Atlantic salmon (*Salmo salar*) migrations in a large hydropower reservoir and the regulated Saint John River

by

Amanda Babin

Master of Science, University of New Brunswick, 2013

Bachelor of Science, Mount Allison University, 2009

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Supervisors:	Tommi Linnansaari, Ph.D., Biology Stephan Peake, Ph.D., Biology
Examining Board:	René Malenfant, Ph.D., Biology Allen Curry, Ph.D., Biology, Forestry and Env. Management Paul Arp, Ph.D., Forestry and Env. Management
External Examiner:	Joseph Zydlewski, Ph.D., Biology, USGS, University of Maine

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ABSTRACT

My research focused on evaluating the impacts of the large Mactaquac Generating Station (MGS) reservoir on the migrations of the endangered Outer Bay of Fundy Atlantic salmon (*Salmo salar*). Salmon respond to flowing waters to determine the direction, timing, and speed of their migrations. A large reach of the Saint John River (SJR) was impounded by the MGS in 1968, transforming the habitat from a free-flowing river to a lacustrine environment with altered and slower flow. I examined all migratory lifestages of Atlantic salmon in the SJR using acoustic telemetry, including pre-smolts, smolts, adults, and post-spawned adults (kelts), as they navigated these environments.

Migration rates were compared between the lentic MGS reservoir and the more lotic reaches upriver and downriver of the MGS to assess whether migration is delayed in the reservoir. Nearly all of the tagged salmon experienced migratory delay within the reservoir (medians: smolts 1.3-6.4 d, kelts 3.5-10.5 d, adults 1.5-5.7 d) due to suppressed migration rates (medians: smolts 5.0-13.3 km d^{-1} vs. 15.4-29.3 km d^{-1}, kelts 4.4-8.9 km d^{-1} vs. 14.9-36.8 km d^{-1}, adults 8.5-20.1 km d^{-1} vs. 19.3-46.9 km d^{-1}). Migration success through the reservoir was higher for downstream migrants (smolts > 81 % and kelts > 82 %) than upstream migrants (adults 47 %).

Recommendations informed by these findings with the aim of aiding recovery of this endangered population are given to hydropower and fisheries managers, including: *i*) changing the spill regime to allow a greater proportion of downstream migrants the option of spillway passage since all but a few smolts and even the earlier kelt migrants were sometimes forced to pass via turbines; *ii*) constructing a downstream surface-

bypass facility which is more economically feasible than increasing spill and is supported by the observed variable passage timing; *iii*) allowing the free-swim of downstream migrants through bypasses in comparison to a trap-and-haul strategy that was not found to increase survival of smolts; and *iv*) maintaining trap-and-haul operations for adults migrating upstream of the MGS due to the high proportion of fallbacks and increased energy expenditure from superfluous movements in the reversed direction to the intended migration observed in the reservoir.

DEDICATION

To my husband, Kraig Babin, who has been there from the beginning.

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List of Symbols, Nomenclature or Abbreviations

Φ – Phi; survival estimate

p – encounter estimate

1SW – one-sea-winter or grilse <63 cm forklength

2SW – two-sea-winter

AIC – Akaike's Information Criterion

ANOVA – ANalysis Of VAriance

BGS – Beechwood Generating Station

CDD – Cumulative Degree Days

CJS – Cormack-Jolly-Seber

CR – Captive reared

CRI – Canadian Rivers Institute

DDT – dichlorodiphenyltrichloroethane

DFO – Department of Fisheries and Oceans

DS – Diversion Sluiceway

ED – Earthen Dam

FS – Free-Swim

FVES – Flow Velocity Enhancement System

GS – Generating Station

HS – Hatchery Smolt

IBoF – inner Bay of Fundy Atlantic salmon population

LMEM – Linear Mixed Effects Model

M – Middle; middle of the river channel

MAES – Mactaquac Aquatic Ecosystem Study

MANOVA – Multivariate ANalysis Of Variance

MBF – Mactaquac Biodiversity Facility

MGS – Mactaquac Generating Station

MSW – multi-sea-winter or large salmon > 63 cm forklength

NBP – New Brunswick Power

NSERC – Natural Sciences and Engineering Research Council of Canada

OBoF – outer Bay of Fundy Atlantic salmon population

ORM – Ordinal Regression Model

PIT – Passive Integrated Transponder

PZT – lead zirconate titanate

Rkm – river kilometer; distance following the centerline of the river

RL – River Left; near the left river bank facing downstream

RR – River Right; near the right river bank facing downstream

RST – Rotary Smolt Trap

SE – Standard Error

SJR – Saint John River

SONAR – SOund Navigation And Ranging

SW – Spillway

TH – Trap-and-Haul

TH2 – Two-way Trap-and-Haul

TNGS – Tobique-Narrows Generating Station

Chapter 1

General Introduction

Atlantic salmon (*Salmo salar*) is an anadromous species, requiring migrations between freshwater and saltwater, often covering hundreds of kilometers to complete their life cycle (Dadswell *et al.* 2010). The migratory lifestage of the juvenile, the smolt, moves from their natal rivers to the sea where they undergo accelerated growth (Gross and Coleman 1988). As adults, they migrate back to freshwater, navigating to their natal stream (with some straying to nearby rivers; Quinn 1993) where they intend to spawn. As an iteroparous species, some adult Atlantic salmon may survive spawning and migrate back to the marine environment as kelts where they can recondition for potential future spawning activites (Ruggles 1980). Along their migratory routes, salmon develop physiologically (*e.g.*, osmoregulation), and ecologically (*e.g.*, optimal ocean entry; McCormick *et al.* 1998), but are challenged by anthropogenic obstacles (*e.g.*, passage through barriers such as hydrogeneration facilities; Marschall *et al.* 2011). This doctoral dissertation examines each migratory lifestage (*i.e.*, pre-smolt, smolt, adult, post-spawn/kelt) of Atlantic salmon as they move through the Saint John River (SJR; New Brunswick, Canada; Figure 1.1) with a focus on the impacts of the Mactaquac Generating Station (MGS; Figure 1.1) and its reservoir on migration success, rates, and delay. The knowledge presented herein is based on field data collected over multiple years; specifically, downstream migrations of smolts (autumn to spring 2014-2016), post-spawned adults known as kelts (autumn to spring 2014-2016), and upstream migrations of adults (summer to autumn 2014-2016).

Chapter 1 provides a general introduction to topics that are essential for understanding the context of these studies. I begin with the broader context of the

Mactaquac Aquatic Ecosystem Study that addresses the whole SJR ecosystem and my project therein. My research questions were explored using telemetry; therefore, the basics of these technologies are described. I summarize the ecology of Atlantic salmon in relation to their migrations, and present evidence on how salmonids can be negatively affected by hydropower generation stations and their reservoirs. I then lay out the current state of Atlantic salmon in the SJR. Lastly, the overarching question of the thesis is stated and broken down into principal objectives, and the purpose of each chapter is described.

1.1 Mactaquac Aquatic Ecosystem Study (MAES)

MAES is a partnership between New Brunswick Power (NBP) and the Canadian Rivers Institute (CRI), with additional funding from the Natural Sciences and Engineering Research Council of Canada (NSERC). All data from MAES has been digitized and is accessible to the public (http://canadarivers-gis.maps.arcgis.com/apps/webappviewer/index.html?id=f4d83a4f66104c36bece0a221d17f832).

NBP is the owner and operator of the Mactaquac Generating Station (MGS; Figure 1.2A). Becoming operational in 1968, the MGS is currently impacted by alkali-aggregate reaction causing its concrete structures to expand. This has reduced its expected lifespan from 100 to 50 years (Stantec Consulting Ltd. 2015). To consider the integrity of the ecosystem services within SJR, NBP partnered with CRI to address relevant scientific questions that will help inform the course for the future of the hydropower station.

The SJR has headwaters in Maine, Quebec, and New Brunswick, and is the second largest river (55,000 km^2) in eastern North America, second only to the Saint Lawrence River (Kidd *et al.* 2011). The MGS is the first (*i.e.*, most downstream; Figure 1.1) dam on the river, located 150 km upstream from the river mouth following the centerline as the channel meanders (river km; rkm). The second dam on the mainstem is the Beechwood Generating Station (BGS; rkm 285; Figure 1.1), upstream of which there is a tributary, the Tobique River, that has approximately 60 % of Atlantic salmon nursery habitat upstream of the MGS (Marshall *et al.* 2014). There is a third major hydropower installation just 1 rkm into mouth of the Tobique River, the Tobique-Narrows Generating Station (TNGS; rkm 315; Figure 1.1). Before the dams were constructed, there was 2,379 ha of juvenile habitat in the SJR (Washburn and Gillis Associates Ltd. 1995), with Grand Falls being a natural barrier (Morse and Dewolf 1974). Dam construction reduced the rearing habitat by 44 % (reduction of 1,032 ha, leaving 1,347 ha) of predicted suitable rearing habitat for Atlantic salmon, with 83 % of the remaining rearing habitat residing in the Tobique River (Figure 1.1; Washburn and Gillis Associates Ltd. 1995).

The MGS is the largest hydropower generating station in New Brunswick and is 15 rkm upstream from the provincial capital of Fredericton (Figures 1.1 and 1.2). The dam is 1,100 m wide with a hydraulic head of approximately 34 m under typical operating conditions. There are six Kaplan turbines that generate up to 672 MW. The dam operation is considered to be a hybrid, incorporating both run-of-the-river and hydropeaking operations. Run-of-the-river dams retain little storage capacity within the reservoir, whereas hydropeaking generates power during peak demand that introduces

artificial short-term flow pulses. The MGS reservoir often exceeds 40 m in depth (average depth 26 m, maximum depth 51 m, volume 1.36 km^3), and dam operations influence water levels as far as 100 rkm upstream to the town of Hartland (Figure 1.1). Such a deep body of water has transformed this section of the river from a lotic to a lentic system, meaning water currents are severely suppressed. The 37 rkm reach upstream of the dam has a drastic decline in water flow from an average of 0.52 m s^{-1} before impoundment to 0.06 m s^{-1} after dam construction (Stantec Consulting Ltd. 2015). This is a potential issue for Atlantic salmon that respond to water currents to guide their downstream and upstream migrations.

NBP initially considered three options for the future of the MGS: 1) Repower with new constructions of the powerhouse and spillway on the opposite side of the river (Figure 1.2B), 2) Retention of the reservoir without power generation (Figure 1.2C), and 3) Restoration of the river to a free-flowing state via dam removal (Figure 1.2D). Removals of large dams are uncommon, but this option is being considered more often worldwide (Chateauvert *et al.* 2015).

Following a Comparative Environmental Review (Stantec Consulting Ltd. 2015), Option 4) Lifetime Achievement was introduced and selected. This strategy was to maintain the *status quo* of the system via repair of the existing concrete structures at the MGS. In all options except the dam removal, the large reservoir would be retained, and therefore the potential impacts of the reservoir on Atlantic salmon during their migrations is a critical component of future decision making.

MAES is a whole-river ecosystem study with three major themes in its first phase: 1) Saint John River ecosystem, 2) Fish passage and 3) Environmental flows. This

dissertation is MAES project 2.2 “Reservoir transit and downstream approaches to a large dam by Atlantic salmon.” The second phase of MAES will monitor baselines while the MGS is modified, and the third phase will monitor the new state of the SJR.

1.2 Atlantic salmon migratory ecology

Anadromous Atlantic salmon spend their juvenile years in freshwater rivers and streams, then migrate to the ocean where they experience accelerated growth, returning as adults to reproduce (Jones 1959; Gross and Coleman 1988). Most salmon populations are evolutionarily adapted to free-flowing rivers, and studies demonstrate that photoperiod and temperature are the main drivers of physiological change and the timing of migration, whereas water flow provide cues for the direction of downstream (smolts and post-spawned adults; Ruggles 1980; McCormick *et al.* 1998) and upstream (adults; Banks 1969) migrations. Smolts also use flowing water as a transport mechanism, drifting passively with the thalweg (the highest flow in the channel; Thorpe and Morgan 1978; Tytler *et al.* 1978). The influence of water flow on salmon migrations is complex, but clearly a determining factor in their survival (Ruggles 1980; Milner *et al.* 2012). Here, the migratory lifestages are introduced with attention to their relationship with water flow.

Salmon transition from a territorial parr (a non-migratory juvenile lifestage) to a schooling smolt that must migrate to the ocean within a specific ‘smolt window’ (McCormick *et al.* 1998). In many river systems, some proportion (12-100 %) of the faster-growing male parr become precocious, and participate in spawning alongside the anadromous males that have grown to adulthood at sea before spawning (Orton *et al.*

1938; Fleming 1996). The precocious male parr have the benefit of breeding, but suffer mortality costs from incurring injury during spawning and/or reduced overwinter survival, and survivors are less likely to smoltify the following spring (Dalley *et al.* 1983).

Smoltification and the downstream migration is regulated by photoperiod (increasing daylength) and water temperature (peak migration typically at 10 °C; McCormick *et al.* 1998). The fish undergo vast changes, including a switch from positive to negative rheotaxis (swimming against versus with the flow), increased salinity tolerance (Na^+, K^+-ATPase activity in the gills), depositing guanine that causes the scales to appear silvery (likely for predator avoidance), and increased olfactory sensitivity as they imprint to the odours of their natal stream during their downstream migration (McCormick *et al.* 1998). Such changes are energetically taxing, causing the fish to be at an increased risk of morality if exposed to further stressors such as dam passage (McCormick *et al.* 1998). These physiological changes last approximately 30 days, known as the physiological smolt window, during which time the smolts attempt to reach the ocean to coincide with appropriate water temperatures and prey availability, the ecological smolt window (McCormick *et al.* 1998). If they cannot successfully migrate to the ocean within the smolt migration window, they could succumb to predation (Ruggles 1980; Jepsen *et al.* 2006), heat stress, and/or reversion of salinity tolerance (McCormick *et al.* 1999). Therefore, delay in the downstream migration of smolts could accumulate to have substantial consequences for their mortality risk and migration success.

Flowing water currents typically provide directional cues and a transport mechanism for smolts traveling in the thalweg, but when these currents are suppressed in a reservoir, the fish could experience migratory delay leading to a multitude of ecological issues that could ultimately be fatal for smolts. Therefore, examining how water flow in the reservoir affects smolt migration is key for understanding the ecological effects of retaining the reservoir. I hypothesize that reduced water currents within the reservoir will reduce smolt migration rates in comparison to rates in the lotic reaches, causing migratory delay.

Smolts enter the sea and spend 1-7 years feeding as they grow to adults. Adult salmon often undertake long migrations from marine feeding grounds to the mouth of their natal river, but with some straying also naturally occurring (Quinn 1993). Their maiden spawning migration can occur after one or more winters at sea (1-sea-winter = 1SW, 2SW), after increasing their weight by 75 times (smolt to 1SW) or greater than 200 times (smolt to 2SW; O'Connell *et al.* 2006). At lengths less than 63 cm they are considered "small" salmon which are more often males, and those greater than 63 cm are designated "large" salmon which are more often females (Chadwick 1985). The mechanisms by which adults find their way at sea are not completely understood, but likely include cues from water currents and detecting magnetic fields (Lohmann *et al.* 2008). Once they reach the river mouth, they use their olfactory system to home to their natal stream between May and October (Hasler *et al.* 1978; Thorstad *et al.* 2008; Byron and Burke 2014). Movement into the river is often triggered by increased water flows, and is also influenced by related environmental variables such as temperature and turbidity (Banks 1969). The spawning migration is not constant but is interspersed with

periods of quiescence. Generally, there are three phases during the migration: 1) upstream movement with short periods of rest, 2) up- and downstream movements while searching for spawning grounds, and 3) a long holding phase before synchronized spawning (Thorstad *et al.* 2008). Migration rates tend to be faster earlier in the migration and slow as they reach the spawning grounds (Thorstad *et al.* 2008).

The adults do not feed in freshwater (Greene 1926), but rather use the energy that would have been spent on digestion to power their muscles while negotiating the currents, and on developing their reproductive tissues along with other spawning activities (Jonsson *et al.* 1997). Migratory delay due to lack of directional cues from flowing water can be energetically costly, leading to lower body condition, pre-spawning mortality, or the interruption of the timing of arrival to the spawning grounds (Geist *et al.* 2000; Mesa and Magie 2006). Females invest approximately six times more energy than males in reproduction, with about 28 % of their total energy going toward egg production as opposed to about 4.5 % of anadromous males energy being invested in sperm production (Fleming 1996). Larger females have higher fecundity (although produce fewer eggs per unit body size) than smaller bodied individuals, and the eggs are also larger and therefore have a greater chance of surviving (Fleming 1996). Female salmon must also invest energy to build multiple redds. Males develop secondary sex characteristics including a hook-like formation on the lower jaw (*i.e.*, a kype) made of connective tissue. They also reshape their skull and replace their feeding teeth with breeding teeth that are used for fighting with other males. Survival to post-spawning is greater for females than males due to injuries and infections incurred during fighting

(Fleming 1996). Larger individuals lose more energy than smaller individuals, and this is reflected in their increased mortality rates (Jonsson *et al.* 1997).

Post-spawned adults or kelts may either return quickly to the ocean or remain in freshwater until the spring (Jonsson *et al.* 1990; Niemelä 2000). Kelts have been shown to be able to tolerate marine water just 4-6 weeks after spawning (Talbot *et al.* 1992; Lacroix 2013). Individuals in relatively poor condition, typically males and larger-bodied fish, tend to leave the river quickly to recondition at sea, but those which still are in relatively good condition tend to overwinter in the river (Halttunen 2011). While overwintering, movements are thought to be minimal (Östergren and Rivinoja 2008; Nyqvist 2016). There is evidence of steelhead (*Oncorhynchus mykiss*) kelts beginning to recondition by feeding in the spring while migrating to the ocean (Penney and Moffitt 2014). Food items can include smolts, other small fish, and invertebrates (Penney and Moffitt 2014). Larger kelts require a greater amount of reconditioning, and therefore are less likely to eventually return to repeat spawn than smaller kelts (Halttunen 2011). Also, the greater mortality rates incurred by males during spawning results in females making up the majority of repeat spawners (Jones 1959).

The iteroparous nature of Atlantic salmon could be an influential factor in the recovery of populations throughout their range. Repeat spawners typically make up less than 10 % of the number of returning adults (Mills 1989). Although their numbers are small, their contribution to recruitment can be a significant safeguard (Saunders and Schom 1985). In small breeding populations, individuals from multiple year classes spawning together decreases inbreeding and provides genetic stability (Saunders and Schom 1985). Repeat spawners may either return after just a few months of

reconditioning in the ocean as consecutive spawners, or after a full year of reconditioning at sea as alternate spawners (Jonsson *et al.* 1990). The extra time at sea where there are greater food resources (Gross and Coleman 1988) allows for larger body sizes than maiden spawners which results in greater fecundity (Ducharme 1969). In the Miramichi River, New Brunswick, consecutive repeat spawners had higher fecundity than maiden or alternate repeat spawners, but their eggs were smaller and had lower survival rates, perhaps owing to the lower condition factor of the spawners which might be expected from a shorter reconditioning period (Reid and Chaput 2012). The variability in the life history of salmon including precocious parr, differing ages of smoltification, the range of time spent at sea, and the ability to repeat spawn can shield against inbreeding depression and the loss of populations (Saunders and Schom 1985).

1.3 Use of telemetry in fish ecology studies

Telemetry means to remotely ("tele") measure ("metry"). When applied to ecological research (biotelemetry), this often means detecting animal locations through space and time. Spatio-temporal data of individually identified animals provides insight into behaviours that can help us to understand migration rates and survival bottlenecks. Tracking devices have also been modified to measure other parameters of interest such as the temperature or depth a fish is experiencing. These data from tagged individuals are useful for predicting population-level responses if the assumption of minimal tagging impacts is not violated (Adams *et al.* 2012).

Biotelemetry began to develop in the 1950s. The first study to use telemetry to track fish was performed by the National Marine Fisheries Service on Chinook salmon

(*Oncorhynchus tshawytscha*) adults during the upstream migration past the Bonneville Dam on the Columbia River (Trefethen 1956). This leading study improved upon the previous method of visual observation of fish as they moved upstream of Columbia River dams. Development continued throughout the 1960s and 1970s, with important contributions from the Marine Biotelemetry Laboratory at the University of New Brunswick, with an ongoing focus on reducing tag size while maintaining useful detection ranges (Adams *et al.* 2012).

Biotelemetry equipment can be passive (energy comes from the receiver) or active (energy comes from the transmitter; Adams *et al.* 2012). One common technology is the Passive Integrated Transponder (PIT) that consists of a rice grain sized tag being detected by antennas. PIT systems are relatively inexpensive, but to be effective for tracking fish there must be a constricted area (< 1 m^2) within which they can be reliably detected (Castro-Santos *et al.* 1996). For applications where individuals need to be monitored from a distance, the most common active biotelemetry technologies are radio and acoustic telemetry. Radio technology began in 1893 when it was first demonstrated by Nikola Tesla, and acoustic telemetry is based on SONAR (sound navigation and ranging) technology originally developed to detect submarines during World War I (Adams *et al.* 2012). Radio telemetry uses frequencies of 30-300 MHz, whereas acoustic telemetry uses the lower frequency range of 30-300 kHz. Both systems use transmitters (hereafter "tags") with built-in batteries, which often produce coded signals for individual identification. The main difference between the two tag types is the presence of an antenna on radio tags that is either trailing from the attachment point on the fish or are coiled inside the fish at the expense of detection range. Using radio equipment,

aquatic animals can be tracked via antennas in the air, as well as in shallow, turbulent waters, but the high frequency signal is ineffective in saline water due to acoustic scattering and absorption (Medwin and Clay 1998). Acoustic telemetry is effective in both fresh and seawater, but the hydrophone of the receiver must be underwater (Adams *et al.* 2012).

Since Atlantic salmon tracked in this dissertation are anadromous, acoustic telemetry was used to allow for a greater detection area than would have been feasible with radio telemetry, as well as allowing for detection in both freshwater and at sea. Other researchers using acoustic telemetry in areas such as the Bay of Fundy, Gulf of Maine, and Atlantic Ocean, were also able to detect salmon tagged in the SJR and share these detections through a data partnership with the Ocean Tracking Network.

Acoustic tags are made of acoustic transducers, batteries, and electronics, housed within a plastic cylinder filled with epoxy. An acoustic transducer is a cylinder of lead zirconate titanate (PZT) that resonates at the transmission frequency, converting electrical energy into acoustic energy (Herman 1975). The hydrophone associated with the receiver then converts this acoustic energy back into electrical energy so that the signal may be decoded into an individual identifying code, along with the timestamp at which the tag was detected.

While the signal is propagating through the water, there are many variables affecting the amount of acoustic energy that reaches the receiver. These include the ambient noise level in the environment within the frequency range of the signal, objects such as aquatic vegetation or large woody debris, and natural phenomenon such as thermoclines and haloclines. Ambient or background noise levels within the frequency

range of the acoustic signal reduce the signal-to-noise ratio, and therefore the detection efficiency of the receiver. Underwater noise can come from natural sources such as wave action or rain, and also from anthropogenic sources such as boat motors and fish finders (Adams *et al.* 2012). Hydropower facilities contribute to noise levels as water flows through the turbines and spillways, and their hard surfaces can also reflect and distort acoustic signals (How and de Lestang 2012). Obstacles such as boulders or aquatic vegetation can impede the acoustic signal since they can create acoustic shadows within which the signal cannot be detected, or they can distort the signal via reflection (hard boulder) or absorption (soft vegetation or sediment). Similarly, changes in water density due to sharp differences in water temperature (thermocline) and/or salinity (halocline) can cause reflection and refraction of acoustic energy that may affect detection efficiency of acoustic signals. For these reasons, site- and equipment-specific range testing is crucial to determine the optimal placement and configuration of the receivers.

Attachment of tags to organisms can have many consequences including direct physical impacts such as increased stress levels, physical abrasions, and death, as well as indirect impacts on fish behaviour, growth, and risk of predation (Greenstreet and Morgan 1989). Generally, impacts are thought to be minimized when the ratio of tag weight to body weight (tag burden) is not allowed to exceed 2 % (Winter 1996) although more recent research suggests that the acceptable tag burden is dictated by the specific study objectives, the tagging method, and the species or lifestage involved (Jepsen *et al.* 2003).

The most common methods of tag attachment in fishes are gastric, external, and internal (see review by Bridger and Booth 2003). Gastric tagging involves placing the tag into an organism's stomach, typically using a lubricated vinyl tube and gentle plunger (Adams *et al.* 2012). Gastric tagging is appropriate for use on organisms that are not feeding (*e.g.,* Atlantic salmon during their spawning migration), are expected to reach their end of life (*e.g.,* Pacific salmon during their spawning migration), or to avoid impacting spawning success. Gastric tagging avoids puncturing the organism's body, but can still affect a fish's buoyancy, swimming performance, feeding, and survival (Kennedy *et al.* 2018). Tag loss via regurgitation is common, but can be reduced by wrapping the tag in rubber bands with vulcanized tape (Rivinoja *et al.* 2006).

External tagging typically involves wrapping the tag in monofilament covered in a smooth epoxy, leaving two tails free to go through two hypodermic needles puncturing the dorsal musculature of a fish (Adams *et al.* 2012). The monofilament is then tied on the opposite side of the fish with a soft rubber barrier between the knot and the fish's skin to protect it from abrasion and to retain integrity of the mucus (Adams *et al.* 2012). Impacting the scales, mucus, or skin of a fish can increase its risk of infection (Adams *et al.* 2012). External tagging also avoids directly impacting spawning success but can impact a fish's swimming performance due to buoyancy changes and the asymmetrical placement of the tag (Adams *et al.* 2012). External tagging is a common method of tag attachment but must be done with care to avoid the attachment from loosening, increasing abrasion, and introducing the risk of the tag being caught on an underwater obstruction (Adams *et al.* 2012).

Internal tagging whereby a tag is inserted into the body cavity is also a common method of tag attachment (see review by Wagner *et al.* 2011). Fish surgery generally involves anesthetizing the fish to achieve loss of reactivity before making a small incision (slightly larger than the diameter of the tag) along the ventral midline, inserting the tag into the peritoneal cavity, and closing the incision with one or two sutures. When using radio tags, the antenna can be coiled inside the fish at the cost of detection range or be allowed to extend outside of the fish via the original or an additional incision. Internal tagging reduces the likelihood of tag loss but may increase the risk of infection from surgery. Other effects can include altered buoyancy, and reduced swimming performance and survival (*e.g.*, Wright *et al.* 2018).

