturally reared smolts were the closest thing to truly *wild* smolts, yet whether they have increased survival relative to hatchery smolts is unknown. Therefore, our objectives were to determine whether hatchery-reared Atlantic salmon smolts released in the Credit River have lower survival yet similar movement strategies as naturally reared smolts when migrating to Lake Ontario. We also wanted to determine if migration initiation was correlated with environmental variables to inform stocking timing, and whether weirs reduce survival and migration speed of smolts.

2 | METHODS

2.1 | Study area and acoustic array

Our study area was located on the Credit River, Ontario, Canada, starting in the upper reach of the Credit River down to Lake Ontario, a distance of approximately 75 river km (rkm; Figure 1). The Credit River drains an area of approx. 850 km^2 and is characterised by a network of glacial spillways containing deposits of gravel with substantial groundwater inputs (Cunjak & Power, 1986). The river is approximately 10 m wide at the release point and widens to approximately 30 m at the river mouth. Historic weirs (specifically mill dams with a 2–3 m vertical drop) with associated fishways are located 35 (Norval) and 60 (Streetsville) rkm downstream from the release point (see Table S1 for spacing).

Hatchery-reared smolts were released, and naturally reared smolts were tagged, at locations previously stocked by OMNRF in the upper reach of the Credit River. In 2017, the release site and naturally reared fish tagging location was on the West Credit branch of the Credit River (43.7958°, −80.0090°; Figure 1). In 2018, the release site and naturally reared fish tagging location was moved 1.5 km downstream to the upper Credit River to obtain larger sample sizes of naturally reared fish (n = 8 in 2017 versus n = 30 in 2018; 43.8021°, −79.9964°; Figure 1). Although release sites were different, for analyses both release sites were set to 0 rkm for simplicity and given the proximity of the release sites for the two years.

An array of VR2W 180 kHz receivers (Vemco Ltd., Halifax, NS) were deployed throughout the Credit River over 75 rkm (n = 27 total sites; n = 23 deployed per year), however, for analyses, 12 sites were used based on grouping sets of receivers and removing those that had low detection probability (described later; Figure 1). Spacing of receivers and weirs are described in Table S1. Four receivers were located close to the release site (West Credit in 2017 and upper Credit in 2018) to indicate the start time and direction of movement as fish left the area. We grouped the release site receivers from both years and the first downstream site (n = 9 receivers total) into a single *start* location for analyses (Table S1). Receiver moorings were deployed in 0.5–2 m depths and cabled to shore with 4.76 mm stainless steel cable. Receiver moorings (*c.* 25 kg) were constructed with a PVC pipe fitted into the open space of a cinderblock, with the remaining openings filled half-way with cement and a U-shaped rebar inserted into the cement to act as a handle/attachment point. Receiver moorings were monitored every month to ensure that they remained in proper positioning in the river, as high flows or people could move the moorings out of the water. Three receivers were deployed at the mouth of the Credit River in Lake Ontario and for analyses were grouped with two receivers at the end of the river into a single *end* location (Figure 1; Table S1). Additionally, six receivers were deployed along the nearshore and 14 deployed in the offshore of the western basin of Lake Ontario to determine general lake movements of successful smolts (Figure 1). The river mouth and nearshore receiver moorings were connected to a *c.* 25–40-kg anchor mooring by a weighted rope to be retrieved via grappling by boat. Offshore receivers were attached to an acoustic release receiver associated with other telemetry projects. River mouth receivers were deployed during both years of the study, however, nearshore and offshore receivers were only deployed during 2018, of which the 14 offshore receivers and one nearshore receiver (Burlington: 43.33060, −79.75633) were deployed prior to the smolt migration (14–25 April 2018). The remaining five nearshore receivers were deployed after the migration by 15 June 2018 and, unfortunately, were not useful for our study (Figure 1).

Range test tags were used in the array to determine the tag detection efficiency within the river and at the river mouth, and

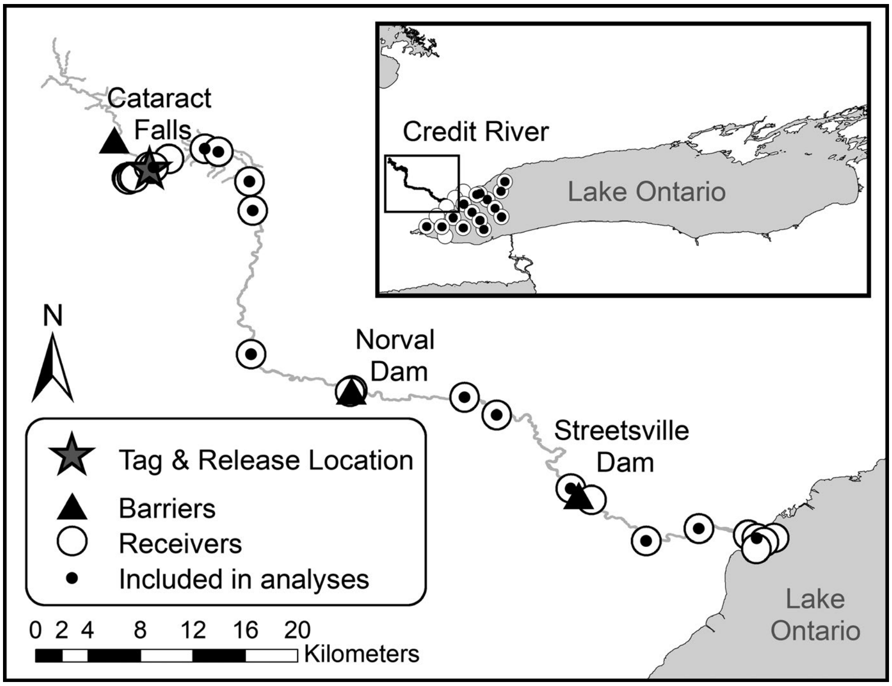


FIGURE 1 Location of acoustic telemetry receivers (and those included in analyses), barriers (labelled), and general tag and release site on the Credit River, Ontario, as well as receivers in the western basin of Lake Ontario (see inset). In 2017 Atlantic salmon (*Salmo salar*) smolts were tagged and released on the West Credit River, while in 2018 smolts were tagged and released on the Upper Credit River (approx. 1.5 km downstream); both locations are depicted by a single symbol

whether we had full detection coverage or if we had to modify analyses based on poor coverage (e.g. keeping sites for analyses, determining site-specific probabilities). Two V9 range test tags (Vemco V9-2H 180 kHz; length: 26 mm; mass in air: 3.7 g; nominal delay: 15 or 30 min), with the same power output yet longer battery life as the V5 and predation tags used and thus representative of tagged fish (Vemco, 2018), were placed at rkm 46.5 (representative of the river) and 74.5 (representative of the river mouth) at approximately 35 and 90 m away from the nearest receiver, respectively, and further away than the width of the river. Tag detection efficiency was determined around the migration period for both 2017 and 2018. Due to the loss of range test tags, full coverage over the migration period was not always possible. Tag detection efficiency within the river was <60% at 35 m (56% in 2017 and 39% in 2018) at the location selected, and thus indicated that fish may migrate undetected at a particular receiver in the river. Tag detection efficiency at the river mouth was >80% at 90 m (85% in 2017 and 82% in 2018). With the high detection efficiency from a longer distance from the range test tag and the general coverage of five receivers (grouped as the *end* point) as fish enter Lake Ontario, it was presumed that there was full detection of fish as they enter the river mouth and Lake Ontario, providing confidence in which fish successfully migrated. Due to our poor within-river range testing and variable habitat within the river, receiver specific detection probabilities were determined from the probability of fish that migrated successfully to Lake Ontario being detected at each receiver location, as not all successful fish were detected at all river receivers. These detection probabilities were later used for within river survival analyses. Receiver locations were removed from analyses if detection probability was unreliable with values <50% at a site (n = 3 sites, where shallow water or tampering reduced detection ability; Table S1). Unfortunately, the locations with poor detection happened to be at sites closest to the weirs.