Biotelemetry has become an effective tool in fish ecology and fisheries research (Heupel *et al.* 2006; Lennox *et al.* 2017). The technology has been proven to provide data on large temporal and spatial scales, furthering our understanding of habitat use, survival, behaviour, and impacts of hydropower systems on fish populations (Lucas and Baras 2000).

1.4 Impacts of hydropower generation on salmonids and their migrations

Rivers have been used by humans throughout history for many purposes including transportation, water supplies, irrigation, flood control, and energy generation. Using flow of rivers to generate hydropower began in the 1800s, most often including dam construction which increased greatly during the period of economic growth after the Second World War and peaked in the 1970s (World Commission on Dams 2000). As of 2000, there were over 45,000 large dams (>15 m high) in operation worldwide

withdrawing an estimated 3,800 km^3 of water from 60 % of the world's rivers (World Commission on Dams 2000). In total, hydropower facilities generate 19 % of the energy utilized by humans (World Commission on Dams 2000).

Flow is considered a master variable that is fundamental to the ecological characteristics of river ecosystems (Poff and Zimmerman 2010). Large dams fundamentally change aquatic ecosystems by shifting the rivers from lotic to lentic environments, trapping water along with sediments and nutrients carried within (Baxter 1977; Thornton *et al.* 1990). While reservoirs are defined as limnological intermediaries between rivers and lakes, and are often grouped with natural lakes because they have similar planktic production and biogeochemical cycling (Wetzel 2001), they differ by having approximately half the hydraulic residence time, half the photic zone, and about 3.7 °C warmer bottom temperatures than comparable lakes (Hayes *et al.* 2017). The deep, slow-moving water in reservoirs may undergo thermal stratification unlike natural rivers where constant flow would negate this process (Baxter 1977; Thornton *et al.* 1990). Slow bodies of water act as heat sinks which can change fish community composition on both sides of the dam (Gregory *et al.* 2002). Also, sediments drop out of suspension in the slow-moving reservoir (Baxter 1977). This will increase the clarity of the water which may be advantageous for visual predators (Gregory *et al.* 2002), but the reduction of sediment load causes significant ecological and hydromorphological changes downstream of dams (Baxter 1977; Petts and Gurnell 2005). Reservoirs now make up 6-11 % of lentic surface area worldwide, increasing the volume of water held

in rivers by 700 % and removing 1 billion metric tons of sediment transport to the ocean each year (Hayes *et al.* 2017).

Dams are one of the greatest threats to freshwater biodiversity (Liermann *et al.* 2012). Impoundment often slows migratory species such as salmon (Gregory *et al.* 2002), and removes spawning and rearing habitats for some fish species (*e.g.*, American shad, *Alosa sapidissima*; Jessop 1975; salmonids; Washburn and Gillis Associates Ltd. 1995) while creating habitat for species benefiting from abundance lentic habitats (*e.g.*, alewife, *Alosa psuedoharengus*; Jessop 1990) including predators of salmonids (*e.g.*, small mouth bass, *Micropterus dolomieu*, chain pickerel, *Esox niger*; Ruggles and Watt 1975).

When flow of a river is subjected to large changes from the natural regime, fish populations nearly always have a negative biological response such as a decrease in diversity or decline in abundance (Banks 1969; Poff and Zimmerman 2010). To compensate for these declines, many systems developed for hydropower have an associated fish hatchery that produces and stocks valuable fish species (often salmonids) in an effort to retain populations. Captive bred and captive reared (CR) fish have been compared to wild fish in many aspects of their life history and are often outperformed by their wild counterparts (Jonsson *et al.* 1991; Fraser 2008). CR salmon have been reported to have lower survival during their downstream migration and at sea, higher straying rates upon return, and lower spawning rates (Jonsson *et al.* 1991; Quinn 1993; Larsson *et al.* 2011). Offspring of CR parents have been found to have decreased fitness compared to those from wild parents, and genetic as well as epigenetic changes have

been shown to occur even over one generation in captivity (Araki *et al.* 2009; Milot *et al.* 2013; Christie *et al.* 2016; Gavery *et al.* 2018). Stocking is also controversial because the artificial environment does not allow for experience with predator avoidance or gaining skills for natural feeding (Álvarez and Nicieza 2003; Larsson *et al.* 2011). The difference in behaviour of CR fish when encountering predators is thought to be an important factor in accounting for their lower survival rates compared to wild fish (Ruggles 1980; Álvarez and Nicieza 2003).

Beyond the changed ecosystem, migratory fishes are faced with a physical obstruction during both upstream and downstream migrations. Arranging fish passage is normally a condition of getting governmental environmental permitting approval for hydropower projects, but passage options are typically only available for select fish species of economic and cultural value (such as salmonids), while the needs of many other species are often ignored (Bunt *et al.* 2012; Noonan *et al.* 2012). The condition for approvals is often considered to be met by engineering upstream and downstream fish passage structures. Much of the research on hydropower impacts on salmonids has taken place in the Pacific Northwest within the Columbia River basin; the U.S. Army Corps of Engineers and many others have studied issues related to hydropower impacts on fish in this system for many decades (see *e.g.*, Williams *et al.* 2005; Whitney *et al.* 2006). While some successes have been achieved in the Columbia River basin for salmonids (Katopodis and Williams 2012; Williams *et al.* 2012), arranging functional passage at hydropower dams has proven to be a challenge despite the significant amount of

research focused on fish passage (Bunt *et al.* 2012; Noonan *et al.* 2012; Linnansaari *et al.* 2015, but see Williams and Katopodis 2016).

Fish passage is a two-way challenge, but upstream passage initially received most of the research and engineering effort. This may be one reason why it has had better success than downstream passage (Williams *et al.* 2012). Upstream migrants cannot pass dams without engineered fish passage solutions. A review of various upstream fish passage structures is provided by (Linnansaari *et al.* 2015) and their efficiency is reviewed by (Bunt *et al.* 2012) and (Noonan *et al.* 2012). Fish ladders are a common solution, coming in a variety of designs including pool-and-weir, vertical-slot, denil, and nature-like fishways (Linnansaari *et al.* 2015). Their efficacy is variable and site-specific (Bunt *et al.* 2012). One of the most critical aspects is siting the structure, and the attraction of fish to the entrance of the fishway (Williams *et al.* 2012; Linnansaari *et al.* 2015). Adults may alternatively be passed upstream using a trap-and-haul (TH) strategy, but this also requires attraction to a collection mechanism such as various fish lifts (Katopodis and Williams 2012).

When considering downstream passage, fish have three general options for successful egress. They may either pass a dam through a spillway, through the turbines, or via engineered structures specifically designed to either collect and/or bypass fish. Research on downstream fish passage has been strongly skewed toward juvenile lifestages rather than the post-spawned adults (Čada 2001). Juvenile salmonids passing multiple dams can experience substantial cumulative mortality (Čada 2001; Gregory *et al.* 2002). Dam passage is also known to elevate the stress levels of already stressed

smolts, leading to a suppressed immune system that makes them more susceptible to disease (Gregory *et al.* 2002).

Downstream fish passage via spillways often has greater survival rates than turbine passage (Muir *et al.* 2001; Jones and Flanagan 2007). Spillways can draw water from the surface (top-spill; Johnson and Dauble 2006), or at depth (bottom-spill; Katopodis and Williams 2012). Both smolts and post-spawned adults tend to be surface-oriented during their downstream migrations and can resist sounding to depths in search for downstream exits; therefore, top-spill is often more effective than bottom-spill (Ruggles 1980; Whitney *et al.* 1997; Wertheimer and Evans 2005). However, the operation of a hydropower dam involves retaining water within the reservoir for future power production and typically the spillways are only opened during periods of high discharge such as the spring freshet or a large rain event. Therefore, this fish passage option with the higher probability of survival can be unavailable at times that are ecologically relevant. Injury or mortality can still occur as fish pass over spillways due to rapid pressure changes, shearing, turbulence, abrasion, rapid deceleration, and striking force once they hit the tailwater (Ruggles 1980). Also, dam passage often disorients fish which are then prone to predation (Jepsen *et al.* 1998).

Passing via turbines can cause direct physical harm with a blade strike or grinding between the blade and its housing, or injury could occur from flow effects such as rapid pressure changes, turbulence, shear stress, and cavitation (Čada 2001). There are generally two types of turbines employed at hydropower generating stations: Francis and Kaplan. Francis turbines typically have a greater number of blades and smaller

diameters, making it more likely that fish would physically encounter the blades more often than in Kaplan turbines, but mortality rates vary greatly for both turbine types (5 to 90 % vs. 5-20 %, respectively; Linnansaari *et al.* 2015). Intuitively, larger-bodied fish have a greater change of encountering the blades than smaller-bodied fish (Franke *et al.* 1997). It is generally thought that the chances of fish survival are maximized when the efficiency of the turbine is also maximized (Čada 2001). This concept has been applied through "fish friendly" turbines including the Alden Turbine and the Voith Minimum Gap Runner which strive to minimize fish mortality while having efficient power production (Hogan *et al.* 2014). These turbines differ from more traditional turbine types by limiting the number of blades, slowing the rate of pressure changes, and maximizing the size of flow passages (Linnansaari *et al.* 2015). The Voith Minimum Gap Runner has been installed in some Columbia River dams where they have been shown to have comparable or lower mortality rates to Kaplan turbines, but with increased power generation efficiencies (Hogan *et al.* 2014). Indirect mortality could also occur as fish become disoriented, which can put them at a higher risk of predation, or if sub-lethal injury occurs, they could succumb to disease shortly after passage (Čada 2001).

During both spillway or turbine passage, fish can experience barotrauma or gas bubble disease due to rapid and large changes in water pressure as they enter the tailrace along with the plunging waters, or as they move through the penstock where they encounter the turbine before exiting into the tailrace (Beeman and Maule 2006; Brown *et al.* 2014). Waters in the tailrace can become supersaturated with atmospheric gases such as nitrogen, which in turn can dissolve into the fish's bodily fluids such as their

blood plasma (Brown *et al.* 2014). Henry's Law states that as a fish rises to the surface and there is a reduction in pressure, solubility will be reduced, and gas will come out of solution (Brown *et al.* 2014). This can cause gas bubbles or emboli to form within the blood, gills, and fins, which cause tissue damage as they expand and can cause hemorrhaging or death (Brown *et al.* 2014).

A variety of mechanisms have been attempted to guide downstream migrants away from spillways and turbines and toward passage routes with higher survival rates. Guidance mechanisms found to be generally ineffective or inconsistent have included lights, sound, air bubble curtains, and electricity (Whitney *et al.* 1997). Screens or racks which were originally designed to minimize trash and debris entering turbine intakes have been modified to divert downstream migrants, with relative success depending on their operation (Coutant and Whitney 2000). Screens are placed to divert smolts away from the turbine intake and into the gatewell where there is an exit to a collection channel that either bypasses them directly to the tailrace or diverts them into trucks or barges to transport them downstream of the dams (Whitney *et al.* 1997; Williams *et al.* 2005; Buchanan *et al.* 2006). Transporting juveniles avoids the cumulative mortality rate from multiple dam passage, but also causes stress (Iversen *et al.* 1998) and could introduce fish to the lower river too early in the smolt window to be optimal for ocean entry (Whitney *et al.* 2006). Allowing smolts to free swim downstream supports active feeding and growing, giving them a better chance of survival upon ocean entry than transported smolts that have not had the extra time to grow (Ruggles 1980). A review of salmonid studies conducted on the Columbia River system with multiple dams

concluded that TH smolts incurred higher mortality rates than free-swimming smolts (Williams *et al.* 2005). Further, transported juveniles may not imprint to their natal streams as strongly as smolts allowed to migrate freely and therefore have greater straying rates when returning as adults (Buchanan *et al.* 2006). When the TH strategy is used for both upstream migrating adults and downstream migrating smolts, it is considered a two-way trap-and-haul (TH2) program (Lusardi and Moyle 2017).

Regardless of the downstream passage options available to fish, managers strive to maximize their survival to maintain healthy ecosystems while generating hydropower. Beyond the option of dam removal, an effective bypass structure may allow fish to pass volitionally with minimal delay and injury. The water used to attract and pass fish to the tailrace via a bypass can also be recovered to a large extent via a dewatering device that allows only a small amount to lubricate the bypass channel, reusing most of the water for power production (Ferguson *et al.* 2005). However, even fully effective dam passage does not address the potential issues arising during fish passage through the reservoir upstream of the dam.

Despite early warnings of the importance of reservoir passage by migrant fish (Eicher 1970), the issue has remained underreported in the literature (Pelicice *et al.* 2014). Suppressed water currents causing migratory delay can be detrimental for juveniles attempting to reach the ocean within the smolt window (McCormick *et al.* 1998), for adults attempting to reach the spawning grounds for synchronized spawning (Thorstad *et al.* 2008), and for kelts which could aid in population recovery as repeat spawners (Jones 1959).

Migration rates reported for juvenile salmonids traveling through low-flow environments including reservoirs, lakes, and fjords, are variable for both wild (0.01-43.5 km d^{-1}) and CR (0.05-82.1 km d^{-1}) fish (Babin and Linnansaari, in prep[1]). These ranges encompass the migration rates reported for juvenile salmonids traveling through free-flowing reaches (0.2-28 km d^{-1}; Ruggles 1980); therefore, it is important to compare migration rates of the same fish moving through both free-flowing and low-flow reaches within the same river system when quantifying migratory delay. Low-flow water bodies have been reported to cause juvenile salmonids to migrate 33-50 % slower than through free-flowing waters (Raymond 1968; Thorpe and Morgan 1978; Carr 2001; Jones and Flanagan 2007). The Penobscot River in the United States has undergone two dam removals and dam upgrades to compensate for energy losses (Stich *et al.* 2015). Migration rates of Atlantic salmon smolts increased (from 67 to 130 km d^{-1}) in areas where dams were removed and decreased (from 50 to 2 km d^{-1}) in areas where dams had been constructed. Juvenile fish that are delayed in their migration are also at an increased risk of predation due to longer residence, increased water clarity, and increasing water temperatures, compounding the mortality risk already experienced during smoltification (Beamesderfer *et al.* 1990; Jepsen *et al.* 1998; Keefer *et al.* 2012). Marschall *et al.* (2011) modeled Atlantic salmon smolt migration and found that

[1] Babin, A. and Linnansaari, T. In prep. Salmonid migrations through low-flow environments: reservoirs, fjords, and lakes – a review.

migratory delay decreased survival beyond direct mortality from dam passage (86 % vs. 73 %).

Dam passage has been reported to be a greater challenge for upstream-migrating adults than reservoir passage (Keefer *et al.* 2004). However, adults attempting to reach spawning grounds may experience an energetic cost when experiencing migratory delay (Geist *et al.* 2000; Mesa and Magie 2006). Spring Chinook salmon moving 510 km through the Columbia River lost 6-17 % of their muscular energy density, and those that had migratory delays lost a further 5-8 % (Mesa and Magie 2006). Migratory delay may expose adults migrating in the summer to high water temperatures which can increase metabolic demands, taking away energy which would otherwise go toward gonadal development, and potentially lead to pre-spawning mortality (Keefer *et al.* 2004). Along the Columbia River, individuals of multiple salmonid species that were unsuccessful in reaching the spawning grounds had longer delays at nearly every dam, after controlling for water flow and temperature (Caudill *et al.* 2007).

Very few studies were found reporting migration rates of kelts through a low-flow area (see above; Babin and Linnansaari, in prep). Wertheimer and Evans (2005) tracked steelhead kelts through the lower Snake and Columbia Rivers. The largest impounded reach (John Day Reservoir) caused fish to move significantly slower than all other reaches, with migration rates being significantly faster in the free-flowing reaches than the impounded reaches (medians 98.6-110.6 km d^{-1} vs. 9.8-64.0 km d^{-1}).

1.5 Current state of the Outer Bay of Fundy Atlantic salmon population in the Saint John River

Wild Atlantic salmon populations have declined throughout eastern Canadian rivers, leading to the conclusion that there has been a reduction in marine survival regardless of river-specific survival rates (Chaput 2012). Return rates of CR fish have also been declining in the SJR, leading to the same conclusion (Jones *et al.* 2014).

Atlantic salmon returning to the SJR are part of the Outer Bay of Fundy (OBoF) population that was known to encompass 20 rivers, one of which is now extirpated (Jones *et al.* 2014). The OBoF population was recommended for designation as endangered in 2010 due to declines of 57 % of 1SW and 82 % of multi-sea-winter (MSW; 64 % overall) within three generations (Committee on the Status of Endangered Wildlife in Canada 2011); however, the population has not yet been listed with any status under the Species At Risk Act.

Historic catch records provide a general idea of the previous abundance of Atlantic salmon in the SJR. Commercial catches were once nearly 250,000 kg per year, but declined to less than 91,000 kg annually by 1960 (Kidd *et al.* 2011). The number of adults returning to the SJR before the 1960s has been estimated as 18,000-30,000 (Ruggles and Watt 1975). Returning adults commonly exceeded 12,000 wild Atlantic salmon in the late 1970s and early 1980s, reaching 15,000-20,000 when including CR adults (Figure 1.3; Ritter 1992; Jones *et al.* 2014).

The nearby Inner Bay of Fundy (IBoF) population of Atlantic salmon return to rivers that flow into the Bay of Fundy east of the City of Saint John (*e.g.*, Big Salmon

River, Upper Salmon River, Stewiacke River). This population has been considered endangered since 2001 and was listed as endangered under the Species At Risk Act in 2003 (Committee on the Status of Endangered Wildlife in Canada 2011). There is a higher prevalence of 2SW maiden spawners in the OBoF population as compared to the IBoF population (Marshall 2014). However, a higher proportion of CR smolts tend to return as 1SW adults than observed from wild smolts (Ritter 2002). In the SJR, 70-90 % of 1SW fish are male, and 80-95 % of MSW fish are female (O'Connell *et al.* 1997). These proportions are similar in the Miramichi River, with some variation based on river entry timing and destination stream (18-80 % of MSW are female; (Chaput *et al.* 2016). Also, alternate spawning is dominant over consecutive spawning in the SJR (Chaput and Jones 2006).

The Tobique River accounts for approximately 60 % of productive rearing habitat for Atlantic salmon upstream of the MGS (Figure 1.1; Marshall *et al.* 2014). The smoltifying juveniles have a long distance to travel (> 300 rkm), which is thought to be a driver of a relative high proportion (45-81 % in 2007-2012; Jones *et al.* 2014) of the population leaving the Tobique River in October-November as pre-smolts. These juveniles presumably overwinter in the mainstem of the SJR before traveling the remaining distance in the spring as smolts (Buck and Youngson 1982; Jones *et al.* 2004). As well as decreasing the distance needed to travel in the spring, the pre-smolt autumn migration strategy may allow for more favorable downstream overwintering locations and increase the overall number of smolts schooling as they migrate in the spring, potentially reducing predation risk (Riddell and Leggett 1981). Prior to the work

presented herein, the overwinter survival of pre-smolts was unknown (Gibson *et al.* 2009).

The conservation requirement for Atlantic salmon within the SJR is currently set at 2.4 eggs m^{-2} by the Department of Fisheries and Oceans (DFO) that manages the stock (Elson 1957; Gibson and Claytor 2012). In the Tobique River, the most recent estimates are that 1SW and MSW female salmon deposit 326 and 6,445 eggs each, respectively (Jones *et al.* 2014). With 7,856,200 m^2 of available habitat, the reference level to achieve the conservation target is 6,970 1SW and 2,580 MSW females depositing 18.9 M eggs along with the corresponding number of males needed to fertilize the eggs (Jones *et al.* 2014). In 1983, it was found that conservation requirements were not being met in many Atlantic Canadian rivers (Chadwick 1985). The response was strong restrictions, closing the commercial fishery and requiring recreational fishers to release any large salmon (MSW) catches (Chadwick 1985). Reduced fishing pressure was expected to have contributed to an increase in return rates, but the recruitment rate of wild salmon continued to decline by 50 % in the early 1990s (1986-1995; Ritter 2002). No clear reason for the decline in the SJR has emerged, with density dependence, competition with CR salmon, predation, pollution, and genetic changes being ruled out (Ritter 2002). However, it is suspected that raising the reservoir water level by 0.9 m in 1983 may have had major impacts on smolt survival via reservoir and dam passage due to less spill (T. Linnansaari, personal communication).

Since 2000, only 10 % of the conservation target described above has been met, compared to 16 % in the Nashwaak River (2005-2007; Gibson *et al.* 2009). The

Nashwaak River is a tributary of the SJR located approximately 20 rkm downstream of the MGS (Figure 1.1) that does not have any hydropower dams, and therefore returns are compared between Nashwaak and upstream of the MGS to distinguish dam-related impacts. Smolt-to-adult return rates for the Nashwaak River (1.5-6.4 % 1SW, 0.3-1.3 % 2SW) have been experiencing declines despite the lack of hydropower impacts (Chaput and Jones 2006). The return rate of repeat spawners to the Nashwaak River is now less than the 10 % average seen in the 1990s (Jones *et al.* 2014). Repeat spawners returning to the MGS made up 7 % of returns in 1982, but has been less than 3 % since the 1990s (Figure 1.4; Chaput and Jones 2006), with no fish spawning more than three times. In the nearby Miramichi River, which also has not been obstructed by dams, the abundance of repeat spawners has increased since the 1970s to 55 % of MSW returns (O'Connell *et al.* 2006). In the SJR, there was a maximum of 7 year classes observed in the 1970s, and it stablized at 5 year classes through the turn of the century, but is now declining (Chaput and Jones 2006).

The OBoF population is threatened by low population phenomena (*i.e.*, inverse density dependence and Allee effects; Courchamp *et al.* 1999), which may lead to inbreeding depression, schooling sizes that are ineffective for reducing predation risk, and an inability to find mates. Therefore, this population is hypersensitive to additional threats (Clarke *et al.* 2014). It is important to note that dichlorodiphenyltrichloroethane (DDT) was used heavily around the SJR watershed from 1952-1967, which could impact salmon development in many ways including disruptions to smoltification, the olfactory system, and kidney structure, potentially affecting migration and reproductive

success (Clarke *et al.* 2014). Another threat to population recovery is illegal poaching; 58 MSW (12.6 % of MSW returns) were lost to gillnetting in 2010 (Clarke *et al.* 2014). Once salmon reach the ocean, they are further challenged by farmed salmon exposing them to an increased abundance of sea lice, infectious salmon anemia, furunculosis, and bacterial kidney disease (Clarke *et al.* 2014). However, habitat fragmentation is the most debilitating factor within the SJR (Kidd *et al.* 2011; Clarke *et al.* 2014). The MGS is an obstacle in reaching much of the salmon rearing habitat, and affects temperature and flow regimes both up- and downstream (Clarke *et al.* 2014). As the MGS reservoir matures, predator populations are growing, including smallmouth bass, chain pickerel, and muskellunge (*Esox masquinongy*; Ritter 2002; Clarke *et al.* 2014).

The three hydropower generating stations along the migratory pathway from the Tobique River are engineered with upstream fish passage solutions but did not have any engineered downstream fish passage structures at the inception of this research. At the MGS, there is a fishlift that is used to place adults into a truck for use in a TH strategy (Figure 1.5). There is a mechanical hoist for upstream passage at the BGS (Gibson *et al.* 2009), and the TNGS has a 274 m vertical slot passageway with 75 pools (Clarke *et al.* 2014). For downstream passage, smolts and kelts must either travel through the powerhouse via the turbines or use the spillway or diversion sluiceway when available during the spring freshet. As of 2017, a bypass is also available to downstream migrants at the TNGS, but its efficacy is not yet known.

Previous studies have been done to estimate the impact of reservoir and dam passage on Atlantic salmon within the SJR (see Chateauvert *et al.* 2018 for a full

review). Smith (1957) reported that adult Atlantic salmon traveling from the BGS to the TNGS (30 rkm) took 8.6 ± 0.6 d [mean ± SE, based on 356 tagged adults], or 3.5 km d^{-1}. Marshall (1975) Carlin tagged over one thousand wild and CR adults and released them either within the MGS reservoir or in Woodstock (approximately 230 rkm; Figure 1.1). Wild adults outperformed the CR fish with significantly more wild fish moving upstream, and more CR fish falling back over the MGS. Wild 1SW adults took a median of 3.5 weeks to travel from the MGS to the BGS (approximately 5.5 km d^{-1}), and wild MSW took a median of 3.1 weeks (approximately 6.2 km d^{-1}). This follows the understanding that larger fish tend to migrate faster (Zabel 2002). For all fish released in Woodstock, it took a median of 2.7 weeks to reach the BGS (approximately 2.9 km d^{-1}).

Smolts, which typically leave the SJR at age 2 (Jones *et al.* 2014), have also been previously studied. Semple (1971) found that CR smolts migrated 17 km d^{-1}, on average, when released in the Tobique River and recaptured at the BGS. Travel from the BGS to the MGS has been estimated to take 10 days (approximately 13.5 km d^{-1}; Montreal Engineering Company 1980). Using acoustic telemetry, migration rates were found to range from 6.4-33.5 km d^{-1} in free-flowing reaches, and from 1.4-25.2 km d^{-1} in the reservoirs, such that smolts traveled 11 times slower in the MGS reservoir than in the river sections; however, these values are anecdotal since the focus of the study was on the effects of the TNGS, and the residual sample sizes remaining in the MGS reservoir were small (n = 5-7; Carr 1999). Smolts from the Nashwaak have previously been acoustically tagged and found to travel the downriver reach at 12-24 km d^{-1} (Nashwaak Watershed Association Inc. 2004).

Smolt mortality due to dam passage has been estimated to range from 8.0-18.3 % at the TNGS (MacEachern 1960; Jones and Flanagan 2007), and is assumed to be 10 % at both the BGS and the MGS based on turbine runner diameter and tailrace elevation differential, although these estimates have not been confirmed (Washburn and Gillis Associates Ltd. 1995; Chateauvert *et al.* 2018). Cumulatively, smolt mortality due to fish passage above these three barriers has been estimated as 33.8 % (Washburn and Gillis Associates Ltd. 1995). Prior to the work reported herein, dam passage mortality of kelts was unknown (Gibson *et al.* 2009).