2.2 | Source of fish

Hatchery-reared fish used for tagging (LaHave strain) were sourced from the OMNRF Normandale Fish Culture Station (Turkey Point, ON). Mean (± *SD*) fork length and mass of hatchery-reared fish in 2017 (n = 32) were 198 ± 12 mm and 93 ± 18 g, and in 2018 (n = 30) were 186 ± 21 mm and 76 ± 22 g. In the Credit River, naturally reared Atlantic salmon were originally stocked as parr the previous spring which survived and grew to smolt size. We captured naturally reared fish using a backpack electrofisher (settings: 250–350 V, 40 Hz, make: Halltech Aquatic Research, Guelph, ON) within a 300 m stretch of the stocking sites in both years. Captured fish were tagged only if fork length was >125 mm to ensure fish would smolt based on the literature and local information (Elson, 1957; Scott & Crossman, 1998; M. Desjardins, OMNRF, personal communication). Mean (± *SD*) fork length and mass of naturally reared fish was 140 ± 8 mm and 31 ± 6 g in 2017 (n = 8), and 143 ± 13 mm and 32 ± 9 g in 2018 (n = 30). Fish were held in an aerated cooler filled with ambient river water prior to and post-tagging. Overall, hatchery-reared fish (192 ± 18 mm) were significantly larger than naturally reared fish (143 ± 12 mm; Mann–Whitney U test: W = 2,292.5; $p < 0.001$); however, they were representative of the size of fish that OMNRF typically stocks in streams and were thus comparable to naturally reared fish.

2.3 | Tagging

Two types of tags were used throughout the study: V5s (Vemco V5-2H 180 kHz; length: 13 mm; mass in air: 0.65 g; estimated battery life: 128–140 days; nominal delay: 40–80 s) and predation tags (Vemco V5D-1H 180 kHz; length: 13 mm; mass in air: 0.68 g; estimated battery life: 108 days; nominal delay: 40–80 s) which trigger a new identification code upon being consumed (Halfyard et al., 2017). In 2017, all tagged fish had V5 tags (n = 40), while in 2018 fish were tagged with either a V5 or predation tag (n = 15 for each tag type, for both hatchery- and naturally reared fish). Due to hatchery protocols and logistics, we anaesthetised individuals using clove oil (50 mg/L) for hatchery-reared fish and MS-222 (100 mg/L) for naturally reared fish. Individuals were weighed (round mass; ± 1 g) and measured (fork length; ± 1 mm). Tags were inserted through a *c*. 1.5 cm incision on the ventral side of the fish off the midline using surgical tools sterilised in a 10% betadine solution. The incision was closed with 2 simple interrupted sutures (5–0 coated Vicryl Plus undyed braided suture; Ethicon, Inc.). Post-surgery, fish were placed in an aerated cooler and observed (<15 min) for recovery from anaesthesia. Hatchery-reared fish were then transferred back to a holding tank until stocking (3–14 days post-surgery) where no mortality occurred during this time. Naturally reared fish were released after electrofishing was completed for the day to prevent additional stress of being recaptured (12–13 April 2017 and 6–7 April 2018). Hatchery-reared fish were transported to the Credit River in a large, aerated holding tank (1 m × 2 m × 1.5 m) and stocked on 21 April 2017 and 12 April 2018. Tagging and release of fish occurred during similar times as OMNRF spring smolt stocking and prior to anticipated migration timing of May–June.

2.4 | Environmental monitoring

Environmental variables were monitored from March to July in 2017 and 2018 to determine if there was any correlation with timing of migration of naturally and hatchery-reared Atlantic salmon. Water temperature (°C) and flow (m^3/s) were logged every 15 min at water quality monitoring stations maintained by the Credit Valley Conservation Authority within 5 km of release sites in which mean daily temperature and flow were calculated. Accumulated thermal units (ATU), the sum of daily mean temperatures, were calculated from 1 March onwards (for each year, respectively) when daily mean temperatures started to rise from 1°C. For hatchery-reared fish, ATUs were calculated from 1 March onwards using daily hatchery water temperatures (8°C) until the stocking dates, after which ATUs were calculated as described above.

2.5 | Data analyses

2.5.1 | Survival analyses

To determine if successful migration varied by fish rearing, we used a logistic regression with rearing (naturally or hatchery reared) and year (2017 and 2018) as categorical variables on the success of migrating to Lake Ontario. An interaction term was not included as it was not significant ($p > 0.05$) but also when included in the model, it created an issue with perfect separation (in which there was only one outcome with naturally reared smolts in 2017).

To determine whether survival varied within the river either at weirs or between receiver locations, we used the Cormack–Jolly–Seber (CJS) model for live recaptures (Cormack, 1964; Jolly, 1965; Seber, 1965) within the program MARK (White & Burnham, 1999) using the RMark package (Laake, 2013) in R (version 3.4.2; R Core Team, 2017). The CJS model calculates a maximum-likelihood estimate (± standard error) for survival (Φ or phi) and probability of recapture (p). As salmon smolts have a unidirectional migration from the river to the lake, the CJS model can be used such that recaptures (i.e. tagged fish detected acoustically downstream from release) occur along a migratory corridor as opposed to distinct capture time periods (Halfyard et al., 2013; Michel et al., 2015). The distance between two receivers was considered the sampling interval for which survival was estimated. Thus, models estimated survival for each passive receiver interval along the progression of smolt migration. Survival estimates were standardised by the length of the receiver interval (i.e. survival per km). This was done by setting the time intervals (in reality, space intervals for this application—Table S1) in the process.data() function of RMark package to a vector of reach lengths (in units of km).

As fish migrate through the system, presence/absence (1,0) was determined at each receiver location for each fish to create a capture history (e.g. 111,010,100,001). The presence of weirs was indicated for the receivers immediately downstream of the Norval and Streetsville weirs (35 and 60 km from release), to determine if weirs explained a reduction in survival (and no effect of p) during the migration. Presence of weirs and receiver location were not used together as model factors as we wished to assess whether weirs or location (i.e. spatial heterogeneity) better explained survival.

Factors that may affect Φ and p were assessed [fish rearing (Φ only), year, receiver location, presence of weirs (Φ only), and receiver specific detection probability (described previously; p only)] using all biologically plausible combinations/interactions, along with a *null* model in which the parameters for Φ and/or p are constant. Each factor-specific CJS model was compared with one another and the *null* model using Akaike information criterion corrected for small sample sizes (AICc). Optimal models were identified as the model with the lowest AICc value and the highest model weights. Candidate models with ΔAICc values < 2 have similar explanatory power (Burnham & Anderson, 2002). Prior to model selection, the global CJS model [Phi(Year*Weir*Rearing*Location) *p*(Year* *Location*Detection)] was tested for goodness-of-fit (i.e. overdispersion) by calculating an overdispersion parameter ($\hat{c}$) from simulating model deviance using a bootstrapping method with $n = 1{,}000$ simulations. We estimated $\hat{c}$ by dividing the deviance estimate from the original global model by the mean of simulated deviances. We obtained a $\hat{c}$ of 0.943, indicating no overdispersion, thus we did not adjust AIC values (Burnham & Anderson, 2002). Only the top 10 models are presented for efficiency.

2.5.2 | Movement analyses

For all movement analyses, we used data associated with the last time a fish was detected at a site to indicate leaving (e.g. migrating) and first time a fish was detected at sites to indicate arriving. Migration initiation time was determined as fish left the *start* site. It was not always possible to determine when unsuccessful fish began migration as some were not seen downstream nor upstream of the release/tagging site and, due to this discrepancy, unsuccessful fish were not considered in the analyses of migration initiation. Due to small sample sizes when split by year and fish rearing, we describe the day number, mean daily water temperature, ATUs, and mean daily flow in which fish initiated migration. Successful hatchery-reared fish in 2018 migrated the day they were released, skewing potential migration initiation trends and were removed from analyses, creating an unbalanced design. We combined year and fish rearing, to have three groups (2017—Hatchery; 2017—Natural; 2018—Natural) within a single environmental variable and conducted a Kruskal–Wallis test, followed by a pairwise Wilcoxon rank-sum comparison with a Bonferroni correction.

Overall migration speed (km/hr) was determined from successfully migrating fish only. Speed was calculated based on the total river distance of 75 km divided by the time taken from leaving the *start* site until arriving at the *end* site. We ran a Kruskal–Wallis test with four groups (combination of year and fish rearing) to determine if there were differences in migration speed between naturally and hatchery-reared smolts and years. To determine if migration speed varied throughout the river, the distance between successive sites was divided by the duration of time taken for an individual fish to leave the previous site and arrive at the next site. This removes any holding time at any one specific receiver and speeds may appear faster than overall migration. All fish (successful or not) were included. We used a linear mixed model to test for significant differences in migration speed between fish rearing, year and receiver location and all two-way interactions, with individual fish as a random factor followed by a post hoc Tukey pairwise comparison of the least squares means to determine differences in migration speed by receiver location.

To determine whether fish migrate at different times of day, we assessed all fish leaving sites other than the *start* site, to ensure we were assessing detections during migration only. Daily hours were broken up into four 6-hr intervals (00–06, 06–12, 12–18, 18–24). These times roughly distinguish between day and night, as dawn and dusk were at 06:00 and 20:00 approximately during the study period. Thus, 00–06 and 18–24 were considered night, while 06–12 and 12–18 intervals were considered day. For each 6-hr interval there were counts of detection events of an individual fish passing. To test for significant differences in detection events per fish during migration between fish rearing and time of day (four 6-hr intervals), we performed a generalised linear mixed model with individual fish as a random effect using a Poisson distribution. A type II analyses of deviance was utilised to determine significant differences between variables followed by a post hoc Tukey pairwise comparisons of the least squares means to determine differences in counts of detection events during the four periods of day.

The subset of fish tagged with predation tags were assessed for predation events (change of identification code) throughout the migration as well as within the lake. Lake Ontario movements were determined using detections from the acoustic telemetry array (described earlier) deployed within the western basin of Lake Ontario (Figure 1). General post-migration lake movements and predation events are described.

All analyses were conducted in R and significance was assessed at $\alpha = 0.05$ or the lack of overlap in 95% confidence intervals (CI). Unless stated otherwise, values are reported in mean ± *SD*. Assumptions of normality and homoscedasity were visually assessed using *qqplot* and fitted versus residual plots.

3 | RESULTS

Naturally reared fish were 13.9 times more likely to successfully migrate to the lake than hatchery fish when controlling for year ($Z = 4.315$, $p < 0.001$). Fish migrating in 2017 were 5.5 times more likely to be successful than migrating in 2018, when controlling for rearing group ($Z = 2.826$, $p = 0.004$; Table 1).

The best-supported CJS model estimated survival per km using fish rearing*year and location, and estimated probability of recapture using our detection probability (Table 2). All top 10 models had fish rearing and location estimating survival, and nine of the top 10 models had year estimating survival, while all top 10 models had detection efficiency estimating probability of recapture (Table 2). The lack of weirs as a factor indicates that there were differences in survival by location that were not attributed to weirs (Figure 2). Based on lack of overlapping 95% CI of survival per km estimates (Φ), the release point (0 km) had significantly lower survival rates than all other locations, except at rkm 4.5, which had large variability in survival (large CIs; Figure 2). Naturally reared smolts generally had greater survival than hatchery-reared smolts in both years, yet naturally reared smolts had a greater reduction in survival in 2018 than 2017 (which was 100%) compared to hatchery-reared smolts as indicated in the top model with the interaction between fish rearing and year. These results corroborate with the logistic regression estimates of differences in overall survival.

Successful, hatchery-reared smolts left on the same day they were stocked in 2018 (11 April; *n* = 4) and were not included for further analyses. Of the successful migrants, date of migration initiation varied between groups ($X^2_2 = 7.390$, $p = 0.025$), and naturally reared fish migrated later in 2018 (May 11 ± 5 days, *n* = 18) than 2017 (May 4 ± 6 days, *n* = 8; *p* = 0.012; Figures 3 and 4a). While migration date of hatchery-reared fish in 2017 (May 10 ± 10 days, *n* = 12) was not significantly different from naturally reared fish

TABLE 1 The proportion and number of acoustically tagged Atlantic salmon (*Salmo salar*) smolts that successfully migrated from the Credit River to Lake Ontario by year and fish rearing group

Year	Fish rearing	Proportion successful	Successful (*n*)	Total tagged (*n*)
2017	Naturally reared	1.00	8	8
	Hatchery-reared	0.38	12	32
2018	Naturally reared	0.60	18	30
	Hatchery-reared	0.13	4	30

TABLE 2 Top 10 models of survival of Atlantic salmon (*Salmo salar*) smolts in the Credit River during the migration to Lake Ontario based on Akaike information criterion corrected for small sample sizes (AICc).

Model	Parameters (*n*)	AICc	ΔAICc	Weight
Phi(~Year * Rearing + Location)*p*(~Detection)	17	908.28	0.00	0.29
Phi(~Year * Rearing + Location)*p*(~Detection * Year)	19	909.37	1.09	0.17
Phi(~Year * Rearing + Location)*p*(~Detection + Year)	18	910.14	1.86	0.12
Phi(~Year + Rearing + Location)*p*(~Detection)	16	910.74	2.46	0.09
Phi(~Year * Location + Rearing)*p*(~Detection)	27	911.13	2.85	0.07
Phi(~Year + Rearing +Location)*p*(~Detection * Year)	18	911.81	3.53	0.05
Phi(~Year * Location + Rearing)*p*(~Detection * Year)	29	912.51	4.23	0.04
Phi(~Year + Rearing + Location)*p*(~Detection + Year)	17	912.59	4.31	0.03
Phi(~Rearing + Location)*p*(~Detection)	15	912.62	4.34	0.03
Phi(~Year * Location + Rearing)*p*(~Detection + Year)	28	913.17	4.89	0.03

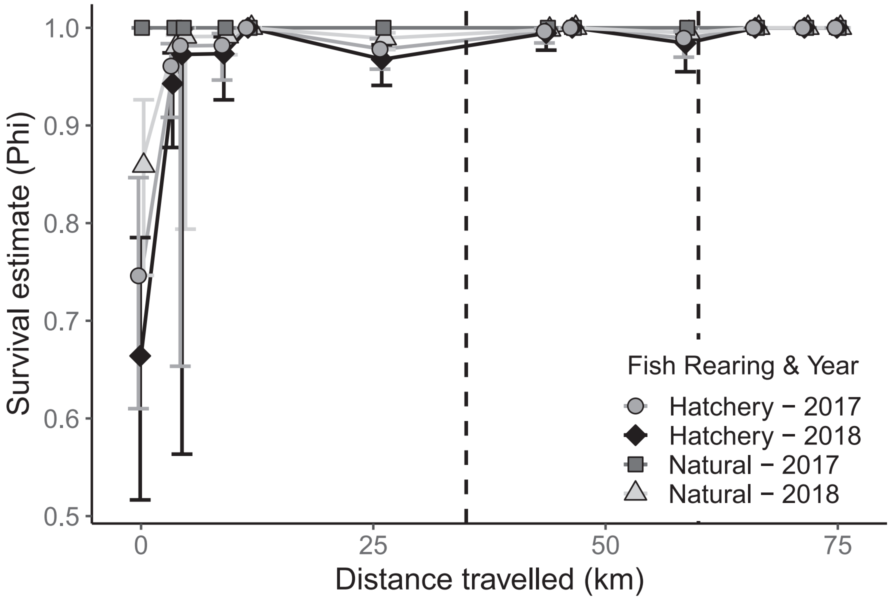


FIGURE 2 Non-cumulative mean (and 95% confidence interval) estimated survival per km (Φ) to reach each receiver location of acoustically tagged hatchery- and naturally reared Atlantic salmon (*Salmo salar*) smolts in 2017 and 2018 as they migrate from the release site in the Credit River (km 0) to Lake Ontario (km 75). Weirs are indicated by a dashed line