Lacroix (2008) examined post-smolt migration within the Bay of Fundy. He found that the migration success of OBoF fish was lower than IBoF fish, with 44-59 % of tagged post-smolts from SJR reaching an array of receivers delineating the Bay of Fundy from the Gulf of Maine. Fish from the SJR were found to have the higher migration rates when traveling through the Bay of Fundy than fish from other rivers (23.4-38.2 km d^{-1} vs. 1-5 km d^{-1}). Smolt-to-adult return rates of OBoF fish were low (3.2 % for the Nashwaak River, 0.45-0.60 % for upstream of the MGS; Lacroix 2008).

A common mitigation strategy to compensate for wild fish loss due to hydropower effects is to supplement salmonid populations with fish artificially raised in hatcheries. To mitigate effects of the MGS, the Mactaquac Biodiversity Facility (MBF) operated by DFO was concurrently built just downstream of the MGS to supplement Atlantic salmon production within the river. At the time, it was the largest Atlantic salmon hatchery in the world (Kidd *et al.* 2011).

Fish stocking has a long history in the SJR, with over 150 million age-0+ fry being widely distributed throughout the river since the 1880s (Clarke *et al.* 2014). Initially, the MBF circumvented the freshwater life stages from spawning to smolt by collecting and spawning wild adults, rearing the eggs, and releasing smolts (Clarke *et al.* 2014). In their natural habitat, egg mortality has been estimated to be 96.2 % in the Tobique River, but at the MBF egg survival was at least 10 % and up to 30 % (Clarke *et al.* 2014). Having a large proportion of artificially spawned eggs survive can remove naturally selected factors that ensure a high fitness of the surviving cohort as they develop (Clarke *et al.* 2014).

The stocking program used 200-500 returning adults that were annually retained as broodstock to produce 500,000 smolts annually to compensate for wild fish losses and reduced CR fitness (Clarke *et al.* 2014). All other wild Atlantic salmon adults returning to the MGS were split into two groups based on their migratory timing for further trap-and-haul upstream of the dam. Returning adults enter the SJR between May-October, and spawn in late October to early November (Clarke *et al.* 2014). The early migrants were thought to be part of the Serpentine River stock that can be distinguished by their dark and deep body, whereas later migrants without these characteristics were considered part of the regular run homing to various other natal streams. The Serpentine River is a tributary in the headwaters of the Tobique River (Figure 1.1), and fish homing to this stream are thought to enter the estuary in November and ascend the river early (May-June) to accommodate their long journey. Adults thought to be from the Serpentine River stock are transported and released near the top of the TNGS reservoir

to bypass the risks of multi-dam and reservoir passage and to shorten their journey, whereas later migrants are released near the town of Woodstock to home to natal streams indistinguishable by managers (Figure 1.1; Clarke *et al.* 2014). As of 2011, the MBF alternates between captive-rearing eggs from Serpentine adults and allowing a free-swim (Clarke *et al.* 2014). With this exception, the adult broodstock program ended in 2004.

Since 2001, the MBF has switched to a strategy circumventing the heightened mortality that occurs during the marine life stage by employing smolt-to-adult supplementation, whereby wild juveniles are captured during the pre-smolt and smolt migrations, reared to maturity at the MBF, and released either just downstream of the Tobique River or upstream of the MGS reservoir (230 rkm) as adults to spawn naturally (Clarke *et al.* 2014). Juvenile pre-smolts and smolts (1,000-3,000 annually) are collected from the Tobique River or the BGS gatewells, and the smolt-to-adult supplementation releases have ranged from 387 to 1,450 adults (Jones *et al*. 2014). Allowing adults to employ natural mate selection is thought to increase fitness (Neff *et al.* 2011).

Gibson *et al.* (2009) highlighted that recovery actions must be undertaken on fish production, fish passage, and marine survival if the population of fish returning to the Tobique River is to recover. Based on their models, it would not be enough to improve one aspect alone, but rather at least two issues need to be improved to see population-level effects. Increasing fish passage survival to 100 % would not be sufficient to create a viable population on its own, and doubling fish production was not enough to offset the combined effects of high passage mortality and low marine survival.

1.6 Synthesis, objectives, and chapter overview

The evaluation of the future options for MGS provides an opportunity to study hydropower impacts on the SJR ecosystem. Through the MAES, multiple projects were undertaken to address the SJR ecosystem as a whole, and to provide recommendations on improving fish passage while managing environmental flows. The endangered OBoF Atlantic salmon that return to the SJR must pass multiple dams and reservoirs in order to complete their lifecycle. Three of the four options under consideration by NBP, Option 1) Repower with new constructions, Option 2) Retention of reservoir, and Option 4) Lifetime Achievement (Figures 1.2 A, B, and D), would all require reservoir and dam passage solutions. The selection of Option 4) Lifetime Achievement will retain the existing structures, including the reservoir, for the next multi-decadal period. Therefore, research on the migratory lifestages of Atlantic salmon was necessary to understand the current state of migrations through the SJR and the MGS reservoir, and to try and find solutions to improve migration success to aid population recovery.

The overarching question of my dissertation was:

Does the MGS reservoir present a problem for Atlantic salmon migration?

This overarching question was broken down into two principal objectives, to:

(1) Quantify migration success, rates, and delay of downstream (smolts and kelts) and upstream (adults) migrants as they navigated through the SJR and the MGS reservoir, and to

(2) Relate smolt, kelt, and adult movements to hydrodynamic conditions that are impacted by MGS operations.

The null hypotheses for the purpose of statistical testing were:

(1) Migration rates would not be significantly different between reaches (upriver, reservoir, downriver) for any lifestage; therefore, there would be no relative delay or impact on migration success from delayed migrations

(2) Movements by all lifestages would be unaffected by hydrodynamic conditions

My predictions were:

(1) Migration rates observed for each individual salmon would be slower within the reservoir than up- or downriver, leading to migratory delay and reduced migration success

(2) Movements of individual salmon between receiver(s) would positively correlate with surface water velocity and angle in relation to the direction of migration.

These questions were examined using acoustic telemetry and therefore the range of detection in the environment was a crucial first step in my studies. Range testing of the receiver and tag types used in these studies was performed at two sites within the SJR (Chapter 2). I report the detection ranges of this equipment at an upriver site, and at a site near the MGS where the hydropower facility has potential to impact detection efficiency.

My doctoral research addresses all migratory lifestages of Atlantic salmon within the SJR. The thesis is structured to address each lifestage separately, starting with downstream migrants (pre-smolts, smolts, and post-spawned adults), then upstream migrants (adults). Chapter 3 addresses downstream migrating smolts over four tagging seasons (2014 spring smolts, 2014 autumn pre-smolts, 2015 autumn pre-smolts, and 2016 spring smolts). A case study was performed on downstream fish passage solutions

under consideration at the TNGS. Chapter 4 compares the migratory survival of 100 tagged autumn pre-smolts (2015), half of which were released just downstream of the TNGS to represent a free-swim through a bypass, and the other half were released just downstream of the MGS to represent a trap-and-haul strategy that would avoid cumulative mortality due to multiple reservoir and dam passages. The migration rates of these fish were reported in the larger smolt study (Chapter 3).

Chapter 5 examines post-spawned adults or kelts over two tagging seasons (2014 and 2015). This lifestage is especially important; if they are able to survive spawning and reach the ocean to recondition and potentially spawn in future years, then they will increase egg deposition and genetic diversity. The iteroparous nature of Atlantic salmon should be highlighted to hydropower managers so that kelts are properly valued for their ability to aid population recovery.

Chapter 6 examines upstream migrating adults over three tagging seasons (2014, 2015, 2016). Adult salmon do not need free-flowing water as a transport mechanism like smolts are thought to, but they do use water currents as a directional cue and can therefore also experience migratory delay in low-flow water bodies.

Chapter 7 discusses the results found within each of the data chapters (2-6) in order to answer the overarching question of whether the MGS reservoir presents a problem for Atlantic salmon migration. Recommendations to NBP that may improve reservoir and dam passage of Atlantic salmon during their encounters with the MGS are given.

These works are presented in a journal article format for submission to peer-reviewed scientific journals. Each of these chapters contains introductory information

obtained from literature reviews and specific objectives respective to each topic that are fit into the context of this thesis. These works were conducted in collaboration with multiple researchers from other university departments and government institutions. The contributions of the authors are described in Appendix 1.

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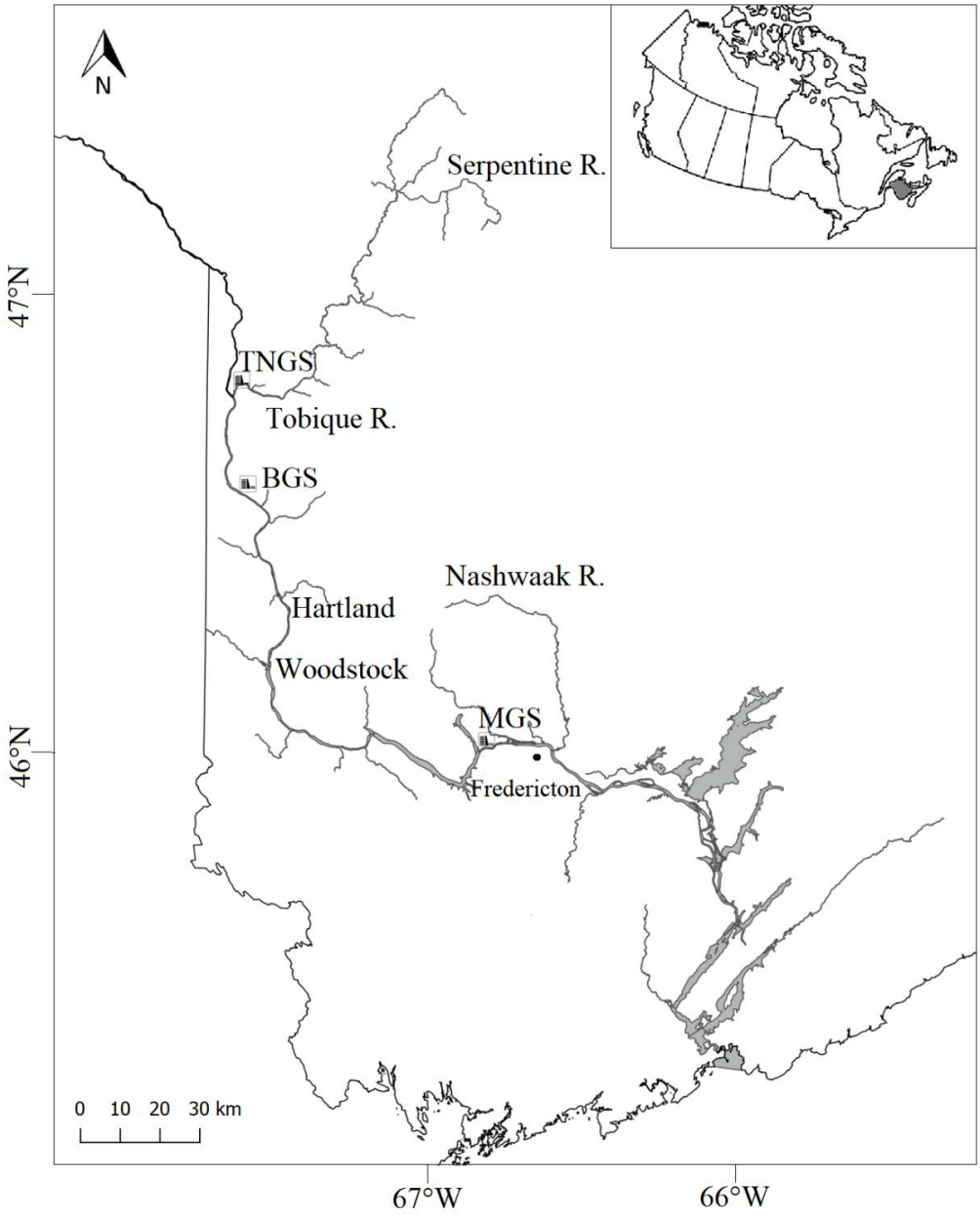

Figure 1.1. A map of the Saint John River in New Brunswick, Canada, showing the major tributaries including the Tobique, Serpentine, and Nashwaak Rivers, as well as the three hydropower generation stations (GS) along the main migratory route of Atlantic salmon (TNGS Tobique-Narrows, BGS Beechwood, MGS Mactaquac), in relation to the provincial capital of Fredericton.

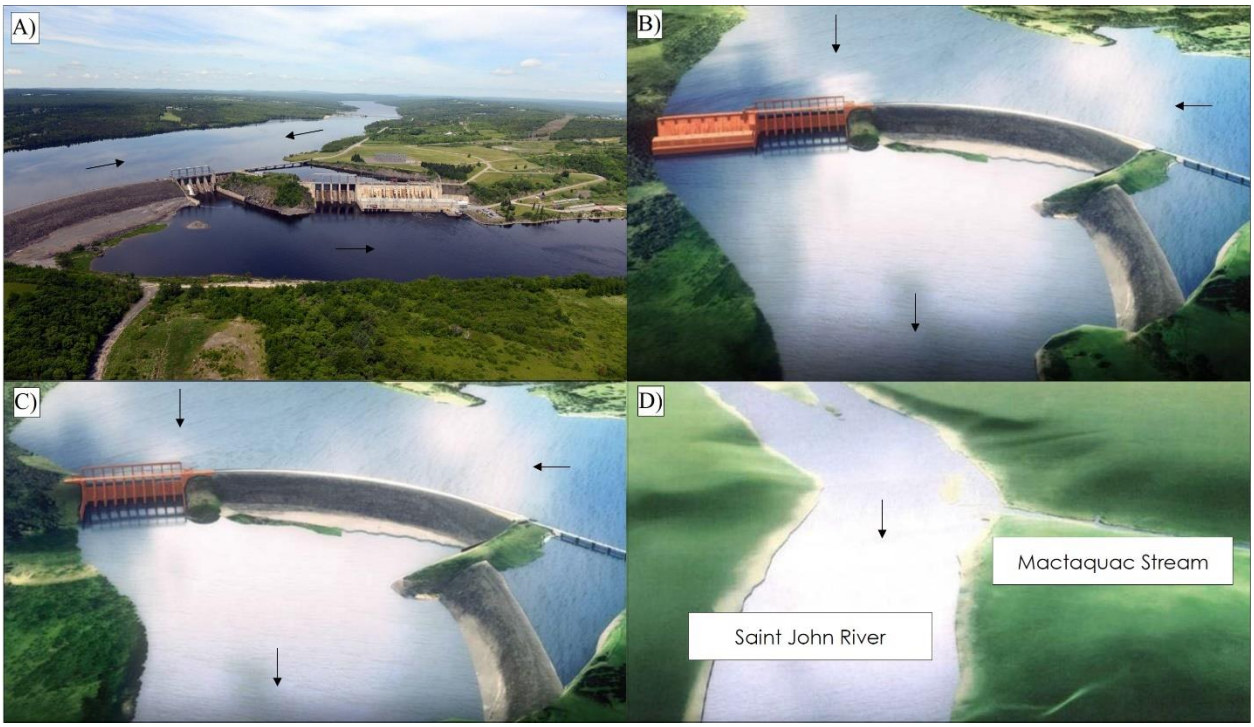

Figure 1.2. A) The Mactaquac Generating Station in the Saint John River, New Brunswick, Canada (Photo Credit: Canadian Rivers Institute/NBP), and conceptual renderings of B) Option 1 – Repower, C) Option 2 – Retention, and D) Option 3 – Restoration (Stantec Consulting Ltd. 2015). Arrows represent the direction of water flow.

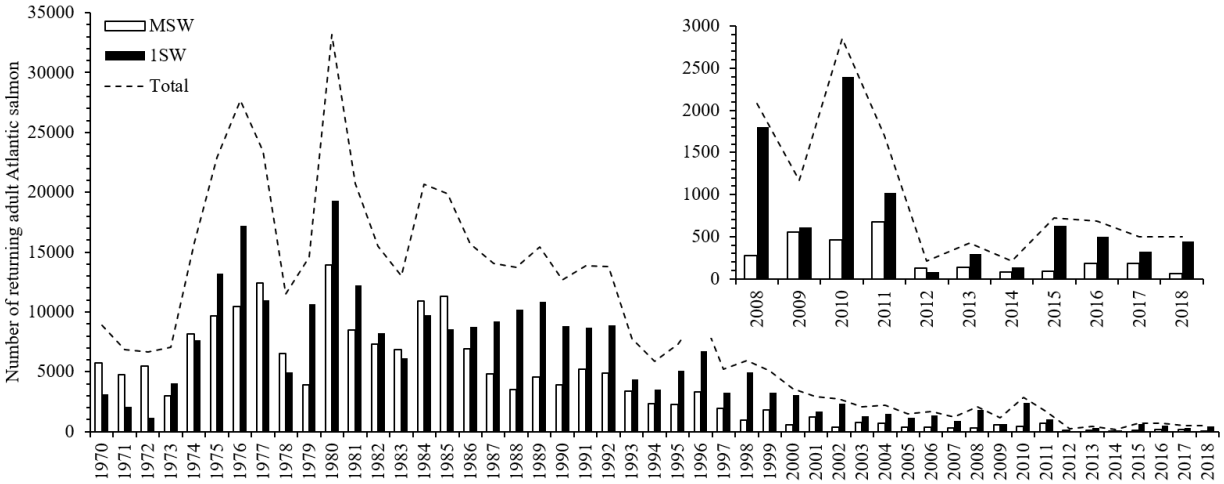

Figure 1.3. Number of wild and captive-reared adult Atlantic salmon (1SW = 1-sea-winter, MSW = multi-sea-winter) returning to the Mactaquac Generating Station since 1970, with a subset of the last decade (2008-2018). Data come from Jones *et al.* (2014) and from the Department of Fisheries and Oceans (https://inter-j01.dfo-mpo.gc.ca/asir/home).

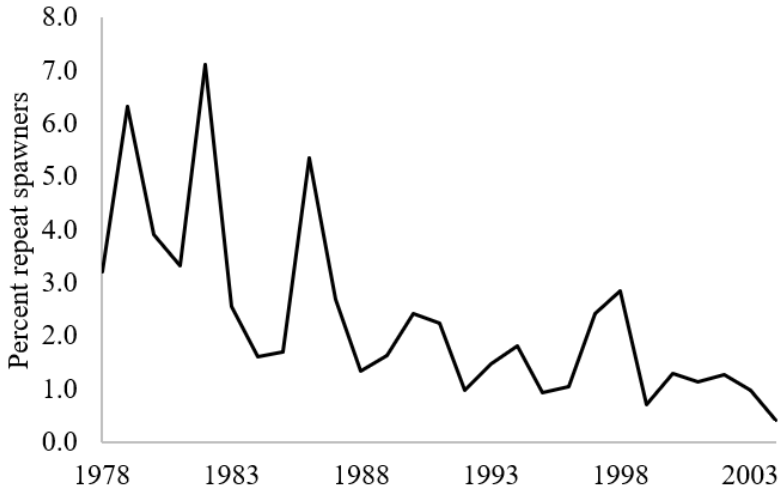

Figure 1.4. Percent of wild and captive-reared repeat spawner adult Atlantic salmon returning to the Mactaquac Generation Station, 1978-2004. Data from Chaput and Jones (2006).

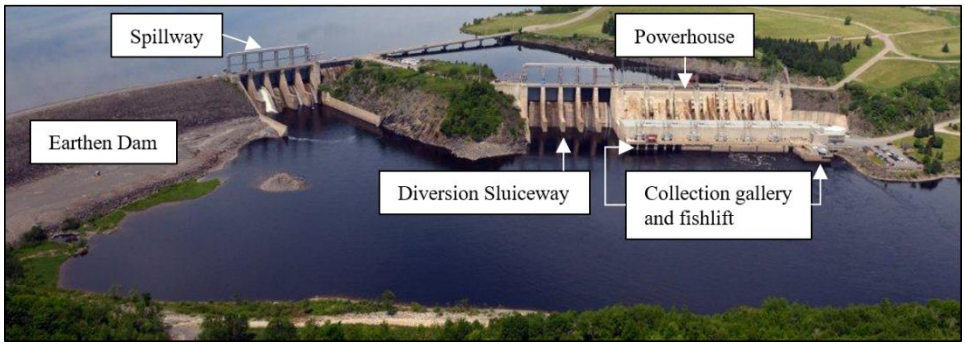

Figure 1.5. Mactaquac Generating Station fish passage structures: fish collection facilities, spillway, diversion sluiceway, earthern dam, and powerhouse. Photo credit: Canadian Rivers Institute/NBP.

Chapter 2

Detection efficiency of acoustic receivers in a large hydropower reservoir

Amanda Babin*

Canadian Rivers Institute, Department of Biology, University of New Brunswick, Fredericton, New Brunswick, Canada, E3B 5A3

Lauren Fitzpatrick

Canadian Rivers Institute, Department of Biology, University of New Brunswick, Fredericton, New Brunswick, Canada, E3B 5A3

Current address: The Michener Institute, 222 St. Patrick Street, Toronto, Ontario, M5T 1V4, 16LF1@michener.ca

Tommi Linnansaari and R. Allen Curry

Canadian Rivers Institute, Department of Biology and Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, New Brunswick, Canada, E3B 5A3

*Corresponding author: amanda@babin-labs.com

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2.1 Abstract

Acoustic telemetry manufacturers report estimated detection ranges under idealized conditions, but environmental conditions such as water depth, substrate type, and turbulence can affect the range of reliable detection. Range testing of low (Vemco V7 136 dB re 1µPa@1m) and high power (V13 147 dB re 1µPa@1m) acoustic transmitters was performed near a hydropower generating station and its associated reservoir using both active (VR100) and passive (VR2W/VR2Tx) receivers. Detection ranges of the low power tags were within 246-351 ± 20-70 m (mean ± SE), and the high power tags were within 537-1106 ± 53-272 m. These ranges often fell within the range of expected values given by the manufacturer for the passive receiver (typically within 40 m) but differed from those expected for the active receiver (typically by 700-800 m). There was evidence of a hydropower effect on detection probability (up to 95 % reduction) of both tag types for the active receiver. Passive receivers were further tested by mooring a fixed sentinel tag (low power) on a receiver line at the hydropower site for 50 days. The sentinel tag detection range of 212 m was less than the expected range of 280-292 m. The results of this study give insight to the initial design of acoustic telemetry studies beyond what can be gathered from manufacturers estimates, but rather nearby hydropower facilities and within large reservoirs; however, detection ranges reported herein do not replace the importance of range testing in site-specific conditions.

2.2 Introduction

Acoustic telemetry is a widely used method for tracking aquatic animals, particularly fish (Heupel et al. 2006; Pincock and Johnston 2012). Detection range between transmitters (henceforth tags) and receivers is dependent on the technical characteristics of the equipment and environmental conditions (Gjelland and Hedger 2013; Kessel et al. 2014). Manufacturers of acoustic telemetry equipment can only provide generalized, estimated detection ranges for 'typical ocean conditions' because of the variability of equipment and environmental factors inherent within each study. At any site, a general understanding of the expected detection ranges is fundamental for ensuring feasibility (*i.e.*, can a fish be tracked effectively), and to determine cost effectiveness (*i.e.*, how many receivers and in what configuration are required to ensure a reasonable detection efficiency). Therefore, site-specific range testing of the equipment in use should be a crucial part of telemetry study design (Gjelland and Hedger 2013; Kessel et al. 2014).

Acoustic environments are influenced by water depth and salinity, substrate types, and surface conditions (*e.g.*, fetch), as well as anthropogenic influences such increases in ambient noise near hydropower dams. Detection efficiency is expected to be lower where salinity levels are high due to increased absorption rates of the acoustic signal (Medwin and Clay 1998; Pincock and Johnston 2012). Environments with substantial wave action that causes air entrapment can increase sound absorption and acoustic signal scattering (Medwin and Clay 1998; Gjelland and Hedger 2013). Deep waters allow an acoustic signal to travel unimpeded through spherical spreading rather than encountering the surface or bottom, at which point the acoustic signal would spread

cylindrically causing it to weaken. Shallow waters where the acoustic signal reaches the bottom could have vegetation that causes attenuation, or substrate types that could dissipate (soft substrates) or reflect/scatter (hard substrates) the signal (Medwin and Clay 1998; Gjelland and Hedger 2013). Anthropogenic activities such as watercraft can also reduce the signal-to-noise ratio.

A specific case in which anthropogenically caused underwater noise may be increased is around hydropower generating stations. Noise is created by water flow through turbines and spillways, as well as by cavitation (How and de Lestang 2012; Pincock and Johnston 2012). Acoustic signals can also be distorted and reflected off concrete and rock structures of dams causing multipath signals (Adams et al 2012; Kessel et al. 2015). While acoustic telemetry is commonly used to examine fish movements close to hydropower facilities (*e.g.*, Coutant and Whitney 2000; Thorstad et al. 2012), specific studies documenting the effects of these facilities on the acoustic environment and subsequent potential effects on acoustic signal detection are not common, and none were considered in a recent detection range testing literature review (Kessel et al. 2014).

Beyond the environmental conditions impacting detection ranges, the type of acoustic telemetry equipment used also impacts the reliability of detecting an acoustic signal. The tags and receivers selected for use in a study depend upon species-specific criteria for tag type and size and behavior to be examined, as well as the environment in which the tags and receivers will be deployed (Adams et al. 2012). Low power tags are smaller, have a relatively short battery life, and are commonly used to tag small fish such as juvenile Atlantic salmon (*Salmo salar*; smolts), whereas high power tags can

accommodate more and/or larger batteries, and are often used to tag large fish. These tag types differ in size to accommodate their respective acoustic transducers, electronics, and batteries. High power tags output an acoustic signal which propagates further underwater than low power tags. Passive and active receiver types vary in tag detection sensitivities. Active receivers generally have a higher sensitivity than passive receivers, especially when using a directional rather than an omnidirectional hydrophone; therefore, active receivers should be able to detect a given tag at a greater distance than passive receivers. Passive receivers are typically moored at a fixed location for extended periods of time because they have internal memory that stores telemetry data including tag identification and datetime stamps. Active receivers are mobile and are used for short periods of time to detect tagged individuals as they move along. Active tracking involves the transport of the receiver and associated hydrophone, most typically using a boat, and is therefore used under more benign environmental conditions that allow for safe operation of such equipment.