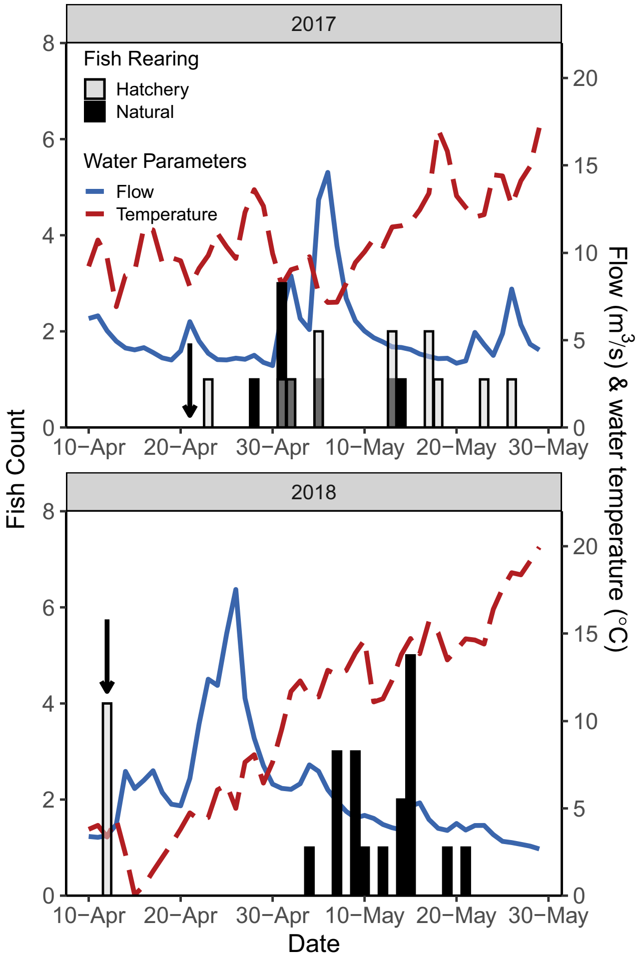


FIGURE 3 Temporal sequence for successful hatchery- (light grey bars) and naturally reared (black bars) Atlantic salmon (*Salmo salar*) smolts initiating the migration in the Credit River to Lake Ontario over time relative to flow (solid line) and water temperatures (dashed line) in 2017 (upper panel) and 2018 (lower panel). Dark grey bars indicate an overlap of hatchery- and naturally reared smolt counts, as bars are not stacked. Arrows represent the release date of hatchery-reared smolts [Colour figure can be viewed at wileyonlinelibrary.com]

in either 2017 or 2018 ($p = 0.120$ and $p = 0.882$, respectively). Water temperatures when fish started migrating were different between groups ($X_2^2 = 15.538$, $p < 0.001$). Water temperatures were similar between naturally (9.7 ± 2.2°C) and hatchery-reared fish (11.2 ± 2.8°C) in 2017 ($p = 0.371$) yet were significantly higher for naturally reared fish in 2018 (13.7 ± 1.1°C; $p = 0.002$ and $p = 0.005$, respectively; Figure 4b). The ATUs when fish began migration varied between groups ($X_2^2 = 23.704$, $p < 0.001$). ATUs did not differ between naturally reared fish in 2017 (393 ± 56°C) and 2018 (355 ± 60°C; $p = 0.209$); however, hatchery-reared fish in 2017 migrated at significantly higher ATUs (626 ± 109°C) than naturally reared fish in 2017 ($p < 0.001$) and 2018 ($p < 0.001$; Figure 4c). Flow did not vary significantly for hatchery-reared fish in 2017, naturally reared fish in 2017, and naturally reared fish in 2018 (6.6 ± 3.4 m^3/s, 6.8 ± 2.9 m^3/s, and 4.8 ± 0.9 m^3/s, respectively; $X_2^2 = 3.928$, $p = 0.140$; Figure 4d).

Although there were differences in survival of naturally and hatchery-reared smolts, overall migration speed did not vary among fish rearing and years ($X_3^2 = 6.562$, $p = 0.087$). Mean migration speed for smolts was 0.70 ± 0.39 km/hr. The migration speed throughout the river also did not vary by fish rearing ($X_1^2 = 0.003$, $p = 0.958$), year ($X_1^2 = 3.039$, $p = 0.081$), fish rearing and year ($X_1^2 = 1.950$, $p = 0.163$), or interact with receiver location (fish rearing * location: $X_{10}^2 = 8.795$, $p = 0.552$; year * location: $X_{10}^2 = 6.924$, $p = 0.733$). However, migration speed did vary by receiver location ($X_{10}^2 = 97.743$, $p < 0.001$). Pairwise comparisons indicated that migration speed at the lower end of the river (except for the last site of entering Lake Ontario) was significantly faster (means ranged from 2.52–3.32 km/hr) than the upper reaches (except for the first site; means ranged from 1.09–1.60 km/hr; Figure 5). As fish reached Lake Ontario, mean migration speed slowed down to 0.92 ± 0.84 km/hr.

When assessing if there were differences in the number of times fish were detected at receivers at different times of day while migrating, there was no significant difference of model fit between

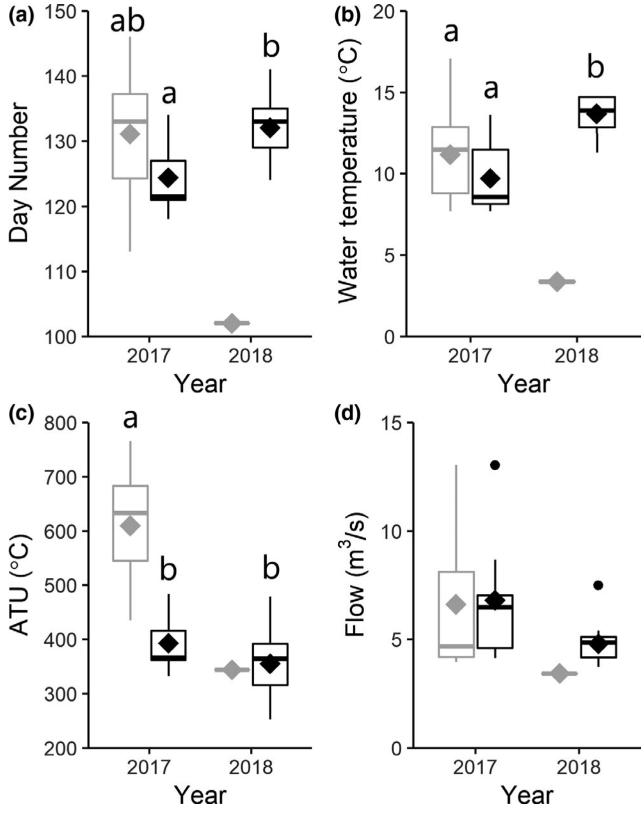


FIGURE 4 Box plots of environmental variables at initiation of migration of successful Atlantic salmon (*Salmo salar*) smolts migrating from Credit River to Lake Ontario in 2017 and 2018. Light grey boxes are hatchery-reared smolts, black boxes are naturally reared smolts. Letters indicate significant differences based on Kruskal–Wallis analyses. Hatchery smolts in 2018 were not included in analyses. ATU, accumulated thermal units

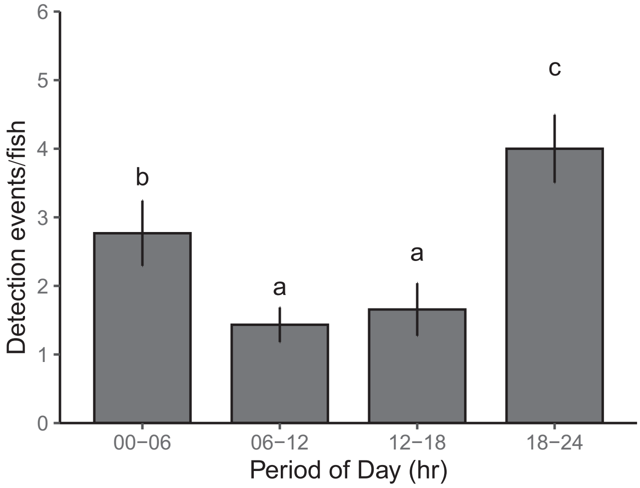


FIGURE 6 Mean (and 95% confidence interval) number of detection events per individual acoustic tagged Atlantic salmon (*Salmo salar*) smolts for different times of day at receivers in the Credit River during migrations in 2017 and 2018

rearing groups on number of detection events ($X_1^2 = 0.587$, $p = 0.444$), nor an interaction between fish rearing and time of day of detection ($X_3^2 = 3.678$, $p = 0.298$). There was a significant difference of model fit in the number of detections events at different times of day ($X_3^2 = 70.216$, $p < 0.001$). Fish were detected more frequently moving past receivers in the hours of 18–24, followed by 00–06, with the 6-hr intervals of 06–12 and 12–18 with the lowest detections of fish (Figure 6).

Smolts were detected in Lake Ontario after leaving the Credit River in 2018. Between the one nearshore and 14 offshore receivers in Lake Ontario deployed at the time of migration, eight receivers detected 7 naturally reared and 1 hatchery-reared smolts (Figure 7). Of the fish that out-migrated to Lake Ontario, 38% of naturally reared and 25% of hatchery-reared smolts were later detected in the lake. Fish were generally detected within a few days to a week of leaving the Credit River; however, two fish were detected later with one detected nearly a month after reaching Lake Ontario and nearing the end of the battery life of the tag. Fish were detected from a range

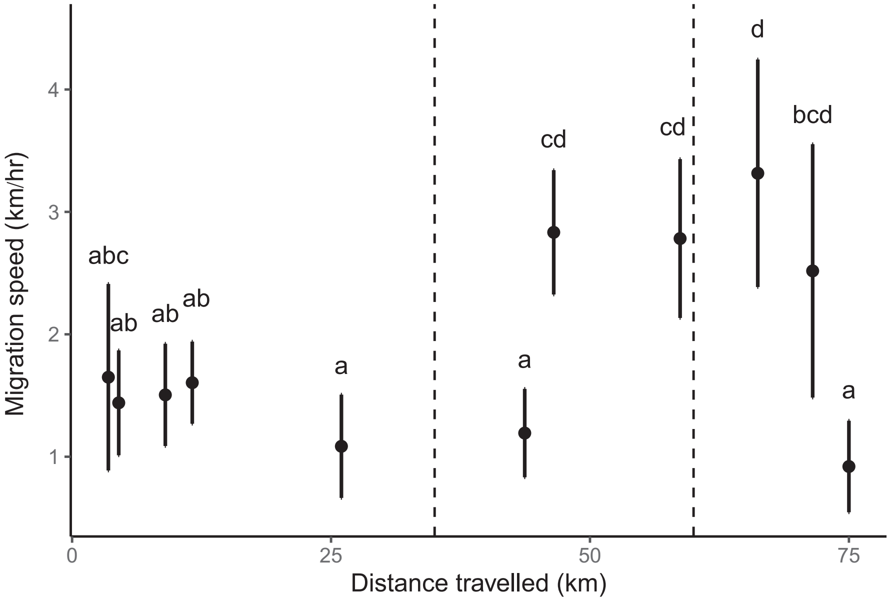
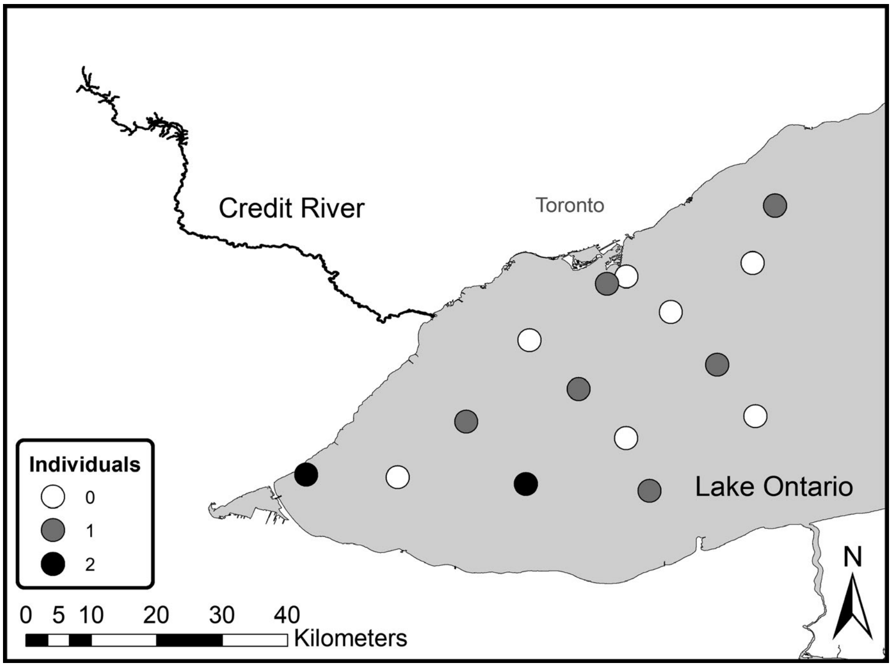


FIGURE 5 Mean (and 95% confidence interval) migration speed of acoustically tagged Atlantic salmon (*Salmo salar*) smolts at different receiver locations as they move from the release site in the Credit River (0 km) to Lake Ontario (km 75). Weirs are indicated by a dashed line. Letters indicate differences based on Tukey's pairwise comparison

FIGURE 7 Number of individual tagged Atlantic salmon (*Salmo salar*) smolts detected at receivers in western Lake Ontario in 2018. Note nearshore receivers not deployed during time of out-migration have been removed



of 15–40 km from the Credit River. Two fish were detected on more than one receiver, in which each fish moved a cumulative 35 and 55 km (linear distance).

From the predation tagged fish, there was no detection of predation events during the smolt migration. Similarly, within Lake Ontario, two naturally reared fish with predation tags were not predated at the time of detection.

4 | DISCUSSION

Overall, using acoustic telemetry we provided a focused assessment of the migration of naturally and hatchery-reared land-locked Atlantic salmon smolts in a Lake Ontario tributary. Naturally reared Atlantic salmon smolts consistently had higher survival and successful migration to Lake Ontario than hatchery-reared smolts and 2017 yielded more successful smolts than 2018. Throughout the river migration, survival was lowest at the release/tagging point and was nearly 100% thereafter, while there did not appear to be any impact with downstream passage over the weirs. Although the 2 years had different temperature and flow regimes, the general movement patterns (speed and time of day) between the two groups were consistent.

4.1 | Migration initiation

We did not have adequate sample sizes of successful smolts to determine whether environmental variables drive migration initiation; however, some trends were noticed when comparing within groups. Successful hatchery-reared smolts began migration later in 2017 than 2018, yet 2018 smolts skewed any correlations with environmental variables by migrating on the day of release. Stich, Kinnison, Kocik, and Zydlewski (2015) found that hatchery-reared Atlantic salmon smolts stocked earlier in the year initiated migration sooner than those released later in the year. Also, hatchery-reared Atlantic salmon smolts stocked later in the year (yet still within the natural smolt timing) had increased survival relative to those stocked earlier (Karppinen, Jounela, Huusko, & Erkinaro, 2014). Although we stocked our hatchery-reared smolts at the same time as the stocking programmes (to relate results to management) it resulted in earlier stocking in 2018 at lower temperatures, with earlier migration and lower survival. We cannot rule out that temperature differences at the time of stocking between years may also contribute to migration timing. The differences seen in the migration timing of our hatchery-reared smolts between years, at least when leaving the day of release in 2018, is more likely attributed to when they were stocked than environmental variables.

Although naturally reared smolts left later in 2018 than 2017, the ATUs were not significantly different between years while mean daily temperature was greater in 2018 than 2017. There is indication that timing of smolt descent is influenced by degree-days or ATUs as opposed to actual water temperature (McCormick, Hansen, Quinn, & Saunders, 1998), or a combination of actual temperature and temperature increase in the water during spring (Jonsson & Jonsson, 2009a; Jonsson & Ruud-Hansen, 1985). In our study, the similar ATUs between years may be a good proxy for the effect of spring temperature trends on migration initiation. Smolt migration initiation has been influenced more strongly by ATU than daily mean temperature in both Chinook salmon (*Oncorhynchus tshawytscha*) (Sykes, Johnson, & Shrimpton, 2009) and Atlantic salmon (Stich, Kinnison, et al., 2015; Zydlewski, Haro, & McCormick, 2005). Brown trout (*Salmo trutta*) migrated later in seasons with lower spring temperatures (Jonsson & Jonsson, 2009b) as was seen here in our study on Atlantic salmon. Although we can only make inferences as temporal trends of water temperature and flow were different between years, it appears that from consistency between years, the initiation of the naturally reared Atlantic salmon smolt migration in our study was also influenced by ATUs or spring temperature trends, rather than daily mean temperatures.

Flow is another factor that can stimulate smolt migration (Jonsson & Jonsson, 2009a; McCormick et al., 1998). In our study, flow was not significantly different between years or naturally or hatchery-reared smolts, yet smolts left at slightly higher mean flows in 2017 than 2018. The increased survival of naturally and hatchery-reared smolts in 2017 may be attributed to higher mean flows or that peak flows occurred during the smolt migration in 2017, while in 2018 peak flows occurred prior to migration. From 2011 to 2016, OMNRF used rotary screw traps on the Credit River to enumerate smolts during out-migration (OMNRF, 2017). Data from the screw traps may be used to further elucidate the consistency of ATUs and flow with migration initiation in Lake Ontario smolts.