The equipment used in this study was chosen based on the applicability of the range testing results to concurrent studies being conducted on Atlantic salmon within a large hydropower reservoir. Both juvenile (smolts) and adults are being tracked with acoustic technology provided by Vemco (Amirix, Bedford, NS). We used low power tags for smolts and high power tags for adults. Here, we report on the detection range of low and high power acoustic tags by passive and active receivers at a site close to a hydropower generating station, and a site upstream away from potential generating station noise but still within a large reservoir. It was hypothesized that: 1) detection ranges for both tag and receiver types would approximate the estimated detection ranges

provided by the manufacturer; 2) detection ranges would be greater for the active than the passive receiver due to the higher sensitivity of the hydrophone; 3) detection ranges would be greater for the high power than the low power tag; 4) detection ranges would decrease with increasing wind speed (due to wave noise); and 5) the hydropower site would have lower detection ranges in comparison to the reservoir site due to higher background underwater noise levels and/or acoustic scattering off reflective surfaces.

2.3 Materials and Methods

Study sites.—

The study took place within the Mactaquac Reservoir created by the Mactaquac Generating Station (MGS) in the Saint John River (SJR), New Brunswick, Canada (Figure 2.1). There were two study sites: a hydropower site (45.94815°N 66.87314°W) near the MGS, and a reservoir site (46.00461°N 67.50419°W) 64 river km (rkm) upstream of the MGS (Figure 2.1). The river channel at the hydropower site was approximately 750 m wide and 30-40 m deep (max 51 m) with soft mud and silt substrates. The maximum fetch was approximately 9 rkm (river kilometers following the meandering channel). Boat traffic was variable and sometimes heavy (10-100 boats per day). The channel at the upstream reservoir site was approximately 300 m wide and 20 m deep with cobble substrate. Trees on shore provided some shelter from wind, which, along with river bends, brought the maximum fetch down to 4 rkm. Boating activity during the range testing trials was rare (1-5 boats per day).

Detection range testing.—

Equipment used in this study was developed and manufactured by Vemco, a division of Amirix (Bedford, Nova Scotia, Canada; https://www.vemco.com/). Range testing tags were the same size and power as the tags used in our tracking studies but had a cap as an attachment point. The low power range testing tag was the V7-4L, being 7 mm in diameter and emitting an acoustic signal (69 kHz, 136 dB re 1µPa@1m) every 10 s. The low power sentinel tag was the same model but transmitted an acoustic signal every 10 min. The high power range testing tag was the V13-1L, being 13 mm diameter and emitting an acoustic signal (69 kHz, 147 dB re 1µPa@1m) every 10 s. The active receiver was the VR100 with a VH165 omnidirectional hydrophone, and the passive receivers were the VR2W and VR2Tx. New batteries were installed before all range testing.

Range testing trials were performed in replicate. They consisted of mooring one of the test tags (either low or high power) in a fixed position 5 m below the surface, placing the passive receiver on one side of an aluminum boat at 10 m depth and the hydrophone of the active receiver on the other side at 10 m depth, and then travelling away from the tag site always along the same transect, stopping to listen every 50 m for 180 s; an example transect at the hydropower site is shown in Figure 2.1. Since the range testing tags transmitted every 10 s, each listening station could theoretically produce 18 detections, which was thus considered as 100 % detection probability. Because the active receiver should theoretically detect the tag from a greater distance than the passive receiver, the transect was followed until the active receiver did not detect any transmissions for two consecutive listening stations. Testing took place at

both sites between 21 July and 18 August 2015 for a total of 26 trials (n = 7 for low power/hydropower, n = 5 for low power/reservoir, n = 8 for high power/hydropower, n = 6 for high power/reservoir).

A longer-term range test was performed at the hydropower site to quantify variability in detection probability of a line of three VR2W passive receivers over 50 days coinciding with the Atlantic salmon smolt run (7 May – 27 June 2015). A low power sentinel tag was moored 6 m below the surface (approximating the position of surface-oriented Atlantic salmon smolts; Fried et al. 1978) and 13 m above a passive receiver on the same mooring line in the river left (RL) position (Figure 2.1). Two additional passive receivers were placed at a horizontal distance of 266 m (middle; M) and 519 m (river right; RR) across the channel (Figure 2.1). The three receivers created a line or gate for detection of smolts passing this location to be tested.

Environmental conditions including depth and substrate type were assessed by the MAES team. Wind speeds were recorded hourly by a nearby meteorological station (45.95919°N 66.84217°W). The average wind speed was calculated for the duration of each trial, and wind speeds were averaged both in 3 and 24 h blocks during the longer-term range test. The presence or absence of boats was also noted during each trial.

Statistical analyses.—

Detection range was defined as the range at which the acoustic signal was detected in 50 % of the possible occurrences (9/18 transmissions detected). This definition is consistent with the manufacturer and other studies (How and de Lestang 2012; Kessel et al. 2014).

For each range testing trial, detection probability was plotted against distance and a logistic curve was fitted to the data. The detection range for that trial was then inferred as the 50 % detection probability on the logistic curve. Idealized logistic curves were also created based on the manufacturers estimates of detection range for each tag-receiver pair. To quantify the difference between observed and expected detection ranges for each tag-receiver pair, median ± SE data from replicate trials were plotted against the expected logistic curve and differences were calculated. Detection ranges for each tag type were compared using two-way ANOVAs of receiver type and site.

Vemco Range Test preliminary software (v 1.9.22.0, Amirix Systems Inc. 2014) was used to analyze the longer-term dataset. Data from each of the passive receivers (Figure 2.1) were partitioned into 3-hour blocks such that each would have 18 potential detections (180 minutes; 10 min transmission interval; n = 420 probability assessment intervals). The effect of wind speed on detection probability (arcsine-squareroot transformed) was visualized through linear regressions.

Analyses were done in R (Version 0.99.878 – © 2009-2016 RStudio, Inc. Packages car, nls2). Normality plots were analyzed for each statistical test, and statistical significance was assumed when *P* was less than or equal to 0.05.

2.4 Results

Range testing trials

Detection ranges and environmental conditions for each tag trial are shown in Table 2.1.

At an average wind speed of 2.7 m/s, the manufacturer estimates a detection range for the low power tag of 280-292 m for the passive receiver, and 1065 m for the active receiver. This study estimated comparable detection ranges for the passive receiver at the hydropower site (mean ± SE; 307 ± 51 m) and slightly lower ranges at the reservoir site (246 ± 48 m), whereas they were much lower for the active receiver (hydropower 232 ± 20 m, reservoir 351 ± 70 m; Figure 2.2). At the same average wind speed, the manufacturer estimates the high power tag would have detection ranges of 522-539 m for the passive receiver, and 1432 m for the active receiver. Current range testing provided comparable or higher estimates for the passive receiver (hydropower 537 ± 53 m, reservoir 897 ± 227 m), and lower estimates for the active receiver (hydropower 677 ± 99 m, reservoir 1106 ± 272 m; Figure 2.3).

Detection ranges did not differ between receiver types for either tag type (two-way ANOVAs, low power $F_{1,20} = 0.00$, $P = 0.99$, high power $F_{1,24} = 1.23$, $P = 0.28$; Figures 2.2 and 2.3), but average detection ranges were higher for the active receiver than the passive receiver in all cases except the low power tag at the hydropower site. As was expected, detection ranges were consistently higher for the high power tag than the low power tag (Figures 2.2 vs. 2.3).

Detection ranges were not significantly different between hydropower and reservoir sites for the low power tag (two-way ANOVA, $F_{1,20} = 0.36$, $P = 0.56$; Figures 2.2 and 2.3), and were significantly different for the high power tag (two-way ANOVA, $F_{1,24} = 6.60$, $P = 0.02$), with ranges generally being lower near the hydropower facility. Observed detection probabilities of replicate trials for each tag and receiver type at the hydropower site were compared with expected values to estimate the effect of the

hydropower facility on ambient noise levels and/or reflective surfaces potentially decreasing detection efficiencies (Figure 2.4). Differences between expected and observed detection probabilities were calculated for the area of the MGS to estimate a 'hydropower effect', noting that differences in detection probabilities due to other environmental factors would be included in these values. Trials at the hydropower site showed consistently drastic and unexpected reductions in detection probabilities coinciding with the concrete structures, such as the diversion sluiceway (DS) of the MGS between 500-700 m (Figures 2.1 and 2.4). Notable also was the subsequent and fairly large increase in detection probability from near zero percent to > 60 % in the 750-1000 m distance along the transect (Figure 2.4). Differences between expected and observed detection probabilities within the area of the hydropower facility were greatest for the active receiver detecting the low power tag (Figure 2.4; median reduction of 95 %), followed by the active receiver detecting the high power tag (Figure 2.4; median 65 %). For the passive receiver detecting the low power tag (Figure 2.4), expected values reached zero detection probability before the hydropower facility situated at 500 m along the transect, thus a hydropower effect was not calculated. The passive receiver detecting the high power tag had expected values greater than observed values between 500-700 m (Figure 2.4; median 8 %), beyond which observed values drastically exceeded expected values.

Longer-term range test

Detection probabilities were greater than 50 % at all times for the receiver 13 m away from the tag (RL; mean ± SE, 79 ± 0.5 %), whereas reliable detection only occurred 43 ± 2 % and 17 ± 2 % of the time for the receivers 266 m (M) and 519 m

(RR) away from the tag, respectively (Figure 2.5). The overall detection range was determined as 212 m, meaning there was 37 % and 31 % overlap between the RL-M and M-RR receivers, respectively (Figure 2.1).

The relationships between average wind speeds and detection probabilities (by 3-hour blocks) for each receiver were weak, with wind speed having no effect on the arcsine-squareroot transformed detection probability of the closest receiver (RL slope = 0.23, $r^2 < 0.001$; Figures 2.1 and 2.6), and progressively more negative although weak relationships with receiver distance (M slope = -2.32, $r^2 = 0.01$; RR slope = -4.72, $r^2 = 0.05$; Figures 2.1 and 2.6). However, there were examples of high detection probabilities by the M and RR receivers being associated with lower average wind speeds (50.9-60.7 %, 0.56 – 0.99 m/s), and low detection probabilities being associated with higher average wind speeds (0.7-21.6 %, 1.71 – 2.81 m/s).

2.5 Discussion

Range testing within a hydropower reservoir established that detection ranges often differed from manufacturer's estimates, generally with detection ranges being higher than expected for the passive receiver, and lower than expected for the active receiver. Deviations from expected detection ranges have been observed in other studies. For example, detection ranges of only 88-111 m for the low power tag and 65 m for the high power tag have been documented in oceanic conditions (How and de Lestang 2012; Pincock and Johnston 2012). Such drastic differences in detection range due to environmental conditions exemplify why site- and equipment-specific range testing is critical for successful study design.

The long-term range test allowed for the quantification of detection range while taking variability of environmental conditions into account. Importantly, this test was performed during the time when tagged Atlantic salmon smolts would be out-migrating. Tagged Atlantic salmon smolts tracked in a concurrent study (transmitting every 60 s on average) took a minimum of 188 s to move through the reliable detection space (212 m) around the receiver line at the hydropower site, and therefore, at least three transmissions were available for detection when receivers were placed using the design in this study, with no undetectable area within a triple receiver line (A. Babin, University of New Brunswick, unpublished data). The number and placement of receivers at any site must be balanced between effectiveness and cost. Using a 50 % threshold for reliable detection allows for optimizing of receiver spacing whereby detection efficiency can be balanced with the number of receivers in the area to minimize financial cost while ensuring reliable data collection. However, researchers should consider the role of their specific study objectives in assessing the optimal orientation of their receiver placement.

Wind speeds encountered during the range testing trials did not reach those recorded during the longer-term range test (maximum 2.7 versus 6.2 m/s). High wind speeds during the long-term test generally coincided with decreased detection ranges, especially as distance between the tag and the receiver increased, although the relationships were weak. Wind speeds high enough to affect detection reliability would probably not be encountered during active tracking in a small boat since the wind speeds would limit safe travel on the water prior to affecting detection probabilities.

Detection ranges significantly differed between sites for the high power tag only, with ranges being generally lower near the hydropower facility than at the reservoir site. This could be partially attributable to the difference in substrate types, where the soft mud and silt bottom at the hydropower site could have attenuated some of the acoustic signals, whereas the cobble bottom at the reservoir site may have propagated the acoustic signal. Overall, the detection probability patterns in the vicinity of the hydropower generating station indicate that decreased detection probabilities were substantial (8-95 %). Reduced detection probabilities have been attributed to increased ambient noise levels caused by discharge flows and cavitation (How and de Lestang 2012; Pincock and Johnston 2012). In the case of the current study, the area in which detection probabilities indicated an abrupt decrease was associated with a diversion sluiceway (DS); however, it is important to note that the DS and spillway (SW) gates were closed during the range testing trials. Therefore, the relationship between the reduction in detection probability and association with the DS could be attributable to acoustic scattering off reflective surfaces rather than increases in ambient noise levels. It was similarly surprising that detection probabilities increased after the significant reduction. Particularly for the passive receiver detecting both tag types, the detection range often exceeded 50 % beyond the distance at which zero-detection probability would have been expected. This surprising result may also be attributable to the presence of the hydropower facility allowing the signal to reflect off of hard surfaces and propagate the signal further than would be expected. These patterns of detection probability in the vicinity of a hydropower generating station lead the authors to recommend that telemetry studies test the detection probabilities under various

(hydropower) operating conditions, as well as different environmental conditions and locations, or that they design their receiver deployments to have greater acoustic space overlap near hydropower dams as a precaution to ensure signals will be reliably detected.

In conclusion, 1) detection ranges were generally lower in both studied sites within the large hydropower reservoir than the expected detection ranges estimated by the manufacturer, especially for the active receiver; 2) detection ranges were generally greater for the active receiver than the passive receiver; 3) detection ranges were greater for the high power tag than the low power tag; 4) detection probabilities were decreased when wind speeds reached 6 m/s, and 5) the hydropower site had generally lower detection ranges in comparison to the reservoir site, with an estimated 8-95 % decrease in detection probability at least partially attributable to the presence of a hydropower facility.

The results of this study will inform the design of telemetry studies performed in hydropower and reservoir settings, although site-specific range testing is recommended. Researchers should carefully consider the conditions of their site, especially in relation to hydropower facilities which could have higher ambient underwater noise and concrete structures causing multipath signals. Range testing should include all tag and receiver types to be used, being careful not to assume that the power output from one tag could represent the power output from another tag type, or only use an active receiver which has a greater sensitivity than passive receivers. Also, range testing should be conducted in a way that captures variability in environmental conditions as well as

during times of the year which are relevant for the species and life-stage which will be tracked.

2.6 Acknowledgements

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Table 2.1. Range testing trials, prevailing environmental conditions and detection range (m) of low power (V7) and high power (V13) tags detected by passive and active receivers at hydropower and reservoir sites as inferred by logistic regression.

Tag-trial	Site	Date (2015)	Boats present	Average wind speed (m/s)/ direction (°)	Detection Range (m) Passive receiver	Active receiver
V7-1	Hydropower	21 July	No	0.96/162.5	318	140
V7-2	Hydropower	24 July	No	1.06/98.1	451	295
V7-3	Hydropower	29 July	Yes	0.66/303.09	67	193
V7-4	Hydropower	10 August	Yes	0.36/292.37	297	248
V7-5	Hydropower	10 August	Yes	0.28/292.88	368	272
V7-6	Reservoir	11 August	Yes	0.45/191.20	159	99
V7-7	Reservoir	11 August	No	0.70/221.40	200	403
V7-8	Reservoir	12 August	No	0.24/294.00	374	493
V7-9	Hydropower	13 August	No	0.42/287.31	440	246
V7-10	Hydropower	13 August	No	0.39/276.00	216	229
V7-11	Reservoir	17 August	Yes	0.68/272.70	351	451
V7-12	Reservoir	18 August	No	0.73/343.88	149	307
V13-1	Hydropower	21 July	Yes	0.98/218.70	584	643
V13-2	Hydropower	24 July	No	0.71/32.30	451	1030
V13-3	Hydropower	24 July	Yes	0.96/91.60	731	635
V13-4	Hydropower	29 July	Yes	0.15/339.45	383	330
V13-5	Reservoir	7 August	Yes	0.39/244.60	1412	1369
V13-6	Reservoir	11 August	No	0.82/154.10	1003	1330
V13-7	Reservoir	12 August	No	0.84/244.60	1678	2222
V13-8	Hydropower	13 August	No	0.44/261.20	457	569
V13-9	Hydropower	13 August	No	0.39/233.90	615	855
V13-10	Reservoir	17 August	No	0.36/39.10	456	554
V13-11	Reservoir	17 August	No	0.31/359.52	406	596
V13-12	Reservoir	18 August	Yes	0.35/265.20	440	567
V13-13	Hydropower	27 August	Yes	0.17/231.20	487	529
V13-14	Hydropower	27 August	No	0.11/167.20	441	747

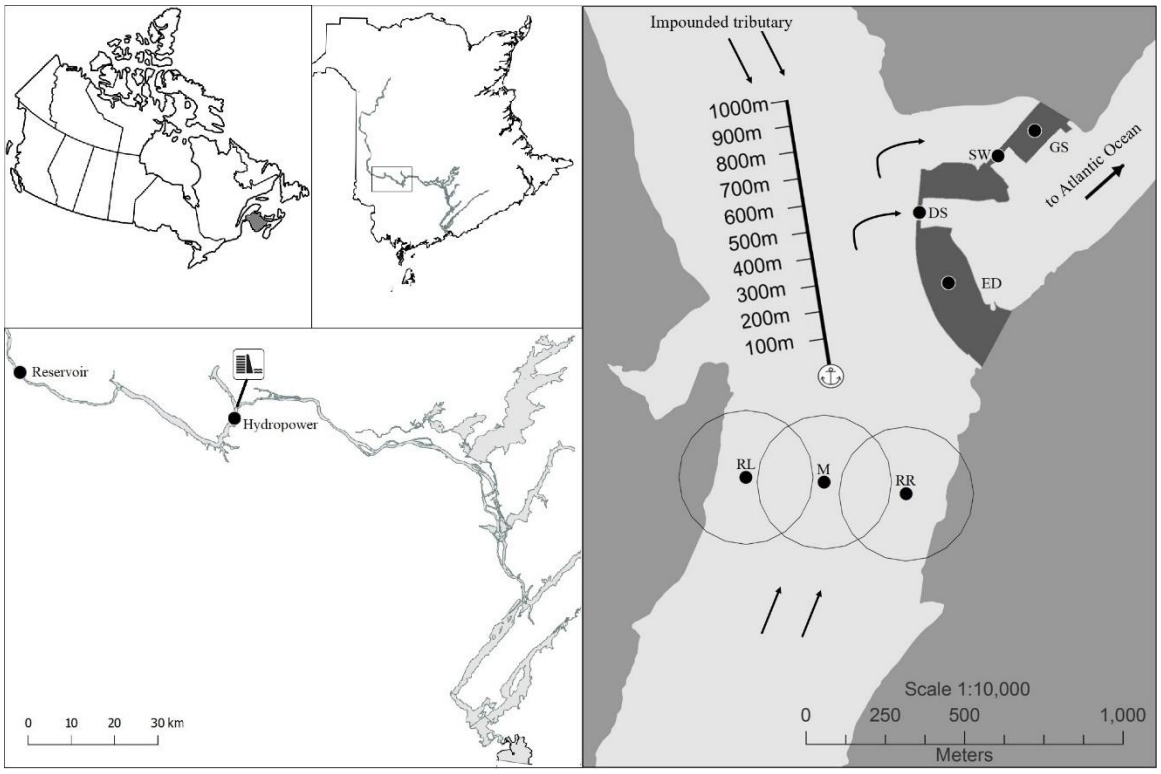

Figure 2.1. Location of hydropower and reservoir sites in the Mactaquac Reservoir, Saint John River, New Brunswick, with a generalized range testing transect along which receivers detected anchored range testing tags (indicated by an anchor symbol) in relation to the hydropower facility (GS = Generating Station; SW = Spillway; DS = Diversion Sluiceway; ED = Earthen Dam). Arrows indicate direction of water flow. Also shown is a passive receiver line (river left RL with low power sentinel tag, middle M, river right RR) showing detection range (212 m) estimated by a long-term range test.

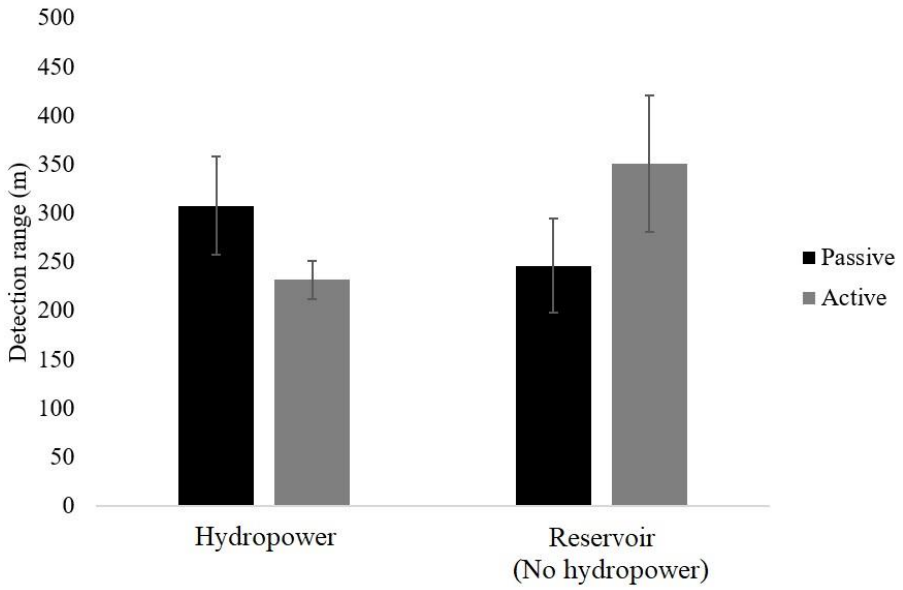

Figure 2.2. Average detection range (m) ± SE for a low power tag being detected by passive and active receivers at hydropower and reservoir sites.

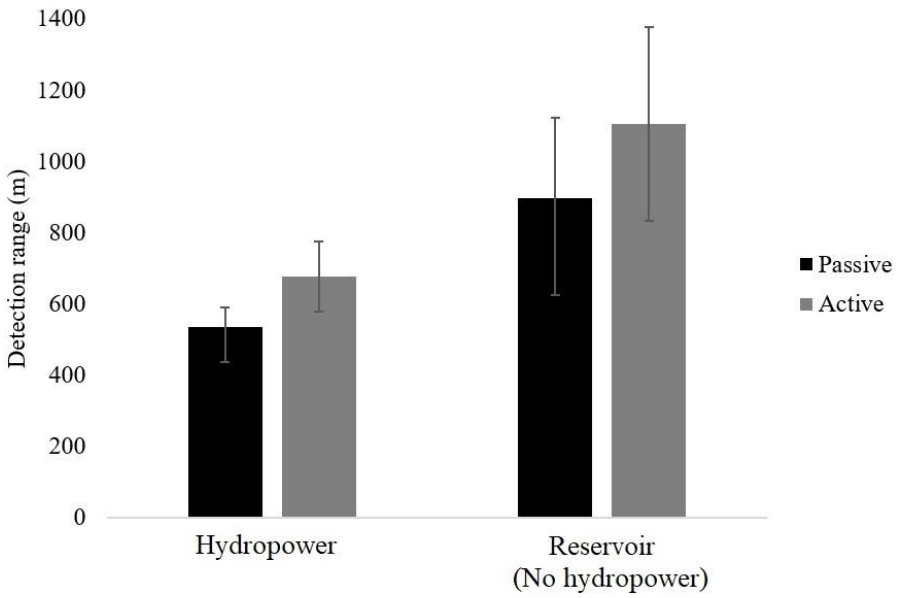

Figure 2.3. Average detection range (m) ± SE for a high power tag being detected by passive and active receivers at hydropower and reservoir sites.

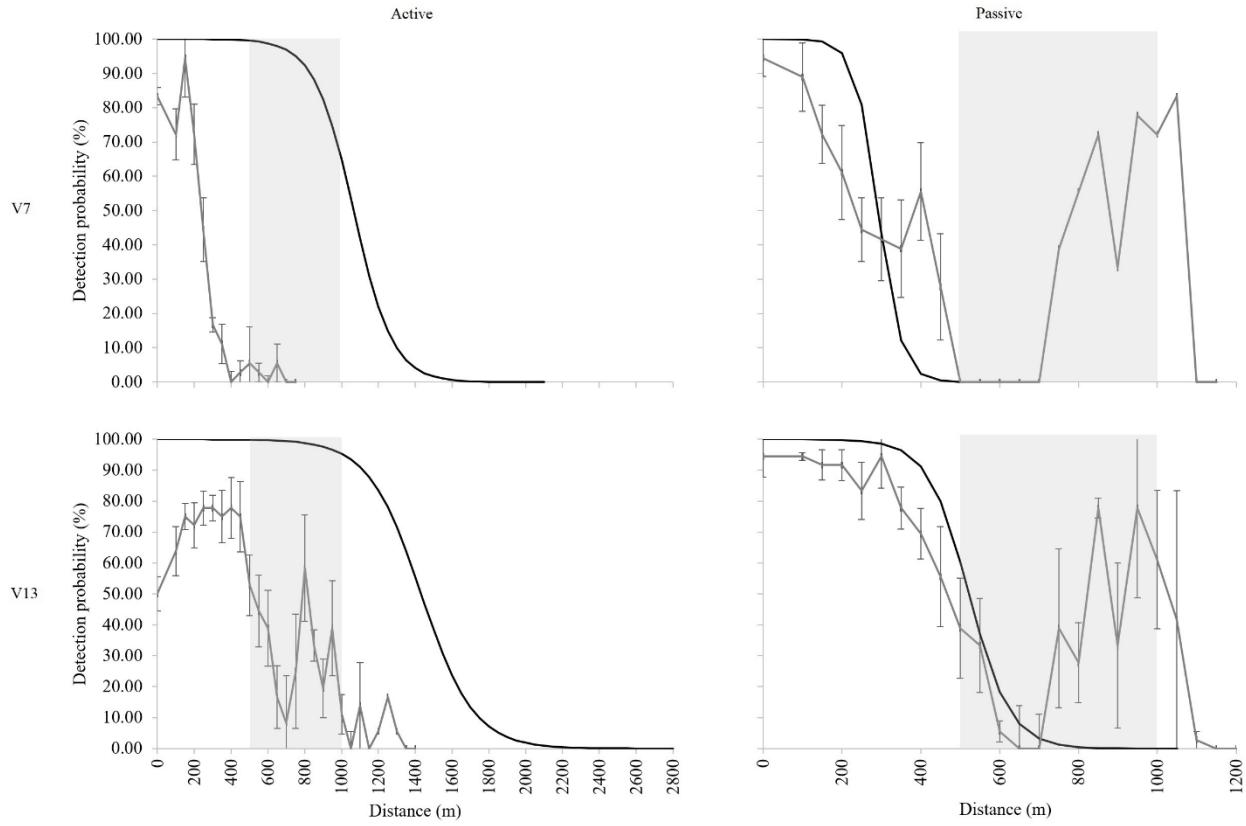

Figure 2.4. Expected (black) and observed (grey; median ± SE) detection probabilities along replicate transects for low (V7) and high (V13) power tags detected by active and passive receivers at the hydropower site. Grey sections indicate the area of potential hydropower impact on ambient noise levels (500-1000 m).