4.2 | Weir effects on smolt survival and speed

The two weirs on the Credit River did not impact downstream movement of smolts, in either survival or speed. Previous studies have shown reduced survival and movement rates of smolts at dammed sections in regulated rivers (Holbrook et al., 2011; Huusko et al., 2018; Stich, Kinnison, et al., 2015). However, in our study, the weirs on the Credit River are relatively small low-head barriers originally constructed for milling operations in the early 1800s. Thus, the mill pond upstream of the weir may not reduce flow or disorient the fish as much as in regulated rivers with hydroelectric dams, nor the vertical drop (maximum of 3 m on the Credit River weirs) going over the weir did not appear to cause mortality (e.g. reduced survival downstream) with the associated flows. With the high flow rates in 2017 and 2018 relative to the Aarestrup and Koed (2003) study, the downstream migration of smolts do not appear to be impacted by weirs on the Credit River. Instead of being slowed down by weirs, migration speed increased in the lower reaches of the river. Unfortunately, receivers deployed immediately downstream of the weirs were tampered with and removed from analyses so obtaining fine details of weir passage was not possible. However, mean survival estimates when passing the weir were >99% while the interval prior to passing the weirs was slightly lower, suggesting other sections of the river incurred more mortality than those associated with the weirs. Generally, our mean mortality rates (1 − mean survival rates) per km throughout the river (ranges from 0 to 5.7% mortality/km) were either lower or within previously observed mortality rates in free-flowing rivers (0.3–7.0% mortality/km; review by Thorstad, Uglem, et al., 2012b; Huusko et al., 2018), further indicating no weir effects on smolt migration or survival.

4.3 | Hatchery- versus naturally reared smolt implications

Naturally reared smolts survived better than hatchery-reared smolts, yet both groups had high initial mortality. Few studies have assessed wild or naturally versus hatchery-reared smolt migration survival in rivers specifically. Of those studies, wild and hatchery smolts migrating the dammed Penobscot River, U.S.A. showed no difference in survival (Holbrook et al., 2011; Stich, Bailey, et al., 2015) while on a free-flowing river, wild smolts had greater survival than hatchery smolts (Hyvärinen & Rodewald, 2013; Urke et al., 2013). Melnychuk et al. (2014) showed similar trends to our study between wild and hatchery-reared steelhead (*Oncorhynchus mykiss*) and also saw the majority of mortality occurring at the start of migration in the river. In our study, the main difference in naturally and hatchery-reared smolt survival was seen at the point of release. As otherwise, throughout the migration, survival as well as migration speeds and preference for migrating at night (18:00 to 06:00) for both naturally and hatchery-reared smolts were similar, as was seen in Urke et al. (2013). This suggests that migratory performance and survival between naturally and hatchery-reared smolts were similar aside from the initial mortality prior to migration. Other tagging studies have also experienced high initial mortality of stocked smolts (Holbrook et al., 2011; Huusko et al., 2018; Thorstad, Uglem, Arechavala-Lopez, Økland, & Finstad, 2011; Thorstad, Uglem, et al., 2012b). We do not believe direct tagging mortality occurred as hatchery fish in 2017 were held for over 2 weeks without incurring any mortality or tag expulsion (and thus only held for 72 hr in 2018). The lack of mortality of naturally reared fish in 2017 further indicates that our capture and tagging methods did not cause tagging effects. There is the possibility of potential indirect tagging effects (e.g. predation) reducing survival of all groups (hatchery-reared more so) and not being detected thereafter. The stocking location in 2018, although having more naturally reared smolts to tag, also had residential adult brown trout (a potential predator) that may have increased mortality relative to 2017 smolts; however, the predation tags in 2018 indicated that this was not the case for those fish that were detected. There was a quick drop in water temperature from 4 to 0°C 3 days after stocking in 2018, which may have provoked additional stress on both hatchery- and naturally reared smolts, relative to 2017. However, those temperatures fall above the lower critical temperature of Atlantic salmon (Elliott, 1991; Jonsson & Jonsson, 2009a) and detections of naturally reared but unsuccessful (i.e. not detected completing the migration) smolts a month after the incident make this seem an unlikely cause of mortality.

The greater initial mortality of the hatchery-reared smolts relative to the naturally reared smolts may be related to hatchery operations. Being raised in a hatchery condition longer and stocked as smolts (hatchery-reared group), as opposed to being stocked as parr (naturally reared group), may have incurred epigenetic effects that were maladaptive upon being released into the river as a smolt.

Genetically, the two groups came from the same strain and would have the same degree of inbreeding depression and domestication selection. However, epigenetic differences have been seen between hatchery and wild coho salmon smolts and may explain the reduced fitness between the groups (Le Loyer et al., 2017). Also, Milot et al. (2013) found that hatchery fish released as smolts had lower fitness than those released earlier as fry. Naturally reared fish being subject to predation and environmental stressors longer may have been more fit at the time of tagging relative to hatchery-reared fish that had not been exposed to such pressures. Melnychuk et al. (2014) also allude to hatchery rainbow trout being less fit, naïve to river environments, and more prone to predation at the start of migration. Predation of hatchery-reared fish may be occurring from avian and mammalian predators, which can predate upon smolts and not be later detected as the tag is physically removed from the river.

Aside from possible epigenetic or fitness differences, additional stocking stress or the time of stocking may cause the increased mortality of the hatchery-reared group. Stocking strategies (e.g. transportation and release methods) or hatchery-rearing methods can increase stress and reduce survival of smolts (Barton, Peter, & Paulencu, 1980; Finstad, Iverson, & Sandodden, 2003; Hyvärinen & Rodewald, 2013; Iverson, Finstad, & Nilssen, 1998). Handling and transportation of fish increases cortisol levels and has been correlated with lower survival of coho salmon smolts (Schreck, Solazzi, Johnson, & Nickelson, 1989; Specker & Schreck, 1980). Thus, the initial lower survival of hatchery smolts may be a factor of stocking stress as performance-wise they were similar to naturally reared smolts. The timing of stocking may also play a role in the increased mortality. Hatchery-reared smolts released earlier in cold waters had lower survival than those released later, closer to the time of natural migration (Karppinen et al., 2014). Karppinen et al. (2014) found that the early release group moved briefly downstream but then ceased migration and had increased exposure to predators. This could explain why we saw no predation, via predation tags, of hatchery-reared smolts near our receivers at the release point yet many smolts were not detected at the next site, 3.5 km downstream. Although we cannot discern it from our study, various factors such as epigenetics, predation risk, transportation stressors, and stocking timing may have contributed towards the lower initial survival of hatchery-reared smolts compared to naturally reared smolts.

Differences in hatchery- and naturally reared smolt survival may be more prominent as they leave the rivers as opposed to during river migration. Relative to wild, hatchery-reared Atlantic salmon post-smolts in the ocean have reduced survival and/or return to natal rivers (Jokikokko et al., 2006; Jonsson et al., 1991; Jonsson, Jonsson, & Hansen, 2003; Kallio-Nyberg, Jutila, Saloniemi, & Jokikokko, 2004; Saloniemi et al., 2004), and hatchery-reared salmonids generally have reduced fitness in the wild (Araki et al., 2008, 2007; Milot et al., 2013). Interestingly, naturally reared smolts had greater fjord survival than wild and hatchery-reared smolts (Flávio, Aarestrup, Jepsen, & Koed, 2019). Whether poor ocean/fjord survival of hatchery-reared smolts similarly translates to poor survival in a large lake, like Lake Ontario, is unknown. Unfortunately, there was a delay in deploying receivers and we did not get full coverage of the movements of smolts when entering Lake Ontario. Of the fish that survived to Lake Ontario, slightly more naturally reared were detected than hatchery-reared smolts and there appeared to be no piscivore predation via the two predation tags detected. However, the array in Lake Ontario was not conducive to providing much detail regarding movement patterns. With increasing coverage of Lake Ontario with acoustic receivers, particularly near sites of river research, future studies could better assess smolt movements and survival in Lake Ontario.

4.4 | Smolt success and Lake Ontario Atlantic salmon restoration

With ongoing restoration efforts of Atlantic salmon in Lake Ontario, it was important to understand the smolt migration success of the stocked fish. The relative survival of both naturally and hatchery-reared smolts can help inform management with regards to stocking strategies and improving Atlantic salmon returns. For instance, whether it is more effective to stock at the parr or smolt life stage, given respective survival rates at each stage and rearing costs, or can timing of stocking be adjusted to improve survival of hatchery-reared smolts. Naturally reared smolts had greater migration survival than hatchery-reared smolts, and weirs were not a factor in migration survival. However, a better understanding of what caused reduced survival at the start of the migration may help improve migration success but also in predicting smolt numbers—whether it be assessing stocking strategies or hatchery-rearing methods. As smolt survival was very high further downstream, previous OMNRF rotary screw trap data could be compared to stocking numbers to obtain population estimates with the aid of our survival estimates. Overall, acoustic telemetry revealed naturally and hatchery-reared Atlantic salmon smolt migration patterns and success in a Lake Ontario tributary in an effort to reveal potential survival bottlenecks to the restoration of Lake Ontario Atlantic salmon.

ACKNOWLEDGMENTS

We would like to acknowledge the Credit Valley Conservation Authority (especially J. Clayton and C. Bird) for providing water quality data and information, access to land, and information for selecting receiver locations, OMNRF Normandale Fish Culture Station for providing Atlantic salmon hatchery smolts for our study, as well as OMNRF staff (M. Heaton and M. Desjardin) for providing advice and logistical support. Thanks to all the field help: R. Corchis-Scott, M. Charone, A. Despenic, T. Fendler, K. Hudelson, N. Klinard, M. Lucas, J. Midwood, S. Pupovac, A. Weinz, A. Wynia, & the Peel Region Police dive team. The authors declare no conflict of interest. All procedures were approved with the University of Windsor Animal Care Committee (permit No. ACC-16-08). Funding for this project was provided through Natural Sciences and Engineering Research Council of Canada (NSERC) via a Strategic Partnership Grant (to A. T. Fisk) and Canada Graduate Scholarship (to S. M. Larocque).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Sarah M. Larocque https://orcid.org/0000-0002-2088-4988
Aaron T. Fisk https://orcid.org/0000-0002-4208-4068

REFERENCES

Aarestrup, K., & Koed, A. (2003). Survival of migrating sea trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) smolts negotiating weirs in small Danish rivers. *Ecology of Freshwater Fish*, *12*(3), 169–176. https://doi.org/10.1034/j.1600-0633.2003.00027.x

Araki, H., Berejikian, B. A., Ford, M. J., & Blouin, M. S. (2008). Fitness of hatchery-reared salmonids in the wild. *Evolutionary Applications*, *1*, 342–355.

Araki, H., Cooper, B., & Blouin, M. S. (2007). Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science*, *318*(5847), 100–103.

Araki, H., & Schmid, C. (2010). Is hatchery stocking a help or harm? Evidence, limitations and future directions in ecological and genetic surveys. *Aquaculture*, *308*, S2–S11. https://doi.org/10.1016/j.aquaculture.2010.05.036

Barton, B. A., Peter, R. E., & Paulencu, C. R. (1980). Plasma cortisol levels of fingerling rainbow trout (*Salmo gairdneri*) at rest, and subjected to handling, confinement, transport, and stocking. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*, 805–811.

Beamish, R. J., Sweeting, R. M., Neville, C. M., Lange, K. L., Beacham, T. D., & Preikshot, D. (2012). Wild chinook salmon survive better than hatchery salmon in a period of poor production. *Environmental Biology of Fishes*, *94*, 135–148. https://doi.org/10.1007/s10641-011-9783-5

Birnie-Gauvin, K., Larsen, M. H., Thomassen, S. T., & Aarestrup, K. (2018). Testing three common stocking methods: Differences in smolt size, migration rate and timing of two strains of stocked Atlantic salmon (*Salmo salar*). *Aquaculture*, *483*, 163–168. https://doi.org/10.1016/j.aquaculture.2017.10.021

Brown, C., & Day, R. (2002). The future of stock enhancements: Lessons for hatchery practice from conservation biology. *Fish and Fisheries*, *3*, 79–94. https://doi.org/10.1046/j.1467-2979.2002.00077.x

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York, NY: Springer.

Cormack, R. M. (1964). Estimates of survival from the sighting of marked animals. *Biometrika*, *51*(3–4), 429–438. https://doi.org/10.1093/biomet/51.3-4.429

Cunjak, R. A., & Power, G. (1986). Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences*, *43*, 1970–1981.

Einum, S., & Fleming, I. A. (2001). Implications of stocking: Ecological interactions between wild and released salmonids. *Nordic Journal of Freshwater Research*, *75*, 56–70.

Elliott, J. M. (1991). Tolerance and resistance to thermal stress in juvenile Atlantic salmon, *Salmo salar*. *Freshwater Biology*, *25*, 61–70. https://doi.org/10.1111/j.1365-2427.1991.tb00473.x

Elson, P. F. (1957). The importance of size in change from parr to smolt in Atlantic salmon. *Canadian Fish Culture*, *21*, 1–6.

Finstad, B., Iverson, M., & Sandodden, R. (2003). Stress-reducing methods for releases of Atlantic salmon (*Salmo salar*) smolts in Norway. *Aquaculture*, *222*, 203–214. https://doi.org/10.1016/S0044-8486(03)00112-1

Flávio, H., Aarestrup, K., Jepsen, N., & Koed, A. (2019). Naturalized Atlantic salmon smolts are more likely to reach the sea than wild smolts in a lowland fjord. *River Research and Applications*, *35*, 216–223.

Halfyard, E. A., Gibson, A. J. F., Stokesbury, M. J. W., Ruzzante, D. E., & Whoriskey, F. G. (2013). Correlates of estuarine survival of Atlantic salmon postsmolts from the Southern Upland, Nova Scotia, Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, *70*, 452–460. https://doi.org/10.1139/cjfas-2012-0287

Halfyard, E. A., Webber, D., Del Papa, J., Leadley, T., Kessel, S. T., Colborne, S. F., & Fisk, A. T. (2017). Evaluation of an acoustic telemetry transmitter designed to identify predation events. *Methods in Ecology and Evolution*, *8*, 1063–1071. https://doi.org/10.1111/2041-210X.12726

Holbrook, C. M., Kinnison, M. T., & Zydlewski, J. (2011). Survival of migrating Atlantic salmon smolts through the Penobscot River, Maine: A prerestoration assessment. *Transactions of the American Fisheries Society*, *140*(5), 1255–1268. https://doi.org/10.1080/00028487.2011.618356

Huusko, R., Hyvärinen, P., Jaukkuri, M., Mäki-Petäys, A., Orell, P., & Erkinaro, J. (2018). Survival and migration speed of radio-tagged Atlantic salmon (*Salmo salar*) smolts in two large rivers: One without and one with dams. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*, 1177–1184.

Hyvärinen, P., & Rodewald, P. (2013). Enriched rearing improves survival of hatchery-reared Atlantic salmon smolts during migration in the River Tornionjoki. *Canadian Journal of Fisheries and Aquatic Sciences*, *70*(9), 1386–1395. https://doi.org/10.1139/cjfas-2013-0147

Iverson, M., Finstad, B., & Nilssen, K. J. (1998). Recovery from loading and transport stress in Atlantic salmon (*Salmo salar* L.) smolts. *Aquaculture*, *168*, 387–394.

Jokikokko, E., Kallio-Nyberg, I., Saloniemi, I., & Jutila, E. (2006). The survival of semi-wild, wild and hatchery-reared Atlantic salmon smolts of the Simojoki River in the Baltic Sea. *Journal of Fish Biology*, *68*(2), 430–442. https://doi.org/10.1111/j.0022-1112.2006.00892.x

Jolly, G. M. (1965). Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika*, *52*(1–2), 225–247. https://doi.org/10.1093/biomet/52.1-2.225

Jonsson, B., & Jonsson, N. (2009a). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology*, *75*, 2381–2447.

Jonsson, B., & Jonsson, N. (2009b). Migratory timing, marine survival and growth of anadromous brown trout *Salmo trutta* in the River Imsa. *Norway. Journal of Fish Biology*, *74*(3), 621–638.

Jonsson, B., Jonsson, N., & Hansen, L. P. (1991). Differences in life history and migratory behaviour between wild and hatchery-reared Atlantic salmon in nature. *Aquaculture*, *98*, 69–78. https://doi.org/10.1016/0044-8486(91)90372-E

Jonsson, B., & Ruud-Hansen, J. (1985). Water temperature as the primary influence on timing of seaward migrations of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, *42*, 593–595.