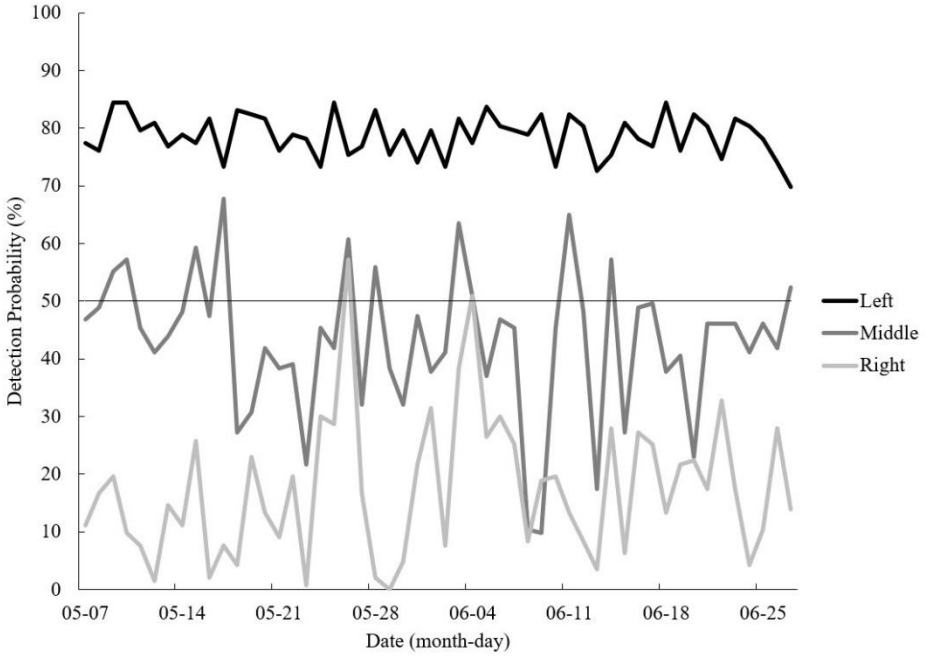

Figure 2.5. Daily average detection probabilities for passive receivers located 6 m (left), 266 m (middle), and 519 m (right) from a low power sentinel tag at the hydropower site. The horizontal line indicates the 50 % detection probability that delineates whether a tag is being reliably detected.

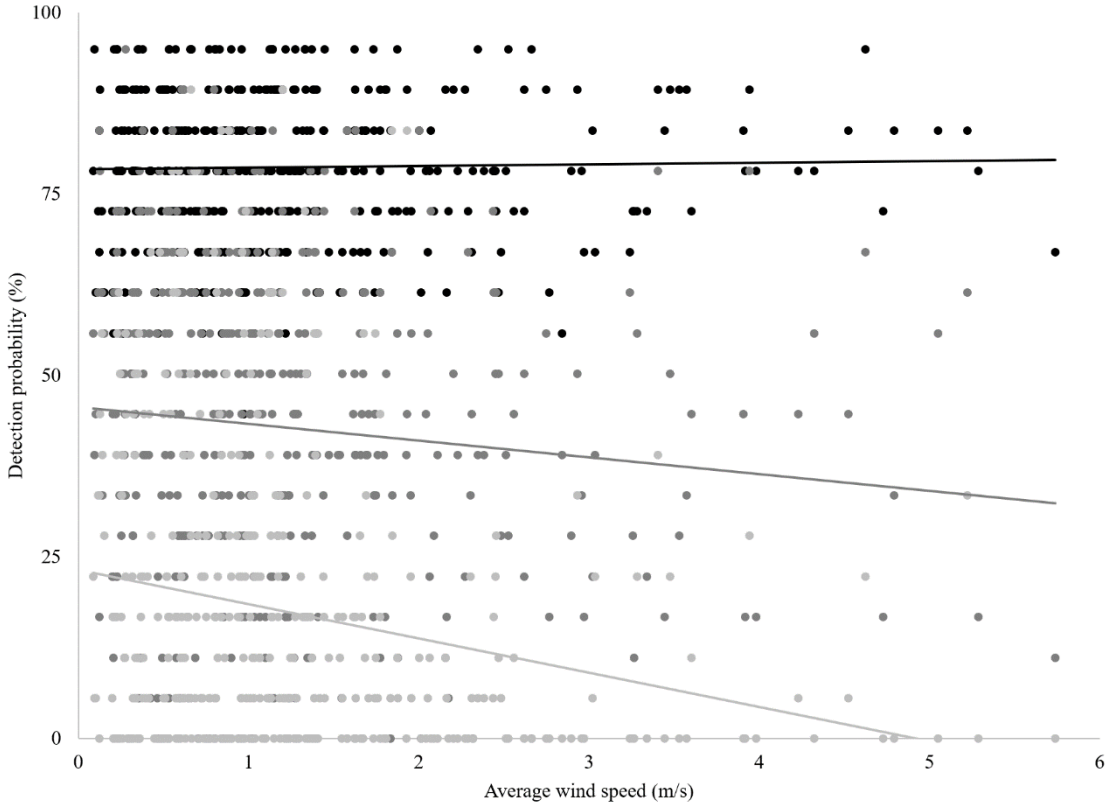

Figure 2.6. Linear regressions of the effect of average wind speed (m/s) on the detection probabilities (%) of receivers located on river left (RL; black), middle (M; dark grey), and river right (RR; light grey) from a low power sentinel tag at the hydropower site.

Chapter 3

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

A. B. Babin[a*], T. Linnansaari[a.b], M. Ndong[c], K. Haralampides[c], S. Peake[a], R. Jones[d], and R. A. Curry[a,b]

Canadian Rivers Institute, Department of Biology[a], Faculty of Forestry and Environmental Management[b], and Department of Engineering[c], University of New Brunswick, Fredericton, New Brunswick, Canada, E3B 5A3

[d]Fisheries and Oceans Canada, Gulf Region, 343 Université Avenue, P.O. Box 5030, Moncton, New Brunswick, Canada, E1C 9B6

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3.1 Abstract

This study examined migration rates, delay, timing and success of acoustically tagged Atlantic salmon (*Salmo salar*) pre-smolts (n = 120) and smolts (n = 57) as they moved through the large Mactaquac Generating Station (MGS) reservoir and subsequently the lower Saint John River (SJR) in spring. The potential relationships between fish movements and the MGS operations were examined directly by comparing migratory timing to the availability of spillway passage, and via a hydrodynamic model by relating fish direction, migration rates, and success to water velocity and direction. Migratory timing was temporally mis-matched with dam operations such that only a few (n = 3) smolts had the option of dam passage via spill. Juvenile salmon tagged as autumn pre-smolts reached the dam 8-28 d earlier, and the estuary 10-30 d sooner, than those tagged as spring smolts. Migration success estimated as apparent survival was high through the reservoir (81-100 %). Downstream passage at the MGS resulted in a 8-32 % decline in apparent survival, and additional losses (27-55 %) occurred during the migration to the lower SJR, such that overall survival to the estuary for the groups tagged as autumn pre-smolts was 61-65 %, and those tagged as spring smolts was 6-10 %. Migration rates were 15.4-29.3 km d^{-1} within the river sections and 5.0-13.3 km d^{-1} through the reservoir; a significant reduction of 73 ± 4 % that was in large part attributable to swimming in the reversed direction from their general migration. Migratory delay was incurred due to suppressed water currents (median 3-4 d), time spent searching in dead-end tributaries (18 h-3 d), and dam passage (up to 2 d searching + 9 h-8 d passage).

3.2 Introduction

Downstream migration by juvenile salmonids in regulated rivers is challenged by hydropower stations and the reservoirs they create (Liermann et al. 2012). Dam passage has been extensively studied (see review Noonan et al. 2012), but less attention has been given to migratory delay or other complications caused by suppressed water currents in large reservoirs (Pelicice et al. 2014). Natural water flow in salmon rivers provides a directional cue to smolts migrating to the ocean, with lotic waters thought to be an important transport mechanism for smolts as they move passively with surface waters (Fried et al. 1978); however, some studies have found that smolts swim actively when flows are insufficient (Thorpe and Morgan 1978; Thorstad et al. 2004), or when they actively feed (Larsson et al. 2011). Inundating sections of a river to create a reservoir for hydropower production decreases water currents which has been shown to lead to migratory delay for smolts in some salmonid populations (Ruggles 1980; Stich et al. 2015). Migratory delay may increase the risk of predation (Poe et al. 1991) and decrease survival rates when smolts cannot reach ocean waters within the physiologically and environmentally determined "smolt window" (McCormick et al. 1998).

As plausible mechanisms exist for how smolt migration may be affected in hydropower regulated rivers, migration success and rates within the impounded Saint John River (SJR), New Brunswick, Canada, are of high interest for conservation efforts of the endangered Outer Bay of Fundy Atlantic salmon (*Salmo salar*) population (Committee on the Status of Endangered Wildlife in Canada 2011).The SJR has three hydropower generating stations along the main migratory route of juvenile Atlantic salmon as they migrate downstream from the tributary with the most nursery habitat, the

Tobique River, to the Bay of Fundy (Marshall et al. 2014; Chateauvert et al. 2018). The migrating pre-smolts and smolts first encounter the Tobique-Narrows Generating Station (TNGS) located 315 river km (rkm; the distance measured on the centerline of the river) from the Bay of Fundy, followed 30 rkm downstream by the Beechwood Generating Station (BGS) at rkm 285, and finally the Mactaquac Generating Station (MGS) after an additional 135 rkm downstream (at 150 rkm) before they enter the free-flowing section of the SJR to the estuary. Of these three hydropower stations along the main migratory route of smolts, the MGS has the largest reservoir (97 rkm), with severely reduced water currents creating a lake-like environment for 37 rkm of its length while the 60 remaining rkm retain some river-like characteristics.

Previous Atlantic salmon pre-smolt and smolt migration and passage studies on the SJR have mainly focused on assessment of the TNGS and BGS reservoir and dam passage success (see review by Chateauvert et al. 2018), with only a few acoustically tagged individuals making it into the MGS reservoir with sufficient battery power remaining to allow for tracking (Carr 1999). Findings in Carr (1999) suggested that the hydropower reservoirs of the SJR may act as "ecological traps" for migrating smolts, with generally high proportions (39-50 % for TNGS, 12.5-100 % for BGS) of acoustically tagged pre-smolts remaining in the first two reservoirs encountered by migrating fish. As the TNGS (but not the BGS) dam passage incurred additional mortality, the ability to assess migration success in the MGS reservoir was limited and haphazard (Carr 1999). However, based on the very small number of individuals tracked ($n = 5$ and $n = 6$ in two years), Carr (1999) observed 0 % migration success through the MGS reservoir suggesting that it may play a role in determining survival of smolts

through the SJR system. Based on these data, Carr (2001) hypothesized that tributary coves (backwater areas) may be significant bottleneck locations where smolt migration ceases.

In addition to the potential effects of the reservoir on smolt migration, dam operations can affect fish migrations by controlling how and when passage options such as spillways and bypasses are available (Coutant and Whitney 2000). Also, controlling the flow of water through the dam could influence the flow patterns in the forebay and reservoir areas (Connor et al. 2003). Currently, downstream passage options at the MGS are limited to the six Kaplan turbines, or the diversion sluiceway and spillway gates that are only temporarily available to migrating juveniles during the spring peak freshet. The ability of Atlantic salmon smolts to pass the MGS through specific routes has not been examined using reliable empirical studies. A theoretical mortality estimate of 10 % has been suggested for the MGS based on the turbine specifications that are similar to other hydropower facilities, and a recent re-analysis of a coded wire tag study suggested a loss of approximately 14 % of smolts (Chateauvert et al. 2018). However, it is not specifically known if the apparent survival of smolts would be affected by their inability to find a suitable egress at the MGS, or whether losses may occur during actual passage through either the spillway structures or turbines.

Another factor contributing to the migration success and timing of smolts from the Tobique River is the high proportion of the population that employs a pre-smolt migration strategy of moving downstream into the mainstem for the winter. The proportion of wild pre-smolts is annually variable and was estimated to vary between 45-81 % in 2007-2012 in the Tobique River (Jones et al. 2014). It is thought that the

pre-smolt strategy may be an adaptation in large river systems where the putative smolts may move out of smaller tributaries that may experience more dynamic winter conditions, and position themselves closer to the river mouth in preparation for the smolt migration the following spring (Riddell and Leggett 1981; Buck and Youngson 1982). In the SJR, the pre-smolt migrations are not thoroughly understood. However, for advising hydropower operations in the SJR, it is important to understand the timing of arrival of migrating smolts at hydropower facilities, as potential passage through either turbines or spillways may incur a different rate of loss and migratory delay. It is not currently known whether the autumn pre-smolts, for example, would be arriving at the MGS at an earlier time, perhaps already by winter, than the spring smolts.

To better understand the relationship between Atlantic salmon smolt migration and the hydropower operations at the MGS, this study quantifies migration rates in relation to water currents within the large hydropower reservoir, and migratory timing of dam passage at the MGS. The main objective was to relate the movements of acoustically tagged Atlantic salmon smolts to hydropower operations at the MGS to examine the extent to which the fish behavior and survival may be influenced by these operations. The second objective was to quantify any delay attributable to the hydropower operations, whether due to reservoir passage or directly by the MGS, and identify any sections of the SJR that may act as migration bottlenecks.

3.3 Materials and Methods

Study site

The SJR is the longest river in New Brunswick (700 rkm, average width 750 m, average depth 2 m; Kidd et al. 2011). Discharge ranges from 280 $m^3 s^{-1}$ in the summer to approximately 10 000 $m^3 s^{-1}$ during the spring freshet (Kidd et al. 2011). The MGS is the lowermost hydropower facility on the SJR (rkm 150; Figure 3.1), along with the BGS (rkm 285; Figure 3.1) on the mainstem and the TNGS (rkm 315; Figure 3.1) near the mouth of the Tobique River tributary. The MGS has a 97 rkm reservoir, with a 37 rkm lake-like section upstream of the dam with depths of 30-40 m and a drastic decline in water velocity from an average of 0.52 m s^{-1} before impoundment to 0.06 m s^{-1} after dam construction (Stantec Consulting Ltd. 2015). Upstream of this reach (Nackawic; reach C; Figure 3.1) the river substantially narrows in width and becomes more shallow in depth (< 20 m), increasing water velocity. Therefore, this study considered reaches C-I (Figure 3.1) to be the lentic section (0.04 cm s^{-1}; M. Ndong, University of New Brunswick, unpublished data) and was termed ‘reservoir’, whereas reach B (Figure 3.1) was a more lotic section (0.14 cm s^{-1}; M. Ndong, University of New Brunswick, unpublished data) and was termed ‘upriver’. Downstream of the MGS was termed ‘downriver’ (reaches J-P; Figure 3.1).

Fish and tagging

Atlantic salmon pre-smolts and smolts from both wild and hatchery origin were acoustically tagged and tracked during 2014-2016 to determine downstream movement

rates and success (Table 3.1). Tagging was performed on the pre-smolt lifestage during their autumn outmigration which allowed for acclimatization over the winter before being tracked in the spring, limiting misinterpretations of the data due to potential tagging impacts that might skew results (Cooke et al. 2011).

Pre-smolts and smolts of wild origin were preferred, but for cases in which wild fish were not captured in sufficient numbers, spring smolts reared in captivity (F1 Hatchery Smolts raised from wild broodstock; HS) were used to supplement the tagging efforts (Table 3.1). In addition, n = 15 migrating wild pre-smolts collected for the Tobique River adult captive-rearing program (Jones et al. 2004) were used in autumn 2014 to supplement tagging. These wild origin, captive-reared smolts (CR) spent < 1 month at the Mactaquac Biodiversity Facility (MBF; 4 rkm downstream of the MGS) in large cobble-bottomed enclosures with river water flow-through to simulate the natural environment prior to tagging and release back into the wild environment (Table 3.1). Wild fish from the Tobique River were sourced from Rotary Smolt Traps (RSTs; Figure 3.1), or from the gatewells of the BGS.

In spring 2014, the first 10 HS fish were tagged at MBF and transported by truck for 2 h and additionally for 1 h by boat to a release site 4 rkm downstream of the BGS (site 1; Figure 3.1). Thereafter, fish were transported by truck for 3 h to a more accessible release site 20 rkm downstream of BGS (site 2; Figure 3.1), avoiding additional handling that was required for boat transport. Wild smolts from the BGS gatewells were tagged on site then transported for 2 h 40 min to release site 2. In autumn 2014, pre-smolts from the BGS gatewells were tagged on site and transported for 15 min to release site 1. CR fish were tagged at MBF, held for three days, then transported for 2

h to either the BGS tailrace while the immediate turbine was off (n = 7), or to release site 1 (n = 8). In the first 10 days of spring 2015, fish were transported for approximately 30 min to a holding tank with gravity-fed flow-through from a nearby brook (triangle; Figure 3.1) where they were observed for 24 h before tagging and allowed to recover for another 24 h before being released at site 2. To reduce transport time, fish captured starting 29 May were either tagged at the capture or release site (2) and observed for 1-4 h before release. During all transport, fish were provided with aeration either in a 45 L cooler or a large transport tank.

In autumn 2015, a study on the migration success of pre-smolts in relation to a newly constructed bypass structure at the TNGS was initiated (see Babin et al. unpublished for full details). The efficacy of a free-swim (FS; released just downstream of TNGS) versus a trap-and-haul (TH; released just downstream of MGS) strategy was compared by assessing apparent survival rates of 50 pre-smolts within each group to the SJR exit. These fish were sourced from the RSTs, transported for 20 min to the gravity-fed holding tank, and observed for 24 h before tagging. Tagged fish were then transported for 30 min for the FS release group, or for 2 h for the TH group.

In spring 2016, wild fish from the RSTs (n = 18) and the BGS gatewells (n = 12), as well as hatchery smolts (n = 7) were observed for 24 h pre- and post-tagging before releasing the wild fish in Hartland (upper reach B; Figure 3.1) and the HS fish in Nackawic (reach C; Figure 3.1).

Acoustic (69 kHz) V7 tags (Vemco, Halifax NS) were 7 mm in diameter, 20 mm in length, weighing 1.6 g in air and 0.75 g in water. The tag:body weight ratio was kept under 5 % (average 3.95 ± 0.69 %) to avoid tagging effects on swimming performance

and survival (Thorsteinsson 2002). Tagging was performed using 40 ppm clove oil as anesthetic (eugenol as active ingredient; ethanol in 1:10 ratio used as carrier; water temperatures ranged from 0.3-7.3 °C in autumn, and from 11.5-16.9 °C in spring, 206 ± 111 s), with surgery lasting 162 ± 76 s for an acoustic tag to be inserted into the body cavity and closed using two monofilament sutures (Monosof 6-0, ce-2 needle). Scale samples were also taken from the standard sampling position for aging (Shearer 1992). When tagging pre-smolts in autumn, tags were programmed to ping at least every 230-370 s for approximately 30 days to ensure the tag was functional and the fish had moved from the release site, then turned off to conserve battery life throughout the winter and resume pinging every 30-90 s during spring migration starting in April, lasting approximately 62-82 d. Due to a logistical error, the tags placed in the pre-smolts in autumn 2014 were reactivated late in spring 2015 when the smolt migration had already begun. Therefore, some upriver and reservoir movements were not detected due to tag inactivity, but their presence can be inferred from detections downriver. For this reason, the 2014/5 pre-smolt group was not included in the apparent survival analysis; however, movement data of those smolts that were detected after tag reactivation were used in other analyses. Smolts tagged in spring always had tags pinging every 30-90s that were estimated to last 132 d.

Pre-smolts and smolts were passively tracked downstream through the SJR and Mactaquac reservoir using a network of passive VR2W receivers (47 in spring 2014, 17 in autumn 2014, 38 in spring 2015, 59 in autumn 2015, 76 in spring 2016; Figure 3.1). The fish were also actively tracked for a total of 63 hydrophone hours using a VR100 receiver. Active tracking was restricted to daylight hours and wind speeds below 25 km

h^{-1}. Through a data partnership with the Ocean Tracking Network, smolts were detected by an additional n = 12 passive receivers in the downriver section during spring 2015, as well as by one receiver in the Saint John Harbour (spring 2016) and two receivers within the Halifax Line (spring 2015).

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

Hydrodynamic model

Fish movements were examined in relation to water velocity and direction by modelling these variables through time and space. The numerical model Delft 3D (Delft3D-FLOW 4.01.00; Deltares 2013) used hourly inputs of tailrace discharge from the BGS, total discharge through the MGS, incoming tributary discharges, wind speed and direction, and bathymetric data to estimate surface (5 m) water velocities (cm s^{-1}, angle from downstream) every two hours 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 3.1) and 233 (reach B; Figure 3.1) 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).

Statistical analyses

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

The fate of each individual was determined based on the presence, duration, and location of detections. This was possible due to the extensive receiver network that was found to produce excellent encounter probabilities upstream of the MGS through CJS modeling (see below and Babin et al. unpublished), ensuring that movements could be inferred from the presence or absence of detections. Three categories were defined:

1) Tag loss or mortality – pre-smolts and smolts were presumed to have either lost their tag or to have died when they were either never detected, detections were near continuous at a single receiver line for the duration of the battery life of the tag, or detections ceased abruptly within the battery life of the tag indicating that the tag or fish

had been lost in an area outside the detection range of any receivers. Tag loss or mortality could be attributed to natural causes such as overwintering stress, tagging effects, dam or reservoir related impacts, or predation. In one case detections indicated active fish movements for a period of time before presumed tag loss, therefore the data before tag loss were included in all analyses except apparent survival estimates.

2) Unsuccessful migrants – smolts were considered to have been unsuccessful in migrating downstream of the reservoir when the last detection came from a receiver upstream of the MGS (reaches A-I; Figure 3.1).

3) Successful migrants – smolts detected downstream of the MGS were known to have passed the dam, but if they were not detected greater than 7 rkm downstream they were considered to have experienced delayed mortality from dam passage. If a fish was detected on the lowermost receivers located 9-20 rkm from the mouth of the SJR (lower SJR; reach P; Figure 3.1), it was considered to have successfully migrated out of the river.

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

Migration success is discussed with absolute numbers of fish reaching key locations (reservoir, dam passage, lower SJR), and number and location of suspected

mortalities. Migratory timing to key locations is visualized and discussed between groups with relation to spill operations at the MGS.

Cormack-Jolly-Seber (CJS; Lebreton et al. 1992; Bowerman and Budy 2012) models were constructed to estimate survival (Φ) and encounter (p) probabilities during the spring migration of four groups: 2014 smolts, 2015/6 FS pre-smolts, 2015/6 TH pre-smolts, and 2016 smolts. When predation was apparent (*e.g.*, abrupt movement away from the main migratory pathway to a side-channel or bay), only those detections determined to have been observed from a smolt were included in the apparent survival analysis. CJS models estimate survival for each reach according to the number of unique tags detected and the detection efficiency of the receivers (Lebreton et al. 1992; Bowerman and Budy 2012). Model assumptions included that, during the spring migration, tagged individuals were representative of the population, survival rates did not differ between tagged and untagged individuals, each tagged individual had equal but independent probabilities of survival and detection, no tags were lost, sampling was instantaneous, and movement was generally unidirectional (downstream). Survival and encounter probability estimates were assessed for 15 reaches with detections of all the receivers within each reach being pooled to reduce model overfitting (Figure 3.1), and encounter probabilities were pooled within study years. Survival over each 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) of each reach. A null model whereby survival and encounter probabilities were not allowed to vary by reach was constructed for base comparison. The comparison of models with or without spatial variability was based on Akaike's Information Criterion corrected for small sample sizes (AIC_c), and the model

with the lowest AIC_c was selected as the best model (Hurvich and Tsai 1993; Burnham and Anderson 2002).

An ordinal regression model (ORM) was used to identify the variables affecting migration success, including the fixed effects of tides (ebb or flow during the last detection, none if not detected in lower SJR), average water temperature throughout the migration, average water velocities in the reservoir, the fish's migration rate through the reservoir, and the proportion of time the fish spent traveling in the reversed direction upstream of the MGS. Overall migration success was coded as an index as follows: 0 = no dam passage, 1 = dam passage, 2 = movement downstream of the MGS (reach J; Figure 3.1), 3 = mid-way downriver (reach L; Figure 3.1), 4 = arrival to the lower SJR (top of reach P; Figure 3.1), 5 = exit of the lower SJR (bottom of reach P; Figure 3.1), 6 = outside of SJR. Continuous variables were scaled using z-scores to account for differences in units and candidate variables were assessed for multicollinearity prior to analysis. Water temperature values were taken from temperature loggers deployed at mid-column alongside the receivers. A proportion (21 %) of fish movements could not be directly linked with concurrent water temperatures, in which case temperature values were interpolated based on the closest spatial and temporal locations.

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

The first LMEM compared overall migration rates (km d^{-1}) within the upriver, reservoir, and downriver reaches. These rates were calculated as: 1) 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 3.1); 2) reservoir; from the last detection as they first entered the reservoir (reach C; Figure 3.1) to the first detection near the MGS (reach I; Figure 3.1); and 3) downriver; from the last detection as they were first detected downstream of the MGS (reach J; Figure 3.1) to the first detection at the last receiver they were observed at downriver. One-way ANOVA was used to compare overall migration rates between wild and HS or CR fish, and among years. Migration rates were further examined by only considering downstream movements between receivers within the upriver and reservoir reaches. These fine-scale movements (km d^{-1}) were related to concurrent water temperatures and velocities (m s^{-1}) through a second LMEM. A third LMEM was used to determine whether smolts were moving passively (fish migration rate < water velocity) or actively (fish migration rate > water velocity) in the upriver and reservoir reaches by subtracting water velocities from fish velocities (km d^{-1}) for each movement between receivers.

The proportion of time that fish spent traveling in the reversed direction to their out-migration and the minimum extra rkm that they swam upstream of the MGS was calculated. Fish direction (upstream or downstream) between receivers was examined using a LME logistic regression model in relation to the associated maximum water angle from downstream in the upriver and reservoir reaches.

Migratory delay was partitioned to components in relation to the causing mechanism, *i.e.*, delay due to the slower than pre-reservoir water currents, time spent

searching within dead-end tributaries, and searching for the downstream exit as well as dam passage itself. Delay was quantified by comparing the expected duration to traverse the reservoir (37 rkm) based on each individual fish's up- and downriver migration rates (assumed pre-reservoir migration rate) to the observed durations. Observed and expected durations based on up- and downriver migration rates were compared using paired t-tests. Delay due to dam passage was quantified in two ways: the duration of time between the first detection at the MGS and the last detection before passing the MGS, and the duration of time between the last detection upstream and the first detection downstream of the MGS.

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

3.4 Results

Wild pre-smolts were significantly heavier (two-way ANOVA, $F_{1,116} = 44.74$, $p < 0.05$) and longer (two-way ANOVA, $F_{1,116} = 71.71$, $p < 0.05$) than CR fish. Those tagged in 2014 were significantly heavier (two-way ANOVA, $F_{2,116} = 4.49$, $p = 0.01$) than those tagged in 2015 in the FS group (TukeyHSD $p = 0.016$) and the TH group (TukeyHSD $p = 0.02$), but these groups did not differ by length (two-way ANOVA, $F_{2,116} = 1.45$, $p = 0.24$). Freshwater age-2+ pre-smolts were approximately 4 g heavier (two-way ANOVA, $F_{1,78} = 7.31$, $p = 0.008$) and 0.6 cm longer (two-way ANOVA, $F_{1,78}$

= 12.24, $p < 0.001$) on average than age-1+ pre-smolts (2014 n = 7, 2015 FS n = 36, 2015 TH n = 41).

Smolt weight (two-way ANOVA, $F_{1,81} = 0.008$, $p = 0.93$) and length (two-way ANOVA, $F_{1,81} = 1.30$, $p = 0.26$) did not differ by origin, but those tagged in 2016 were significantly heavier by 4 g (two-way ANOVA, $F_{2.81} = 4.59$, $p = 0.01$) and longer by 1 cm (two-way ANOVA, $F_{2,81} = 6.24$, $p = 0.003$), on average than those tagged in 2014 (TukeyHSD weight $p = 0.02$, length $p = 0.04$) or 2015 (TukeyHSD weight $p = 0.04$, length $p = 0.003$).

Dummy-tagged control groups held over the 2014/5 winter season (see Babin et al. unpublished) indicated that overwinter mortality and tag loss was expected to be 36 %. Of the groups released upstream of the MGS, 20 (14 %) tags were never detected and 53 (36 %) individuals were determined to have either lost their tag or experienced mortality. Many (n = 35) of these individuals were not detected moving from their respective release sites, and the majority (n = 65) were lost within a week with other tags not being observed until active tracking in the spring when their presence in close proximity of the release site and immobility therein was confirmed. With one exception of clear fish movements before tag loss, all of these individuals were removed from analyses to avoid methodological bias on the results.

Overwinter

Overwintering locations were determined for the pre-smolts for the two winters in 2014/5 and 2015/6. The upriver section (reach B; Figure 3.1) was used for overwintering by eight pre-smolts, whereas the majority of fish (n = 18) overwintered in

the upriver-top of reservoir transition area (reach B-C; Figure 3.1). Entry into the MGS reservoir was infrequent, but one fish was detected entering the reservoir in the winter with its first spring detection just 17 rkm upstream of the MGS, and another pre-smolt overwintered within the reservoir only 12 rkm upstream of the MGS (reach G; Figure 3.1). Additionally, two fish from the 2015/6 FS pre-smolt group released at the tailrace of the TNGS remained within the BGS reservoir over winter. No winter movement through the MGS was documented in this study. In the group released downstream of the MGS (2015/6 TH pre-smolt group), only two moved downstream of their release site during the winter, being detected up to 17 rkm away (reach K; Figure 3.1); however, neither of these fish were detected in the spring.

Migration success and timing

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

CJS estimates of detection efficiency and survival were best explained with spatial variability (Table 3.2). Encounter estimates were less than 50 % in areas outside of the reservoir that were covered by a single receiver (mainly in the downriver reach) but were greater than 50 % for lines of multiple receivers within the reservoir (reach B; Figure 3.1).

Apparent survival estimates were greater for the groups tagged as autumn pre-smolts than those tagged as spring smolts (Figure 3.2B). Overall, apparent survival estimates were 95-100 % as they entered the reservoir (reaches B-C; Figure 3.2B) and

remained stable within each group as they travelled through the reservoir with the exception of the 2016 smolt group that declined by 12.5 % (reaches C-I; Figure 3.2B). Apparent survival estimates declined by 8-32 % during dam passage (reaches I-J; Figure 3.2B), with smaller losses (8 %) in the group tagged as pre-smolts, and the greater losses (2014; 32 %, 2016; 20 %) being incurred by the groups tagged in the spring. Downriver, survival estimates declined by 27-55 % (reaches J-P; Figure 3.2B). It appeared as though the last reaches (N-P; Figure 3.1) incurred losses of 10-20 % for most groups but was higher for the 2014 smolts (53 %). Cumulative survival estimates to the lower SJR ranged from 60-65 % for groups tagged as autumn pre-smolts, and from 6-10 % for groups tagged as spring smolts (Figure 3.2B). Two CR fish from the 2014/5 pre-smolt group continued on to the Bay of Fundy and were detected off the Halifax Line (9 and 26 June).

Migration success was not affected by average water temperature (ORM, p = 0.08; Table 3.3a) or velocity (ORM, p = 0.85; Table 3.3a), individual migration rates through the reservoir (ORM, p = 0.42; Table 3.3a), or the proportion of time that individual fish spent traveling upstream instead of downstream (ORM, p = 0.60; Table 3.3a). Fish that reached the lower SJR were assigned an ebb or flood state whereas those that did not reach the lower SJR were assigned a null tide state because the tidal effect was not expected to be strong enough to affect fish movements upstream of this area. As expected, migration success was significantly different between null and ebb or flood states (ORM, $p < 0.001$; Table 3.3a), but migration success was not significantly different between fish that reached the lower SJR during ebb or flood states (ORM, p = 0.65; Table 3.3a).

The declines in apparent survival in the downriver reaches were likely attributable to delayed MGS passage mortality (n = 3) and potential predation (n = 18). Predation events were inferred from detections of acoustic tags in non-typical areas away from the main SJR channel, and thus the migratory route. The areas of atypical movements involved the Grand Lake (n = 1), the Washademoak Lake (n = 5), the Belleisle Bay (n = 6), and the Kennebecasis Bay (n = 1; Figure 3.1). In addition, avian predation was the suspected fate for smolts (n = 5) that were detected by receivers upstream of receivers from which they were detected earlier. The most extreme example would be one smolt that was detected in reach P then subsequently in reach J without any detections from the 16 receivers between these reaches (Figure 3.1).

The timing of migration initiation and arrival to the MGS of each tagging group is visualized in Figure 3.3. Fish tagged as autumn pre-smolts initiated their spring migration (identified by directed downstream movements) earlier than fish tagged in the spring as smolts (22 Apr-29 May vs. 16 May-1 Jun) with associated median water temperatures of 8.0-11.1 °C (SE; 0.5-0.8 °C) for smolts tagged as autumn pre-smolts and 10.1 ± 0.2 °C for smolts tagged in the spring. Pre-smolt groups entered the reservoir earlier (reach C; Figure 3.1; 25 Apr-30 May vs. 18 May-12 Jun), and reached the MGS (28 Apr-16 Jun vs. 20 May-12 Jul) and the lower SJR (4-29 May vs. 28 May-22 Jun) sooner in comparison to groups tagged as spring smolts. Reaching the MGS earlier in the year allowed three fish tagged as pre-smolts the option of passing via spill (either the outer diversion sluiceway or the spillways within the forebay), although there were only 4-6 days to do so before the spill was closed (22 May 2014, 15 May 2015, 3 May 2016). Fish tagged as smolts did not encounter the MGS before spill was closed. Those that

successfully passed the MGS experienced median water temperatures of 9.3-16.1 °C (SE; 0.5-0.8 °C) near the MGS, and those that remained in the reservoir experienced median water temperatures of 9.6-18.0 °C (SE; 1.0-1.1 °C), and up to 20.4°C near the end of the tracking period.

Migration rate and delay

Juvenile salmon migrants traveling through the reservoir experienced suppressed migration rates (medians 5.0-13.3 km d^{-1}) when compared to sections up- (18.7-23.4 km d^{-1}) or downriver (15.4-29.3 km d^{-1}), likely due to decreased water current (Figure 3.4). Migration rates were significantly different between reaches (LMEM, $p < 0.001$; Table 3.3b), but did not significantly differ between wild and HS or CR origin (one-way ANOVA, $F_{1,157} = 2.00$, $p = 0.16$). Only 1.04 % of the variation in overall migration rates was attributed to individual fish.

Migration rates between each receiver as the fish were moving downstream were tested to determine dependence on concurrent water velocities. Individual fish only accounted for 1.12 % of the variance among downstream migration rates. When only downstream movements between receivers were considered, there was no effect of reach (LMEM, $p = 0.81$; Table 3.3c) or concurrent water velocities (LMEM, $p = 0.19$; Table 3.3c); however, greater water temperatures were found to have a positive and significant effect (LMEM, $p < 0.001$; Table 3.3c).

Migration rates were further compared with concurrent water velocities to determine where and how often fish were moving passively (fish migration rate < water velocity), or actively (fish migration rate > water velocity). The variance in velocity

differences was attributed 8.26 % with individual fish. Velocity differences were significantly different between reaches (LMEM; $p < 0.0014$; Table 3.3d), with smolts more often swimming actively in the reservoir than upriver (93 % vs. 68 %).

Slow water currents removed directional cues, as was evidenced by the large proportion of time smolts spent reversing direction, *i.e.*, swimming upstream rather than making downstream progress. The majority of the tracked fish (n = 46 of 84) spent 17-49 % of their time reversing direction in areas upstream of the MGS during the migratory period (Figure 3.5). Compared to the minimum distance the fish would need to travel to exit the reservoir (37 rkm), reversed direction swimming added medians of 24-302 ± 14-217 extra rkm, and up to 519 extra rkm to the migration. Reversals were less common once fish had passed the MGS (median 11-41 ± 2-14 % of time; 7-64 ± 7-55 extra rkm).

Variation of fish direction (upstream or downstream) between receivers was attributed 3.51 % with individual fish. Fish direction was not detectably affected by the water direction as measured by the maximum angle away from the downstream direction (LMEM, $p = 0.93$; Table 3.3e), but upstream movement between receivers was more common in the reservoir than upriver (35 vs. 3 %; LMEM, $p = 0.008$; Table 3.3e).

While searching for the downstream exit, many migrating fish journeyed into and spent time within the dead-end Longs Creek tributary (Table 3.4), situated at a large, almost 90° bend in the MGS reservoir between reaches G and H (Figure 3.1). One tagged fish each spring were last detected in Longs Creek where they presumably died. Another dead-end tributary, the Mactaquac Arm to the east of the MGS, was also

searched by two smolts (both tagged in the spring of 2016) that visited once for a total of 11.3 h and 1.4 d.

A pre-MGS reservoir migration rate was estimated for each tagged fish by applying their respective up- or downriver migration rate to the distance of the reservoir (37 rkm), providing a duration of time that the fish would have been expected to be able to traverse this distance if the water was flowing at a river rate as opposed to a slow-moving reservoir. These expected durations were compared to the observed duration of time each fish used to travel over that distance (from Nackawic to their first encounter with the MGS) to provide an estimate of delay due to reduced water currents (Table 3.5). Expected durations to traverse the MGS reservoir for all three studied springs ranged between 1.8 and 2.8 d (Table 3.5). However, the observed durations to pass the reservoir were longer than expected (paired t-test; vs. upriver $p < 0.001$, vs. downriver $p = 0.009$; Table 3.5). The tagged fish migrating in spring 2014 and 2015 migrated at similar rates (one-way ANOVA, $p = 0.96$) and took approximately 4.5 d to traverse the reservoir, whereas the reservoir migration was significantly slower in 2016 (by 3.5 d; one-way ANOVA, $p = 0.005$; Table 3.5). Overall, delay within the reservoir could be calculated for 53 smolts, with estimated delays attributable to water flow being 3.74 ± 0.94 d based on upriver migration rates, and 3.54 ± 0.88 d based on downriver migration rates.

Compounding the delay during reservoir passage was the additional delay incurred at the vicinity of the MGS. During each of the three studied springs, tagged smolts made multiple attempts to approach the MGS (up to 7 attempts), with most attempts taking place during daylight hours (pooled 76 %). All fish were delayed to

some extent as evidenced by the duration between their first and last detections in the forebay area, but the median time spent at the MGS prior to passage varied between years (2014; 18.7 ± 28.5 h, range 7 min to 16 d; 2015; 30 min; 2016 pre-smolt group; 40 min; 2016 smolt group; 14 h, range 43 min to 43 d). Following the delay in the forebay, additional delay was observed during the actual passage of MGS (*i.e.*, last detection upstream of the MGS and first detection downstream of the MGS) that ranged between 2 min and 44 d (median 5.3 h ± 1.1 d) for all years studied.

3.5 Discussion

The outer Bay of Fundy population of Atlantic salmon is experiencing severe decline, partly due to challenges associated with dam operations (Clarke et al. 2014). This study found that survival rate was relatively high throughout the MGS reservoir (81-100 %) but declined during dam passage (by 8-32 %) with the greater losses being incurred by groups acoustically tagged as spring smolts in comparison to those tagged during the pre-smolt lifestage. Cumulative apparent survival to the lower SJR was also greater for groups tagged as autumn pre-smolts over groups tagged as spring smolts (60-65 % vs. 6-10 %). Migration rates were suppressed within the reservoir (5.0-13.3 km d^{-1}) compared to river reaches (15.4-29.3 km d^{-1}), causing migratory delay (3-4 d). Migratory timing in the spring was largely mis-matched with the availability of fish passage through the spillways such that only three fish tagged as autumn pre-smolts had the option of spillway passage due to initiating migration 4-6 d earlier, whereas all fish tagged as spring smolts were forced to pass via the turbines.

The inferred overwintering location of pre-smolts was observed to be in the upriver to top of reservoir transition area as the tagged fish were generally not detected moving into the reservoir until spring. Juvenile salmonids in other river systems have been observed to pass through dams in the winter, during which time the passage options are the turbines or specific bypasses (that the MGS lacks) because spill is typically restricted to the spring freshet (Tiffan et al. 2012). There was evidence for a few fish choosing to overwinter within the reservoirs, either upstream of the BGS or the MGS, and some fish (the 2014/5 FS pre-smolt group) passed the MGS before their tags re-activated, but the passage likely occurred early in the spring as was observed for the other groups tagged as pre-smolts. The pre-smolts that were transported to overwinter downstream of the MGS remained near the release site with only two fish moving downstream (up to 17 rkm), neither of which were detected in the spring.

Reservoir passage of salmonids has been reported to be associated with greater survival rates than dam passage (*e.g.*, 69-86 % vs. 14-33 %; Beeman et al. 2013). This study found apparent survival rates were fairly stable throughout the reservoir (95-100 %; except for a 12.5 % decline among the 2016 smolt group). None of the tagged groups experienced greater mortality rates while passing the reservoir than when passing the MGS. Previous studies in the SJR have estimated smolt mortality due to reservoir and dam passage as 24.7 % at the TNGS, 13.6 % at the BGS, and 15.9 % at the MGS (Carr 2001), reaching up to 45.3 % for smolts emigrating past the three dams cumulatively (Carr 1999; Chateauvert et al. 2018). This study represents the first estimates using telemetry for apparent survival at the MGS reservoir and dam, with dam passage through the MGS being found to reduce survival rates by 8-32 %. This encompasses the

previous estimates that were based on coded wire tag mass markings for estimating passage success at the MGS (Carr 2001; Chateauvert et al. 2018). These losses suggest that the MGS facility, but not the reservoir, may be a considerable migration bottleneck for Atlantic salmon smolts in the SJR system. It should be noted, however, that fish that were tagged as autumn pre-smolts incurred smaller losses than those tagged as spring smolts. This could be in part due to the earlier arrival timing at the MGS when they could utilize the potentially safer spillway for passage. The earlier arrival of smolts tagged as pre-smolts, in turn, may be a true ecological phenomenon but could also be a methodological artifact related to the timing of tagging and potentially delays it may cause (see below).

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

When comparing the migratory timing of fish tagged as smolts in the spring versus those tagged as pre-smolts in the autumn, it appears as though smolts that waited until spring to initiate their migration moved later in the season than those that moved into the mainstem in the autumn. However, the apparent differences in migratory timing

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

Migration rates of wild juvenile salmonids in free-flowing and low-flow waters are highly variable, ranging from 0.01 to 43.5 km d^{-1} (Babin, unpublished data), with rates of smolts that have spent time in captivity being even more variable (0.05 to 82 km d^{-1}; Babin, unpublished data). A previous study examining pre-smolts within the SJR

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

When both low- and free-flowing reaches have been compared within the same study, low-flow water bodies have been reported to cause juvenile salmonids to migrate 33-50 % slower than through free-flowing waters (Raymond 1968; Thorpe and Morgan 1978; Raymond 1979; Stich et al. 2015). This study found similar values with smolts moving 73 ± 4 % slower in the reservoir than the up- and downriver reaches which had a more lotic character. These reductions are hypothesized to be related to the reduced

water currents within the reservoir, lacking the directional cues juvenile salmon use to find their way to the ocean. However, our analyses did not detect a direct association between individual downstream movements between receivers and concurrent water velocities. Rather, it was found that the rates of downstream movements between receivers were not different within each reach, but the back-and-forth movements termed reversals seemed to have led to decreased migration rates within the reservoir as a whole.

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

When directional cues are lacking, out-migrating smolts need to actively search for the downstream exit, contributing to migratory delay. Migratory delay has been estimated to increase mortality rates by 13 % over dam passage alone (Marschall et al. 2011), and decrease smolt-to-adult survival by 16.5 % (Zabel 2002). Aarestrup et al. (1999) observed upstream-directed movements by Atlantic salmon smolts in a reservoir that took 16 % of their migration time and was associated with strong winds. The hydrodynamic model used in this study incorporated wind speeds and direction in the outputs of water speed and direction, but these variables did not appear to be related to fish direction. The variables were estimated for the surface 5 m of the water column

where the fish were assumed to travel, but the actual location of the fish in 3D space could have caused a mismatch with concurrent hydrodynamic conditions. However, it was observed that up to half of the total migration time upstream of the MGS was spent traveling upstream rather than downstream, covering tens or hundreds of extra rkm in comparison to swimming downstream in the most direct route. Upstream movements between receivers was more common in the reservoir than upriver (35 % vs. 3 %). These movements included searching in dead-end tributaries such as the Longs Creek and the Mactaquac Arm. The latter tributary could only be accessed through large culverts at a causeway and contains ideal, shallow, vegetated habitat for predators such as the smallmouth bass (*Micropterus dolomieu*) and the recently introduced largemouth bass (*M. salmoides*; M. Gautreau, University of New Brunswick, unpublished data).

Predation may be increased within reservoirs due to high water transparency as compared to river reaches (Pelicice et al. 2014), along with increasing water temperatures and increasing smolt disorientation and searching behaviour (Beamesderfer et al. 1990, Smith et al. 2003). Areas where predators congregate, such as tailrace areas of hydropower dams, may introduce bottlenecks to the survival of smolts during their migration (Blackwell and Juanes 1998; Naughton et al. 2004). Previous studies examining the predation of Atlantic salmon smolts downstream of the MGS have concluded that the predation threat is negligible downstream of the MGS in spring (Curry et al. 2007; Andrews et al. 2018), although Babin et al. unpublished hypothesized potential predation in late autumn. However, predation of Atlantic salmon smolts has not been thoroughly examined in the lower parts of the SJR during their migration. In this study, it was estimated that 12-46 % of mortalities of the tagged fish actively

migrating downstream of the MGS could be attributed to predation. Predation was inferred from detections where smolts were showing unidirectional and consistent mainstem migration towards the sea, until a migration reversal and entry into non-typical smolt habitat, such as Grand Lake, Washademoak Lake, Belleisle Bay, and Kennebecasis River in the lower reaches of the SJR which appeared to be a substantial migration bottleneck in the spring. Inference of predation events was more difficult in the reservoir due to frequent migratory reversal behaviour and smolt entry to dead-end tributaries. However, predators such as smallmouth bass, chain pickerel (*Esox niger*), and muskellunge (*Esox masquinongy*) are known to reside in the reservoir (Ritter 2002, Clarke et al. 2014).

Another source of migratory delay occurred after fish encountered the MGS but presumably continued to search for a downstream exit through the dam. At the MGS, smolts left and returned to the forebay area up to seven times and waited up to 43 d before being detected downriver. To aid smolts in identifying the direction of the downstream exit, Flow Velocity Enhancement Systems (FVES) have been installed in other hydropower systems to induce water currents toward the direction of migration (Coutant 2001) and could be tried at the MGS to expedite smolt migration. Contrary to the prevailing literature (Brege and Absolon 1996; Aarestrup et al. 1999; Beeman et al. 2013), dam passage occurred mostly during daylight hours (76 %). Successful passage of the MGS itself took approximately 5 h, *i.e.*, the time differential between the last detection in the forebay and the first detection in the vicinity of the tailrace. Part of the delay inherent in dam passage is the time spent travelling through the dam structures,

such as gatewells. In this study, there was an effort to track smolts of wild origin in the spring of 2015 that were sourced from the gatewells of the BGS by using a specifically designed net that could be lowered into the structure. Although 20 wild smolts were tagged, only one reached the MGS reservoir and did not make it as far as the MGS. These tagged fish were removed from all analyses due to potential tagging-related bias. It is important to note that smolts sourced in the spring had most likely already undergone one dam passage at the TNGS and were in the process of passing the BGS, and thus may not have been able to persist after the additional stressors associated with capture, tagging, and transport. This highlights the physiologically sensitive nature of this lifestage (Carey and McCormick 1998), and that researchers should attempt to target the pre-smolt population wherever possible to allow for acclimatization over winter and avoid adding to the cumulative stress of spring smolts migrating in hydropower-regulated systems.

Following many other hydropower systems, a fish hatchery (MBF) was tasked with producing and releasing Atlantic salmon with the goal of mitigating losses due to hydropower effects (Young 2013; Maynard and Trial 2014). The current management practice in the SJR includes both captive rearing of wild juveniles from the Tobique River into mature adults that are then released to spawn naturally, or used as a broodstock in a traditional juvenile (age-0 fall parr) hatchery stocking program with releases back into the tributary of origin (Jones et al. 2014). Along with suppressed water currents and dam operations, rearing conditions can also affect migration timing, rates, and success of juvenile salmonids (Monzyk et al. 2009). Hatchery-raised fish are less adapted to the natural environment; therefore, they often travel at slower rates and

experience higher mortality rates during the spring migration than their wild counterparts (Jonsson et al. 1991; Chittenden et al. 2008). However, no clear pattern of this result emerged from the two tagging groups of spring smolts that spent their entire lives in captivity and were used to supplement the wild pre-smolts and smolts in our study. The current study was not designed as a comparative study between the success of wild and hatchery smolts, and the hatchery fish were only used to supplement the tagging numbers, and as such, our study had no analytical capacity to analyze differences by origin.

The main objective of this study was to quantify juvenile Atlantic salmon migration rates within the MGS reservoir in comparison to lotic portions of the SJR, and to relate fish movements to dam operations to inform practices affecting survival rates. Migration rates were found to be 73 ± 4 % lower within the reservoir compared to the river reaches. Estimated delays of 3-4 d were incurred by low water flow, reversed swimming direction, and dam passage. Migration success and rates were not detected to be influenced by specific hydrodynamic conditions influenced by hydropower operations at the MGS; therefore, changes to management practices with the goal of increasing water flows, and therefore directional cues to smolts, are not directly supported by this study. Currently, dam operations at the MGS are not managed to allow for downstream passage of smolts via spill or bypass which could produce higher survival rates than through turbines. Migration success could be aided by providing spill passage further into the smolt migration window but could potentially be cost-prohibitive. However, construction of a functional bypass system that would allow volitional passage at all times could minimize the expenditure in water lost for

generation but may offer a safe route through the MGS for migrating Atlantic salmon smolts.

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Table 3.1. Weight (g) and fork length (cm) [mean ± SE] of wild, hatchery-reared (*i.e.*, hatchery smolts; HS), and captive-reared (CR) Atlantic salmon pre-smolts and smolts tagged between 2014-2016. FS = Free-Swim, TH = Trap-and-Haul.