Jonsson, N., Jonsson, B., & Hansen, L. P. (2003). The marine survival and growth of wild and hatchery-reared Atlantic salmon. *Journal of Applied Ecology*, *40*, 900–911. https://doi.org/10.1046/j.1365-2664.2003.00851.x

Kallio-Nyberg, I., Jutila, E., Saloniemi, I., & Jokikokko, E. (2004). Association between environmental factors, smolt size and the survival of wild and reared Atlantic salmon from the Simojoki River in the Baltic Sea. *Journal of Fish Biology*, *65*, 122–134. https://doi.org/10.1111/j.0022-1112.2004.00435.x

Karppinen, P., Jounela, P., Huusko, R., & Erkinaro, J. (2014). Effects of release timing on migration behaviour and survival of hatchery-reared Atlantic salmon smolts in a regulated river. *Ecology of Freshwater Fish*, *23*(3), 438–452. https://doi.org/10.1111/eff.12097

Klemetsen, A., Amundsen, P. A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F., & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): A review of aspects of their life histories. *Ecology of Freshwater Fish*, *12*(1), 1–59.

Laake, J. L. (2013). *RMark: An R interface for analysis of capture-recapture data with MARK*. Alaska Fisheries Science Centre Processed Report, 2013–01.

Le Loyer, J., Laporte, M., Beacham, T. D., Kaukinen, K. H., Withler, R. E., Leong, J. S., … Bernatchez, L. (2017). Parallel epigenetic modifications induced by hatchery rearing in a Pacific salmon. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, 12964–12969. https://doi.org/10.1073/pnas.1711229114

McCormick, S. D., Hansen, L. P., Quinn, T. P., & Saunders, R. L. (1998). Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(S1), 77–92.

Melnychuk, M. C., Korman, J., Hausch, S., Welch, D. W., McCubbing, D. J. F., & Walters, C. J. (2014). Marine survival difference between wild and hatchery-reared steelhead trout determined during early downstream migration. *Canadian Journal of Fisheries and Aquatic Sciences*, *71*, 831–846. https://doi.org/10.1139/cjfas-2013-0165

Michel, C. J., Ammann, A. J., Lindley, S. T., Sandstrom, P. T., Chapman, E. D., Thomas, M. J., … MacFarlane, R. B. (2015). Chinook salmon outmigration survival in wet and dry years in California's Sacramento River. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*, 1749–1759. https://doi.org/10.1139/cjfas-2014-0528

Milot, E., Perrier, C., Papillon, L., Dodson, J. J., & Bernatchez, L. (2013). Reduced fitness of Atlantic salmon released in the wild after one generation of captive breeding. *Evolutionary Applications*, *6*, 472–485. https://doi.org/10.1111/eva.12028

Minckley, W. L. (1995). Translocation as a tool for conserving imperiled fishes: Experiences in western United States. *Biological Conservation*, *72*, 297–309. https://doi.org/10.1016/0006-3207(94)00091-4

Molony, B. W., Lenanton, R., Jackson, G., & Norriss, J. (2003). Stock enhancement as a fisheries management tool. *Reviews in Fish Biology and Fisheries*, *13*, 409–432. https://doi.org/10.1007/s11160-004-1886-z

Ontario Ministry of Natural Resources and Forestry (2016). *Lake Ontario fish communities and fisheries: 2015 annual report of the Lake Ontario management unit*. Picton, ON: Ontario Ministry of Natural Resources and Forestry.

Ontario Ministry of Natural Resources and Forestry (2017). *Lake Ontario Fish communities and fisheries: 2016 annual report of the Lake Ontario management unit*. Picton, ON: Ontario Ministry of Natural Resources and Forestry.

Parrish, D. L., Behnke, R. J., Gephard, S. R., McCormick, S. D., & Reeves, G. H. (1998). Why aren't there more Atlantic salmon (*Salmo salar*)? *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(S1), 281–287.

R Core Team (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Saloniemi, I., Jokikokko, E., Kallio-Nyberg, I., Jutila, E., & Psanen, P. (2004). Survival of reared and wild Atlantic salmon smolts: Size matters more in bad years. *ICES Journal of Marine Science*, *61*(5), 782–787. https://doi.org/10.1016/j.icesjms.2004.03.032

Saltveit, S. J. (2006). The effects of stocking Atlantic salmon, *Salmo salar*, in a Norwegian regulated river. *Fisheries Management and Ecology*, *13*, 197–205. https://doi.org/10.1111/j.1365-2400.2006.00494.x

Schreck, C. B., Solazzi, M. F., Johnson, S. L., & Nickelson, T. E. (1989). Transportation stress affects performance of coho salmon, *Oncorhynchus kisutch*. *Aquaculture*, *82*, 15–20. https://doi.org/10.1016/0044-8486(89)90391-8

Scott, W. B., & Crossman, E. J. (1998). *Freshwater fishes of Canada*. Oakville, ON: Galt House Publications.

Seber, G. A. F. (1965). A note on the multiple-recapture census. *Biometrika*, *52*(1/2), 249–259. https://doi.org/10.1093/biomet/52.1-2.249

Specker, J. L., & Schreck, C. B. (1980). Stress responses to transportation and fitness for marine survival in coho salmon (*Oncorhynchus kisutch*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*, 765–769.

Stich, D. S., Bailey, M. M., Holbrook, C. M., Kinnison, M. T., & Zydlewski, J. D. (2015). Catchment-wide survival of wild- and hatchery-reared Atlantic salmon smolts in a changing system. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(9), 1352–1365. https://doi.org/10.1139/cjfas-2014-0573

Stich, D. S., Kinnison, M. T., Kocik, J. F., & Zydlewski, J. D. (2015). Initiation of migration and movement rates of Atlantic salmon smolts in fresh water. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(9), 1339–1351. https://doi.org/10.1139/cjfas-2014-0570

Sykes, G. E., Johnson, C. J., & Shrimpton, M. J. (2009). Temperature and flow effects on migration timing of Chinook salmon smolts. *Transactions of the American Fisheries Society*, *138*, 1252–1265. https://doi.org/10.1577/T08-180.1

Thériault, V., Moyer, G. R., & Banks, M. A. (2010). Survival and life history characteristics among wild and hatchery coho salmon (*Oncorhynchus kisutch*) returns: How do unfed fry differ from smolt releases? *Canadian Journal of Fisheries and Aquatic Sciences*, *67*, 486–497.

Thorstad, E. B., Uglem, I., Arechavala-Lopez, P., Økland, F., & Finstad, B. (2011). Low survival of hatchery-released Atlantic salmon smolts during initial river and fjord migration. *Boreal Environment Research*, *16*(2), 115–120.

Thorstad, E. B., Uglem, I., Finstad, B., Chittenden, C. M., Nilsen, R., Økland, F., & Bjørn, P. A. (2012b). Stocking location and predation by marine fishes affect survival of hatchery-reared Atlantic salmon smolts. *Fisheries Management and Ecology*, *19*, 400–409. https://doi.org/10.1111/j.1365-2400.2012.00854.x

Thorstad, E. B., Whoriskey, F. G., Rikardsen, A. H., & Aarestrup, K. (2011). Aquatic nomads: The life and migrations of the Atlantic salmon. In Ø. Aas, S. Einum, A. Klemetsen, & J. Skurdal (Eds.), *Atlantic salmon ecology* (pp. 1–32). Oxford, UK: Wiley-Blackwell.

Thorstad, E. B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H., & Finstad, B. (2012). A critical life stage of the Atlantic salmon *Salmo salar*: Behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*, *81*(2), 500–542. https://doi.org/10.1111/j.1095-8649.2012.03370.x

Urke, H. A., Kristensen, T., Ulvund, J. B., & Alfredsen, J. A. (2013). Riverine and fjord migration of wild and hatchery-reared Atlantic salmon smolts. *Fisheries Management and Ecology*, *20*(6), 544–552. https://doi.org/10.1111/fme.12042

Vemco (2018). *V9 / V9TP-180 kHz coded transmitters datasheet*. Retrieved from https://www.vemco.com/wp-content/uploads/2015/09/v9-180khz.pdf

White, G. C., & Burnham, K. P. (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study*, *46*(Suppl 1), S120–S139. https://doi.org/10.1080/00063659909477239

Zydlewski, G. B., Haro, A., & McCormick, S. D. (2005). Evidence for cumulative temperature as an initiating and terminating factor in downstream migratory behavior of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*, 68–78.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Larocque SM, Johnson TB, Fisk AT. Survival and migration patterns of naturally and hatchery-reared Atlantic salmon (*Salmo salar*) smolts in a Lake Ontario tributary using acoustic telemetry. *Freshwater Biology*. 2020;65:835–848. https://doi.org/10.1111/fwb.13467