Date	Origin	N	Weight (g)	Fork length (cm)
21-26 May 2014	HS	20	41.7 ± 1.7	16.8 ± 0.2
29 May-1 Jun 2014	Wild	20	41.4 ± 2.3	17.2 ± 0.3
17-20 Nov 2014	Wild	5	67.7 ± 12.9[a]	19.3 ± 1.2[a]
8 Dec 2014	CR[b]	15	39.4 ± 2.0	15.6 ± 0.2
19 May-2 Jun 2015	Wild	20	41.0 ± 1.6	16.5 ± 0.2
28 Oct-25 Nov 2015	Wild (FS)	50	40.4 ± 0.9	16.2 ± 0.1
28 Oct-25 Nov 2015	Wild (TH)	50	40.6 ± 0.8	16.1 ± 0.1
31 May 2016	HS	7	48.7 ± 2.2[c]	17.5 ± 0.3[c]
15-27 May 2016	Wild	30	44.9 ± 2.4[c]	17.4 ± 0.3[c]

[a]Wild pre-smolts significantly larger than CR fish (two-way ANOVA, $F_{1,116} = 71.71$, $p < 0.05$)

[b]Wild pre-smolts held at the Mactaquac Biodiversity Facility for approx. 1 month prior to acoustic tagging

[c]Smolts tagged in spring 2016 significantly heavier (two-way ANOVA, $F_{2.81} = 4.59$, $p = 0.01$) and longer (two-way ANOVA, $F_{2,81} = 6.24$, $p = 0.003$) than other smolt groups

Table 3.2. Model selection of Cormack-Jolly-Seber survival (Φ) and encounter (p) probabilities with (s) and without (.) spatial variability, Akaike Information Criteria corrected for small sample sizes (AIC_c), and model weight (w_i).

Model	AIC_c	w_i	Evidence ratio
Φ(s)p(s)	970.1952	1.00000	$5.19x10^{37}$
Φ(s)p(.)	1124.3836	0.00000	17126
Φ(.)p(.)	1143.8804	0.00000	1

Note: Evidence ratio describes how well the evidence supports the model

Table 3.3 Model type, formula, sample size, and coefficient estimates, standard errors (SE), z- (ordinal regression model; ORM) or t-values (linear mixed effects models; LMEM, and linear mixed effects (LME) logistic regression model), and *p*-values, assessing Atlantic salmon smolt migration success, rates, and fine-scale direction.

Coefficient	Estimate	SE	z/t	*p*
a) ORM; success index ~ tide + temperature_avg + water_velocity_avg + fish_km_d + proportion_upstream, n = 64				
tides ebb vs. flood	-0.16179	0.35405	-0.457	0.65
tides overall	-4.85893	0.98379	-4.939	<0.0001
temperature_avg	-0.83411	0.48017	-1.737	0.08
water_velocity_avg	0.06902	0.36907	0.187	0.85
fish_km_d	0.27384	0.34296	0.798	0.42
proportion_upstream	-0.18623	0.35170	-0.530	0.60
b) LMEM; fish_km_d ~ reach + (1|fish_id), n = 159 from 76 fish				
reach	4.162	1.078	3.860	<0.0001
c) LMEM; fish_km_d ~ reach * temperature_avg * water_velocity_avg + (1|fish_id)[1], n = 867 from 65 fish				
reach	0.5308	2.2648	0.234	0.81
temperature_avg	10.8308	3.0467	3.555	0.0004
water_velocity_avg	2.6082	1.9935	1.308	0.19
d) LME; velocity_difference ~ reach + (1|fish_id), n = 1279 from 65 fish				
reach	6.044	1.309	4.618	<0.0001
e) LME logistic regression model; fish_direction ~ reach * water_angle + (1|fish_id)[1], n = 1279 from 65 fish				
reach	0.014	0.005	2.666	0.008
water_angle	0.006	0.008	0.082	0.93

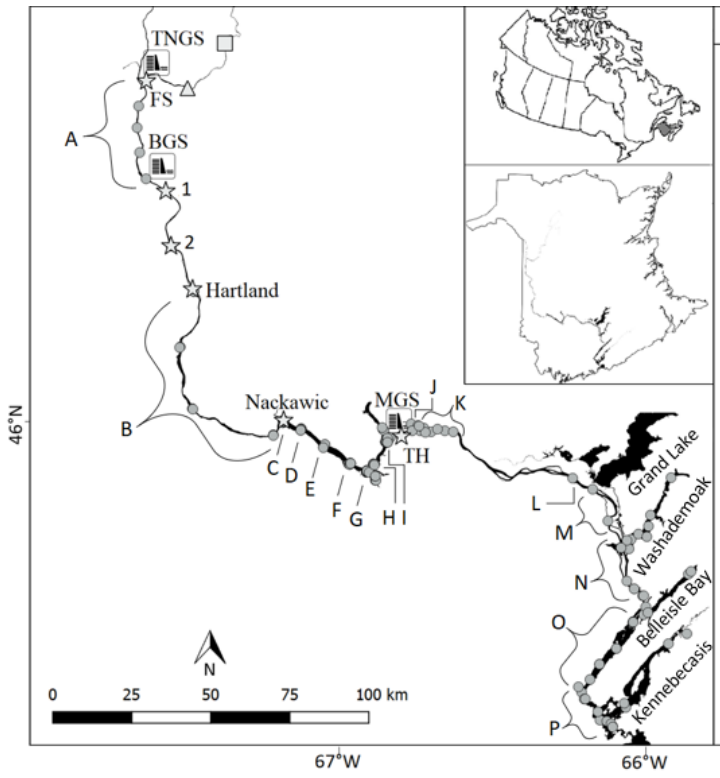
[1]Interactions (not shown) were non-significant

Table 3.4. Number of tagged Atlantic salmon smolts that entered or bypassed Longs Creek, with the number of tagged smolts that entered upon their first encounter, and the mean ± standard error duration of time spent in the tributary.

Tagging Group	N bypassed	N entered	N first encounter	Duration (d)
2014 smolt	4	15	9	0.8 ± 0.1
2014/5 pre-smolt	2	2	1	1.3 ± 0.8
2015/6 pre-smolt	15	10	6	1.5 ± 0.3
2016 smolt	8	6	4	2.5 ± 0.8

Table 3.5. Observed – Expected duration (d; mean ± SE) that smolt groups (FS = Free-Swim) spent traversing the MGS reservoir (37 rkm) based on individual up- and downriver migration rates (km d^{-1}).

		Based on upriver		Based on downriver	
Tagging Group	Observed (d)	Expected (d)	Delay (d)	Expected (d)	Delay (d)
2014 smolts	4.3 ± 1.0	2.8 ± 0.5	1.6 ± 1.2	2.5 ± 0.2	2.0 ± 1.2
2014/5 pre-smolts	4.6 ± 1.4	1.8 ± 0.4	2.5 ± 1.6	12.2 ± 9.8	-9.6 ± 10.9
2015/6 FS pre-smolts	7.8 ± 1.6	1.9 ± 0.3	6.2 ± 1.7	1.2 ± 0.2	4.2 ± 0.8
2016 smolts	8.0 ± 1.4	2.3 ± 0.4	6.9 ± 1.6	1.8 ± 0.7	9.1 ± 3.9



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

Figure 3.1. Locations of receivers (circles), hydropower generation stations (TNGS = Tobique-Narrows, BGS = Beechwood, MGS = Mactaquac), Atlantic salmon pre-smolt and smolt capture (Rotary Smolt Traps at square, gatewells at BGS), tagging (triangle), and release sites (stars; FS = Free-Swim, 1 = release site 1, 2 = release site 2, TH = Trap-and-Haul) along the Saint John River, New Brunswick, Canada. Associated table delineates CJS groupings with maximum number of receivers in the mainstem in any given study year.

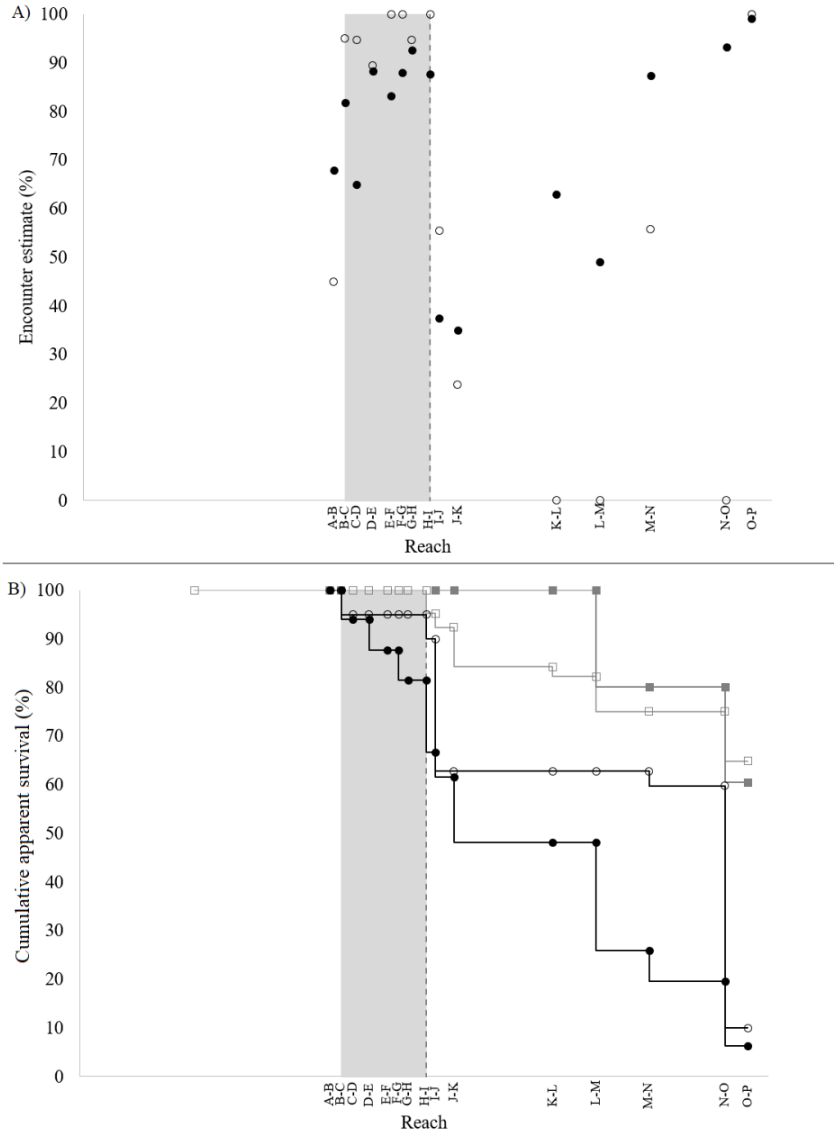


Figure 3.2. Cormack-Jolly-Seber A) encounter probability estimates in 2014 (open circles) and 2016 (closed circles) and B) cumulative apparent survival estimates (%) during the spring migration in 15 river reaches (Figure 3.1) of Atlantic salmon smolts tagged as autumn pre-smolts (grey lines; 2015/6 pre-smolts free-swim open squares, trap-and-haul closed squares) or spring smolts (black lines; 2014 open circles, 2016 closed circles). The shaded section represents the Mactaquac reservoir and the dashed vertical line represents the location of the Mactaquac Generating Station.

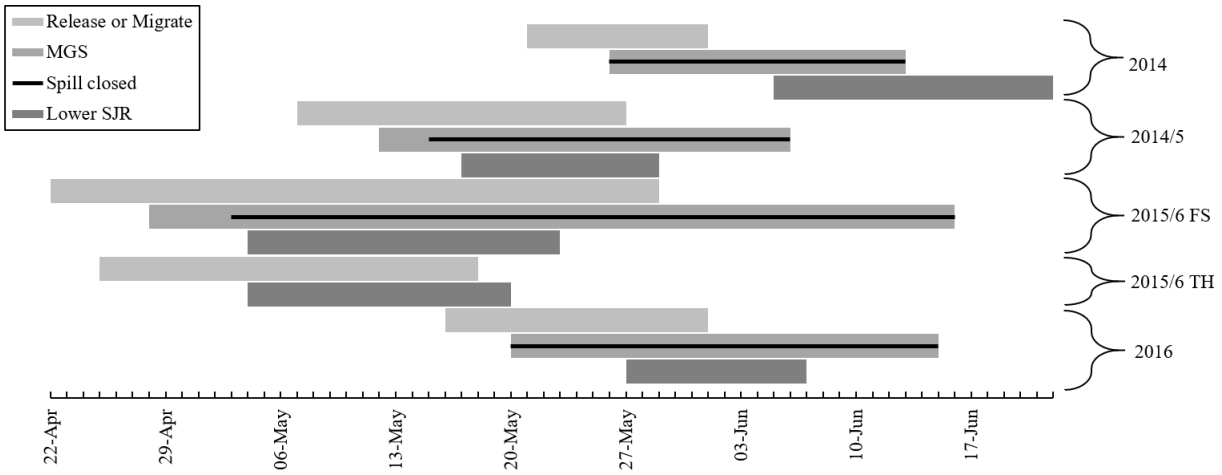


Figure 3.3. Migration timing of Atlantic salmon tagged as pre-smolts (2014/5, 2015/6 FS = Free-Swim, TH = Trap-and-Haul) or smolts (2014, 2016) including release (smolts) or initiation of spring migration (pre-smolts; light grey), arrival to the Mactaquac Generating Station (MGS; medium grey) with closed spill (black), and arrival to the lower Saint John River (SJR; dark grey).

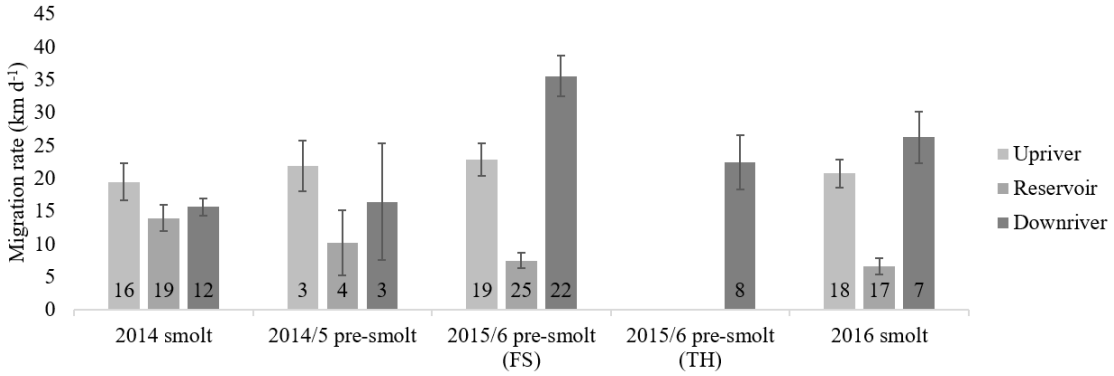


Figure 3.4. Mean migration rate (km d^{-1}) of Atlantic salmon tagged as autumn pre-smolts or spring smolts as they migrated through the Saint John River from 2014-2016. FS = Free-Swim, TH = Trap-and-Haul. Error bars represent standard error and sample sizes are in shown.

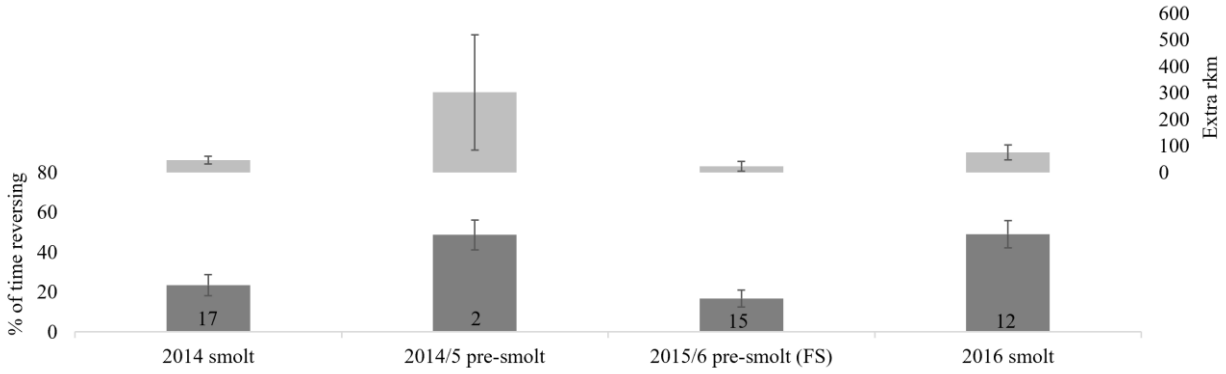


Figure 3.5. Median proportion of time Atlantic salmon smolts spent reversing (moving upstream; dark grey) within the MGS reservoir in 2014-2016, and the accompanying minimum distance of extra rkm added to the migration due to reversal behaviour (greater than the 37 rkm of the reservoir; light grey); error bars represent standard error and sample sizes are in shown.

Chapter 4

Evaluation of downstream passage management strategies for Atlantic salmon *Salmo salar* smolts in a regulated river: free-swim versus trap-and-haul

Amanda B. Babin, Stephan Peake

Canadian Rivers Institute, Biology Department, University of New Brunswick, Bailey Hall, 10 Bailey Drive, P.O. Box 4400, Fredericton, New Brunswick, Canada, E3B 5A3

Tommi Linnansaari, R. Allen Curry

Canadian Rivers Institute, Biology Department, Faculty of Forestry and Environmental Management, University of New Brunswick, Bailey Hall, 10 Bailey Drive, P.O. Box 4400, Fredericton, New Brunswick, Canada, E3B 5A3

Ross Jones

Fisheries and Oceans Canada, Gulf Region, 343 Université Avenue, P.O. Box 5030, Moncton, New Brunswick, Canada, E1C 9B6

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4.1 Abstract

Downstream-migrating, juvenile salmonids often pass through hydropower generating stations when they must reach the sea within an ecological window. Dams delay passage and often lack bypass facilities, adding stress of turbine or spillway passage to a physiologically sensitive lifestage. Contemporary dam operations can have facilities for fish to bypass dam structures or capture and transport them downstream. Free-swimming (FS) allows for imprinting during the downstream migration, whereas fish that are trapped-and-hauled (TH) avoid dam passage issues but they may experience stress and altered migratory timing from handling and transport. In this study, Atlantic salmon (*Salmo salar*) from the Tobique River, New Brunswick, Canada, were acoustically tagged during the 2015 autumn pre-smolt migration and released either downstream of the Tobique-Narrows Generation Station (FS group; n = 50), or downstream of the Mactaquac Generating Station (TH group; n = 50). The FS group migrated through two reservoirs and hydropower generating stations with no bypass facilities to reach the river exit (total of 315 rkm), whereas the TH group had direct access to the estuary (total of 146 rkm). Two control groups were held in captivity to estimate overwinter survival (untagged; n = 50) and tagging-related mortality and tag loss (dummy-tagged; n = 50). The two release groups reached the lower river (< 20 rkm from river exit) within a similar timeframe (FS from 4-23 May, TH from 4-20 May). The TH group may have experienced high predation rates upon release but cumulative apparent survival to the lower river were similar between the FS (65.5 %) and TH (64.8 %) groups, and the survival rate curves in the downriver reach were not significantly different between the release groups. Given the similarity of migration timing and

survival, it is recommended that the natural processes of imprinting during free-swimming be the preferred management option at this time.

4.2 Introduction

Global renewable energy production has been increasing in an effort to reduce greenhouse gas emissions, with hydropower supplying 86 % of electricity from renewable sources worldwide (IPCC 2011). However, it is well documented that generation of power through hydro-dams can impede the migration of diadromous fishes both up- and downstream (Bunt et al. 2012; Liermann et al. 2012; Noonan et al. 2012). Salmonids are economically (Mills 1989), culturally (Naves et al. 2015), and ecologically (Willson and Halupka 1995; Hilderbrand et al. 2004) valuable, but their ability to complete migrations either up- or downstream is often challenged by the issues related to fish passage at hydropower generating stations (Marschall et al. 2011; Bunt et al. 2012; Noonan et al. 2012).

Upstream passage structures such as fishways or lifts at hydropower facilities can be effective at passing strong swimmers such as adult salmonids, but their efficiency more often depends on how well they attract fish to the entrance rather than how the structure itself is engineered (Bunt et al. 2012; Noonan et al. 2012). Attraction efficiencies are highly variable and tend to be driven by the species characteristics (Bunt et al. 2012). As the fish search for the entrance to the upstream passage structure, migrations can be delayed or halted, decreasing the energy reserves that would otherwise be used to reach natal spawning grounds and successfully spawn (Caudill et al. 2007; Roscoe and Hinch 2010). To avoid such delays and to aid adults in reaching

the spawning grounds, a common management strategy is to trap-and-haul (TH) individuals upstream of the hydropower facility (Marshall et al. 1994; George et al. 2009; Lusardi and Moyle 2017).

Similar to upstream passage at hydropower facilities, efficient downstream passage often suffers from structure location and attraction issues (Bunt et al. 2012; Noonan et al. 2012). Downstream passage is typically achieved via one of three general forms: migrating fish go downstream through the turbines; egress is achieved with the spill (either from the surface 'top-spill' or the subsurface 'bottom-spill'); or fish are guided downstream through designed bypass structures. Passing through turbines has a high mortality risk, especially for larger-bodied fish (Čada 2001; Wertheimer and Evans 2005). Atlantic salmon (*Salmo salar*) downstream migrants (juvenile smolts and post-spawned adults/kelts) tend to be surface-orienting, and thus passage via top-spill can have lower mortality rates, albeit an economically costly option (Muir et al. 2001; Fjeldstad et al. 2014; Nyqvist 2016). Bottom-spill can be effective, but salmonids can be resistant to sounding to depth to find the entrance (Ruggles 1980; Coutant and Whitney 2000). Some hydropower facilities have bypass structures that have been constructed specifically for fish passage (*e.g.*, Lower Granite, Little Goose, and Lower Monumental dams in the Snake River-Columbia River system; Muir et al. 2001). Bypass facilities must also contend with the issues of entrance location and attraction, but the water volume lost to the bypass is less than the spilling, and in some cases is partially recovered for power generation with an added turbine (Johnson and Dauble 2006). Fish passing via bypass facilities experience relatively low mortality risk (Whitney et al. 1997; Buchanan et al. 2006). Passage via a bypass includes a further fisheries

management consideration or option. Migrating fish that enter a bypass may be allowed to freely continue migration through the bypass, *i.e.*, a free-swim management strategy (FS; Johnson and Dauble 2006), or managers can include a collection facility whereby fish may be captured for assessment and/or research purposes, then diverted to hauling platforms such as barges or trucks for transport downstream to avoid subsequent migration obstacle(s) (TH; Evans et al. 2008).

Free-swimming after bypass passage may be advantageous for salmonid smolts that imprint to the chemistry of their natal stream and river while migrating downstream and thus aid navigation during their eventual returning spawning migration (Hasler et al. 1978; Keefer and Caudill 2014). Smolts can also feed during their downstream migration, increasing their body size and their probability of survival during their early marine migration (Larsson et al. 2011; Manel-la et al. 2011). Fish that pass through multiple dams have a compounded risk of mortality (Williams et al. 2005) which the TH strategy overcomes, but other issues can arise such as the shortened travel time of transported smolts (relative to FS smolts) that may place fish within the estuary too early for their developmental stage or at a time when ocean conditions are less than ideal (Williams et al. 2003; Whitney et al. 2006). Also, there are risks associated with handling and transport that will increase stress in a stressful lifestage (Iversen et al. 1998; Hoar 1988). The reduced opportunity for imprinting in a TH strategy may increase rates of adults straying to other tributaries upon their return, thereby reducing the number of adults to tributaries (Buchanan et al. 2006; Keefer et al. 2008). In either case, disorientation upon release may increase the risk of immediate predation (Muir et al. 2006; Whitney et al. 2006). Regardless, two-way TH (TH2) of both adults upstream

and smolts downstream can be an effective management strategy in some systems (Aurdaul et al. 2001; Lusardi and Moyle 2017).

Hydropower was developed in the Saint John River (SJR) starting in 1930s with the construction of the Grand Falls Generating Station on an impassable waterfall where diadromous fishes would have encountered this natural obstacle, continuing into the 1950s with the Tobique-Narrows Generating Station (TNGS) located approximately 1 km upstream from the SJR-Tobique River confluence, and the Beechwood Generating Station (BGS) located 30 river km (rkm) downstream of this confluence (Figure 4.1). The Mactaquac Generating Station (MGS) was the last dam constructed (1968) a further 135 rkm downstream on the mainstem. The Tobique River is important for smolt production, holding 60 % of the nursery habitat within the SJR upstream of the MGS (Marshall et al. 2014). Juveniles from the Tobique River must migrate past these three hydropower stations and reservoirs along their downstream migration of over 300 rkm in total. Currently, two of the three hydropower facilities do not have dedicated passage structures for the downstream migrants.

Atlantic salmon returning to tributaries upstream of the MGS have been declining in numbers since the 1980s, decreasing from annual returns of 10,000 before construction of the MGS to less than 3,000 by the 2000s, and only a few hundred wild adults have been returning over the last decade (Jones et al. 2014). Consequently, the population has been listed as endangered (Committee on the Status of Endangered Wildlife in Canada 2011). Fisheries managers are strongly motivated to improve the status of the population, in part by addressing downstream passage issues associated with hydropower facilities. The first step being taken was the installation of a

downstream fish surface bypass facility on the first dam (*i.e.*, TNGS) encountered by out-migrating juveniles from the Tobique River.

In this study, we examined the implications for Atlantic salmon smolts of a bypass facility being installed at the first dam (*i.e.*, TNGS) encountered by out-migrating juveniles from the Tobique River. When built, and if successful in collecting downstream migrants, the fisheries management must determine whether they will allow volitional passage of Atlantic salmon pre-smolts and smolts to the tailrace of the TNGS (*i.e.*, FS strategy), or collect the smolts for transport, thus bypassing the two subsequent hydropower dams and reservoirs (*i.e.*, TH strategy). We compared an assumed successful bypass of TNGS and then FS to the sea versus a TH strategy with fish being released 165 rkm downstream, below the lowermost dam. The objective was to identify which strategy, FS or TH, produced a higher likelihood of successful arrival of Atlantic salmon smolts to the Saint John River estuary downstream of all migration barriers. The FS group migrated a longer distance and navigated two dams and reservoirs; therefore, we predicted that the FS group would take longer to reach the estuary and have a lower survival rate than the TH group.

4.3 Materials and Methods

Study site.– The Tobique River is a tributary of the SJR in New Brunswick, Canada (Figure 4.1), and is the largest nursery habitat of the endangered Atlantic salmon upstream of the MGS (Committee on the Status of Endangered Wildlife in Canada 2011; Marshall et al. 2014). From the Tobique River, downstream migrating pre-smolts and smolts must pass three hydropower reservoirs and generating stations (TNGS 315

rkm, BGS, 285 rkm, and MGS 150 rkm; reaches A, B, and I in Figure 4.1), a distance of approximately 300 river km (rkm) before reaching the mouth of the SJR. This long-distance migration is thought to be one of the reasons driving a relatively high proportion (45-81 %) of the juvenile Atlantic salmon population to initiate their downstream migration in the autumn months as pre-smolts with movements into the mainstem of the SJR where they are thought to overwinter (Jones and Flanagan 2007). In the spring, typically in May-June, the pre-smolts resume their long-distance migration as smolts to the Bay of Fundy and the Atlantic Ocean (Jones et al. 2014).

At the time of conducting this study, there were no downstream passage solutions at the TNGS; a bypass structure was installed in 2017 that is currently being evaluated for efficiency (H. MacLean et al., University of New Brunswick, unpublished data). Pre-smolts in the Tobique River rarely have the option of passing via the four spillways of the TNGS because these are generally not operating in autumn, but rather must travel through one of two Kaplan turbines with intakes at 6.3 and 8.1 m depth (Jones and Flanagan 2007).

Tagging and tracking.– Wild Atlantic salmon pre-smolts used in this study were sourced from rotary smolt traps at Three Brooks, Tobique River (Figure 4.1) operated by the Department of Fisheries and Oceans Canada (DFO) in partnership with Tobique First Nations and the Tobique Salmon Protective Association. Overall, 200 pre-smolts were used between two experimental groups (FS and TH), a dummy-tagged control group and a non-tagged control group (Table 4.1).

After capture at Three Brooks, fish were transported for 20 minutes to a tagging site (Figure 4.1) in an aerated transport tank, placed into a large circular tank for

recovery from capture and transport, and observed for 24 h before tagging. Wild pre-smolts that were used as controls were transported approximately two hours to the Mactaquac Biodiversity Facility (MBF; Figure 4.1) where they were held for approximately three weeks before further handling and/or tagging.

The tags used in this study were acoustic (69 kHz) V7 tags (Vemco, Bedford, N.S.) measuring 7 mm in diameter and 20 mm in length, weighing 1.6 g in air and 0.75 g in water. Tags were pre-programmed to remain active for the first month after tagging, then turn off until re-activation in late April 2016 to save battery power for tracking during the spring migration. During the active state the tags transmitted a signal on average every 60 s, and battery life was expected to last 60-62 d in the spring. Pre-smolts were anaesthetized in an aqueous solution of 40 ppm clove oil (eugenol as active ingredient; ethanol in 1:10 ratio used as carrier), measured for fork length and weight (Table 4.1), had a scale sample was taken from the standard sampling position for aging (Shearer 1992), and had acoustic tags surgically inserted into the body cavity then closed using two monofilament sutures (Monosof 6-0, ce-2 needle). On average, surgery lasted 194 ± 31 s (SE), and the tag-to-body weight ratio was kept under 5 % (3.95 ± 0.61 %) to avoid tagging effects on swimming performance and survival (Thorsteinsson 2002). The tagged fish recovered for 24 h in a floating live-well within a large circular tank with gravity-fed flow-through from a nearby brook.

Tagged fish were alternately sorted into the experimental groups (FS and TH) and then transported in a large aerated transport tank for approximately 30 min to the TNGS (FS group; reach A; Figure 4.1) or approximately 2 h to the MGS (TH group;

reach J; Figure 4.1) and released to the downstream vicinity of these generating stations in daylight hours from shore using small dipnets.

After their release, the acoustically tagged fish in experimental groups were passively tracked downstream through the SJR using a network of 57 VR2W receivers (Figure 4.1) to determine downstream movement rates, migration timing and success. Range-testing of the receiver setup was performed and reported in a separate study (Babin et al. unpublished), documenting average detection ranges of 246 – 307 m for V7 tags using VR2W receivers.

The two control groups were composed of wild pre-smolts originally sourced from the same location as fish used in the experimental groups; however, the majority of the dummy-tagged control group (45/50) and the untagged control group (46/50) had spent an approximate three week period at the MBF on a commercial pellet feed prior to length and weight measurements. Using the methods above, the untagged control group was anaesthetized at the MBF for length and weight measurements. Similarly, the dummy-tagged control group underwent the same tagging procedure as the experimental groups using tags that had the same composition and size as the live tags, but that did not emit an acoustic signal. These groups were held over winter at the MBF from 27 October 2015 to 1 May 2016 to quantify mortality due to surgery and transport, tag loss, and overwinter mortality.

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

Statistical analyses.– Differences in fork length, weight, and condition, were compared between groups (experimental groups FS and TH, control groups dummy-tagged and untagged) using a MANOVA. Upon significance, the response variables were examined separately using ANOVA with adjusted Holm-Bonferroni alpha's and Tukey's Honestly Significant Difference post-hoc test.

Overwintering mortality of fish in the release groups was assumed when tags were last detected in the autumn but no spring migration was observed. Presumed mortality causes were natural overwinter stressors or tagging and handling stress. Observed overwinter mortality of both experimental groups was compared to expected tag loss and mortality rates from control groups using a Chi-square test.

Cormack-Jolly-Seber (CJS; Lebreton et al. 1992; Bowerman and Budy 2012) models were run to estimate survival (Φ) and encounter (p) probabilities of the FS and TH groups during their active spring migration period. CJS uses the number of unique tags detected on receivers and the detection efficiency of the receivers to estimate survival for each reach (Lebreton et al. 1992; Bowerman and Budy 2012). Model assumptions included that tagged individuals migrating in the spring (*i.e.*, tagged fish alive for greater than five months post-tagging) were representative of the population, spring survival rates did not differ between tagged and untagged individuals, each tagged individual had equal but independent probabilities of survival and detection, no tags were lost, sampling was instantaneous, and movement was generally unidirectional (downstream). To meet the assumption of no tags being lost, tags that were assessed to have been lost prior to the active spring migration were removed from the analysis. Survival and encounter probabilities estimates were allowed to vary over 16 river

reaches (A to P; Figure 4.1) with detections of all the receivers within each reach being pooled to reduce model overfitting, and encounter probabilities were pooled. Survival over each river 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) of each reach. Survival estimates of the TH group were fixed at 100 % upstream of the MGS (*i.e.*, no transport mortality). A null model whereby neither survival nor encounter probabilities were allowed to vary by reach was constructed for the base comparison. The comparison of models with or without spatial variability was based on Akaike's Information Criterion corrected for small sample sizes (AIC_c), and the model with the lowest AIC_c was selected as the best model (Hurvich and Tsai 1993; Burnham and Anderson 2002). Survival rate curves in the downriver reach were compared between groups using a log rank test (Kaplan and Meier 1958). Timing of arrival to the lower SJR (< 20 rkm from the river exit; reach P; Figure 4.1) was compared between groups using the Watson test for differences in circular orientation (Jammalamadaka et al. 2001).

Analyses were done in R (Version 1.0.136 © 2009-2016 RStudio, Inc. Packages car, circular), with the exception of CJS analyses done in Program MARK (Version 8.2; White and Burnham 1999) , and statistical significance was assumed when *p* was less than or equal to 0.05.

4.4 Results

The majority of the pre-smolts tagged in this study were age 2+ (FS 75 %, TH 68 %). Body size differed (MANOVA, Phillai's trace = 0.10, $F_{3,192} = 2.23$, $p = 0.02$) between groups in weight (ANOVA, $F_{3,192} = 3.29$, Holm-Bonferroni adjusted $p = 0.04$)

and condition factor (ANOVA, $F_{3,192} = 5.50$, Holm-Bonferroni adjusted $p = 0.004$), but not in length (ANOVA, $F_{3,192} = 0.37$, Holm-Bonferroni adjusted $p = 0.77$). The dummy-tagged control group was significantly heavier (average 44.6 g; Table 4.1) than the FS experimental group (40.4 g; Table 4.1; TukeyHSD $p = 0.04$) and subsequently had higher condition factors (1.02; Table 4.1) than both the FS (0.95; Table 4.1; TukeyHSD $p = 0.001$) and TH (0.96; Table 4.1; TukeyHSD $p = 0.02$) experimental groups, likely as a result of the commercial feed. All groups were considered sufficiently similar and assumed to respond similarly to the tag burden.

Tagging mortality occurred in 22 % of the dummy-tagged individuals (13-50 d post-tagging) with additional tag loss without mortality in 14 % of the dummy-tagged fish (28-94 d post-tagging), with no mortality or tag loss coinciding with the spring migration period of the experimental groups. The untagged control group experienced only 2 % (n = 1) mortality after approximately 159 d presumably due to natural reasons. Based on the control groups, the over winter loss of tagged individuals due to tagging-related incidences (mortality and tag loss) was expected to be 36 % of the in-river tagged smolts.

Within the FS group, 6 % of the tags were never detected and 38 % of the fish were not detected moving downstream in the spring. This was 8 % greater, but not significantly higher, than the expected 36 % loss due to tagging/handling/tag loss effects ($\chi^2 = 0.66$, df = 1, $p = 0.42$). Of the TH group, 10 % of the tags were never detected and 67 % were not detected moving more than one rkm downstream of the release site. This additional 41 % loss was significantly greater than the 36 % that could be explained by tagging-related mortality or tag loss ($\chi^2 = 16.93$, df = 1, $p < 0.001$).

Overall, 28 tagged smolts from the FS group were tracked through their spring migration. Three smolts (10.7 %) passed the MGS during the period of tag inactivity (their first spring detections were downstream of the MGS). Based on the locations of first detections in the spring, inferred overwintering locations included areas upriver (3.6 % in reach A, 17.9 % at the upper end of reach B; Figure 4.1), but the majority of smolts in the FS group (64.3 %) were first detected in the spring by the two receiver locations in the downstream section of reach B as well as reach C (Figure 4.1). Overwintering in the MGS reservoir was not common (3.6 %; reaches G-H; Figure 4.1). For the TH group, 11 tagged smolts were detected during their spring migration. One (9.1 %) did not move downstream from the release site, two (18.2 %) were first detected in backchannel habitat nearby the release site (K; Figure 4.1), whereas four (36.4 %) were first detected mid-way downriver (L; Figure 4.1), and a few were first detected further downriver (three in reach N and one in reach P; Figure 4.1).

The CJS model with highest support included spatial variation (distance between receivers) of the survival (Φ) and encounter (p) probabilities (Table 4.2). Encounter probability (p) was estimated to be greater than 50 % in all reaches except I-K and L-M where the minimum estimate was 33 % (Figure 4.2).

Apparent survival of the FS group did not decrease until they encountered the MGS where a 5.7 % decline was estimated (reach I-J; Figure 4.2). The largest decrease (8.3 %) in apparent survival occurred in the K-L reach. Survival decreased in the M-N reach where the TH group also experienced their greatest mortality decrease (FS = 7.8 %, TH = 20.1 %; Figure 4.2). Kaplan-Meier survival rate curves in the downriver reach

were not significantly different between the FS and TH groups (65.5 % vs. 64.8 %; z = 0.36, p = 0.72).

FS smolts entered the MGS reservoir (reach C; Figure 4.1) mainly in the first two weeks of May as water temperatures increased from approximately 5 to 12 °C (full range between 25 April and 30 May 2016). Of the migrating smolts, 36 % (n = 10) entered a dead-end tributary of the MGS reservoir (Longs Creek) located at the bend between reaches G-H (Figure 4.1). This delayed their migration by 2.6 h to 3 d (median 1.5 d). Detections indicated a wide arrival timeframe to the vicinity of the MGS between 28 April and 16 June 2016 (Figure 4.3). A group of smolts (14 %) was unable to negotiate the MGS as their last detections were at receivers close to the upstream side of the MGS (reaches H-J; Figure 4.1). Fish did not always pass the dam upon first encounter but made multiple attempts (1-7) and were delayed for up to 9 d (median 40 min; n = 10) before passing. The time it took to pass the dam was estimated from the first detection downstream of the MGS and the last detection in the forebay area, ranging from 1 h to over 4 d (median 14 h; n = 20). Two fish from the FS group were last detected 12 rkm downstream of the MGS indicating mortality potentially due to dam passage or avian predation as inferred for one tag that was detected downstream before being last detected upstream in the vicinity of the MGS. There was additional evidence of predation when smolts were detected in unlikely areas such as Belleisle Bay, but the majority (76 %) of the tagged smolts that passed the MGS were detected at the upstream end (n = 19) or exit (n = 14) of reach P (Figure 4.1).

Only seven (64 %) smolts from the TH group were detected at the upstream end of reach P (Figure 4.1), and five (45 %) were detected at the exit from this reach. Smolts

from both groups reached the lower SJR (reach P; Figure 4.1) within a similar time frame: 4-20 May 2016 and 4-23 May 2016, FS and TH respectively (Watson test statistic = 0.12, $p > 0.10$; Figure 4.3).

4.5 Discussion

A downstream fish bypass facility began operating at the TNGS in 2017. This offered two smolt migration strategies that had not previously existed: the use of the bypass to provide a free-swim (FS) of 315 rkm past two reservoirs and dams (without passage structures), or the use of the bypass to trap-and-haul (TH) smolts past the dams and reservoirs leaving 146 rkm to free-swim to the sea. We predicted that the TH strategy would result in higher survival to the river estuary because dams and reservoirs were avoided, and that the TH smolts would arrive at the estuary earlier because of the shorter distance to cover without potential delays caused by dams and reservoirs. We documented no difference in survival rates or in the timing of arrival to the river mouth between the two strategies. It was observed that migrating FS smolts initiated their migration later than the TH smolts, and experienced delays in at least the largest (MGS) reservoir. However, the overall data suggests that no benefits from trap-and-haul operations appeared to be achieved.

The FS strategy is biologically advantageous as it allows smolts to overwinter in a habitat that is naturally experienced by the wild population. The current study identified that some pre-smolts passed the MGS before the tags had activated in the spring due to their first spring detections being downriver. It was also observed that the reservoir did not seem to be a preferred overwintering habitat because only one smolt

moved into the mid-reservoir whereas the majority overwintered just upstream of the reservoir. In the spring, FS smolts can feed, grow, and importantly, imprint to their natal route during their downstream migration which presumably reduces straying during the return migration (Keefer et al. 2008; Bond et al. 2017). However, there are two more reservoirs and generating stations on the SJR that FS fish have to navigate before their entry to the sea, and it was conceivable based on previous studies that some level of direct or indirect mortality would be inflicted at both facilities (Chateauvert et al. 2018). Theoretical estimates for mortality at the BGS and MGS are 10 % (Washburn and Gillis Associates Ltd. 1995), but only anecdotal empirical evidence exists for mortality at these two facilities (Chateauvert et al. 2018). A coded wire tag study carried out in the 1990s with recent data re-analysis estimated the mortality at BGS as less than 13 % and less than 14 % at MGS (Washburn and Gillis Associates Ltd. 1995 reassessed by Chateauvert et al. 2018). Previous telemetry work in the SJR system used radio telemetry to track 77 pre-smolts in the Tobique River (346 rkm) and observed 74 % of the pre-smolts successfully descended from the TNGS in autumn and 26 % passed the BGS in the late autumn/winter (Jones and Flanagan 2007). This previous study did not provide a mortality estimate at the BGS, and the fate of the whole population could not be determined due to the expiry of the transmitters prior to the spring (Jones and Flanagan 2007). The vast majority (82 %) of the pre-smolts in the current study, which were released just downstream of the TNGS, passed the BGS in the winter to use the reach upriver of the MGS reservoir to overwinter. The additional loss of 8 % of tagged individuals in the FS group may be attributed to many factors including passage at the BGS. The dam passage mortality at the MGS was estimated as 6 % in spring. Additional

studies will be required to further evaluate the individual and cumulative dam mortality rates for Atlantic salmon smolts. Taken together, the generating stations in the SJR appear to inflict at least some level of mortality during turbine passage, and therefore, avoiding the risk of multiplicative loss at hydropower facilities is used as justification to consider a TH over a FS strategy in a general case, provided that the TH strategy would avoid similar losses and would therefore provide a survival benefit.

However, the decision to employ the TH vs. the FS strategy is intimately related to the relative success of the TH, *i.e.*, in a situation where the FS strategy can be shown to result in *de facto* losses of fish at hydropower facilities or their associated reservoirs, the TH should produce a tangible survival benefit. However, the interpretation between survival benefits between FS and TH strategies are not as clear. For example, Williams et al. (2005) concluded that salmonids transported downstream of Columbia River dams have lower survival rates than those that were allowed to free-swim. In the current study, contrary to our prediction and despite the documented losses of tagged smolts in the hydropower generating stations in the FS group, the downriver survival rate curves indicated similar apparent survival for the FS group and the TH group as the approached the sea (FS = 66 % and TH = 65 %). In fact, by examining not only the proportion of fish migrating in the spring, but the absolute values observed in the SJR estuary in spring (n = 19 for FS and n = 7 for TH), it is apparent that the TH strategy did not impact greater survival benefits over the FS strategy, which corroborates the findings by Williams et al. (2005). While the TH strategy avoids the issues from multiple passages, the fish would have to undergo the stress of collection, handling, and transport (Carey and McCormick 1998; Iversen et al. 1998), and would not have imprinted on 165 rkm of

habitat. In this study, the transport did not result in direct mortality and all tagged fish were released in apparent good condition. However, the TH group experienced a drastic decline in numbers in the late autumn/winter that was beyond what could be reasonably explained by tagged/tag expulsion related losses. Even when accounting for natural overwinter mortality and tagging effects, survival to spring migration of the TH group was 41 % lower than expected. A large proportion of the TH release group was initially observed by the receiver network in the downstream vicinity of the MGS; however, the acoustic tracks ceased in the autumn or did not re-emerge in the spring once the acoustic tags reactivated.

The SJR is home for a number of predatory fish species, such as the introduced muskellunge (*Esox masquinongy*), and the native striped bass (*Morone saxatilis*). The effects of predation of these two predator species has been examined in spring and summer, and Atlantic salmon have been shown to play a negligible role in their diets (Curry et al. 2007; Andrews et al. 2018a). However, concurrent movement studies tracking both predators using telemetry methods suggest a large presence just downstream of the MGS during the release period in autumn (K. Zelman and S. Andrews, University of New Brunswick, personal communications). Tagged striped bass extensively use the MGS area until the water temperature drops below 10 °C, at which time they move *en masse* to apparent overwintering habitat in the large bays downstream (Andrews et al. 2018b). During the release of the TH group, water temperatures were 10.5-12.4 °C and concurrent striped bass and muskellunge tracking studies indicated their high-density presence around the TH release area (T. Linnansaari, unpublished data). While the predation is only a hypothetical cause for the

disappearance of the large proportion of the pre-smolts in the TH group in this study, future studies should be conducted to examine the validity of this hypothesis, for example using acoustic "predation tags" (Halfyard et al. 2017). If predation plays a role in reducing the apparent survival of pre-smolts in the TH strategy, a selection of alternative release locations and timing should be studied to reduce mortality risk.

The results of this study also showed that by using the TH strategy, the pre-smolts will be overwintering in habitat much further downstream than what appeared to be their naturally chosen affinity, although the habitat quality in the approximate 20 rkm section immediately downstream of the MGS provides habitats that are generally suitable for juvenile salmon in winter (Wegscheider et al. 2018). In the winter, large-sized salmon parr are known to prefer low-flow areas potentially to conserve energy (Heggenes and Dokk 2001). This may have been the situation observed for a few TH pre-smolts in this study that appeared to have overwintered in the backchannel habitat available downstream of the MGS.

Chinook salmon (*Oncorhynchus tshawytscha*) smolts that were transported downstream in the Snake River system had compressed migration times that did not allow for the growth experienced by in-river migrants, leading to size selective predation (Muir et al. 2006). However, in-river migrants delayed by multiple dam passages that reached downstream later in the migratory window also experienced increased mortality risk (Muir et al. 2006). Based on this and previous studies of the TH strategy in other systems, it was predicted that the TH group could potentially reach the mouth of the river at an earlier time in their migratory window in the spring than they would have normally (Whitney et al. 2006). However, the timing of arrival to the

estuary was not found to be accelerated for the TH group relative to the successful migrants in the FS group, with arrival to the lowermost receivers occurring within similar timeframes for both groups.

A caveat to this analysis is that it is a technical possibility that the tagged smolts in the TH group could have moved into the estuary in the winter when the acoustic tags entered their non-transmitting mode, and would have then further emigrated from the river in very cold water temperatures prior to the tags resuming transmissions. Successful estuarine residency prior to smolt migration has been documented for Atlantic salmon parr, particularly in smaller rivers (Cunjak et al. 1989). However, the locations where the TH tags activated in the spring, and the general observations of winter movements of juvenile Atlantic salmon (Linnansaari et al. 2009; Linnansaari and Cunjak 2013) suggests that the results of this study are not biased by winter-time migration that would have occurred prior to acoustic tag activation in spring.

Salmonid migrations worldwide are impeded by dam obstruction (Liermann et al. 2012) and there is a general understanding that the cumulative effects of dams and reservoirs combined with multiple additional stressors can impact salmonid populations (Norrgård et al. 2013). Endangered populations, such as the outer Bay of Fundy Atlantic salmon studied herein, must be protected by ensuring safe passage, especially when multiple dams obstruct their migratory pathway (Committee on the Status of Endangered Wildlife in Canada 2011). While various threats to the SJR Atlantic salmon population and recovery actions have been identified, hydropower dams are of the highest concern due to extensive habitat alterations and cumulative mortality from fish passage (Clarke et al. 2014). We assessed the behavior and survival of free-swimming

(through two dams and reservoirs) and trapped-and-hauled (past all dams) smolts and found survival rates and migratory timing to be similar between the two strategies. While not conclusive, this study suggests that successful free-swimming passage by smolts can be achieved and that provision of effective dam passage via a bypass could reduce mortality during their out-migration. This may be the preferred management strategy in the SJR. However, we do not yet know the condition of free-swim versus trap-and-haul smolts as they enter the sea, *e.g.*, TH smolts may have had greater energy reserves owing to the shorter migration distance and without dams and reservoirs to navigate.

4.6 Acknowledgements

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Table 4.1. Sample size (N), tagging date (2015), weight (g), fork length (cm), and condition factor (mean ± SE) of Atlantic salmon pre-smolts in experimental (Free-Swim and Trap-and-Haul release groups), and control (Dummy-tagged and Untagged) groups. Letters represent significant differences.

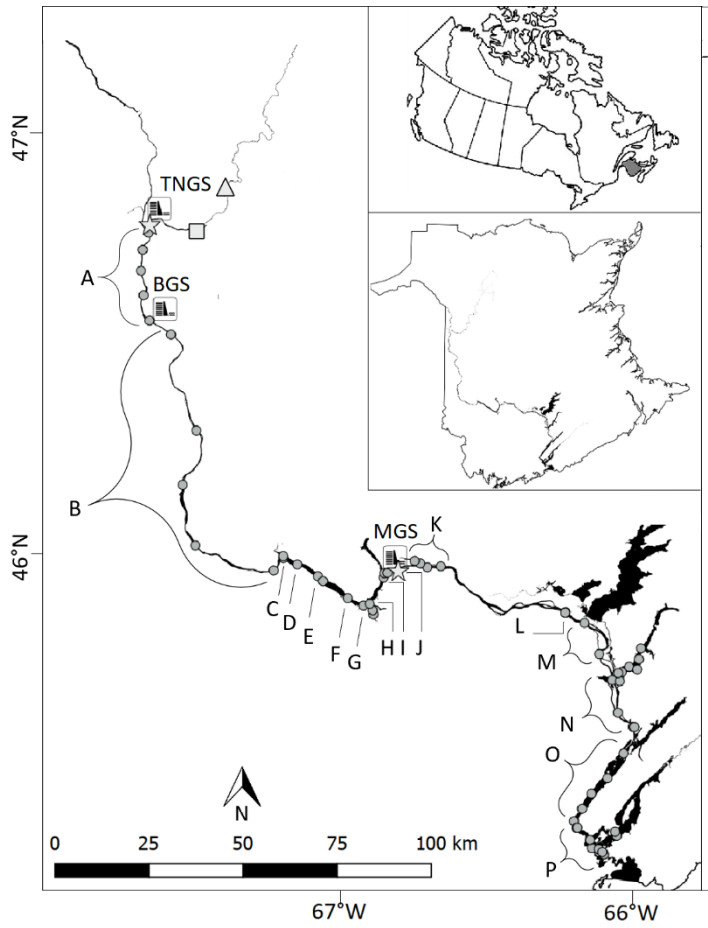
Group	N	Tagging Date	Weight (g)	Fork length (cm)	Condition
Free-Swim (FS)	50	28 Oct – 25 Nov	40.4 ± 0.9 z	16.2 ± 0.1 z	0.95 ± 0.01 z
Trap-and-Haul (TH)	50	28 Oct – 25 Nov	40.6 ± 0.8 z	16.1 ± 0.1 z	0.96 ± 0.01 z
Dummy-tagged[1]	50	27 Oct – 9 Dec	44.6 ± 1.2 y	16.3 ± 0.1 z	1.02 ± 0.02 y
Untagged[1]	50	5 Nov – 10 Dec	42.9 ± 1.6 y	16.2 ± 0.2 z	0.99 ± 0.02 y

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

Table 4.2. Model selection of Cormack-Jolly-Seber survival (Φ) and encounter (p) probabilities with (s) and without (.) spatial variability, Akaike Information Criteria corrected for small sample sizes (AIC_c), and model weight (w_i).

Model	AIC_c	w_i	Evidence ratio
Φ(s)p(s)	605.5523	0.99917	$3.300x10^7$
Φ(.)p(.)	619.7303	0.00083	27530
Φ(s)p(.)	640.1764	0.00000	1

Note: Evidence ratio describes how well the evidence supports the model



Reach	Rkm	Number of receivers
A	288-313	6
B	192-250	5
C	187	2
D	182	1
E	175	4
F	167	3
G	162	2
H	158	3
I	151	4
J	146	2
K	138-144	5
L	95	1
M	76-89	2
N	53-69	6
O	20-50	6
P	9-15	5

Figure 4.1. Location of fish capture at Three Brooks (triangle), tagging (square), and release (stars), along with three generating stations (Tobique Narrows, TNGS; Beechwood, BGS; Mactaquac, MGS) in the Saint John River, New Brunswick, Canada. The location of the Mactaquac Biodiversity Facility (MBF), where control groups were monitored, overlaps with the release location downstream of the MGS. Also shown are the locations of VR2W receivers (circles) and Cormack-Jolly-Seber groupings of receivers in river reaches.

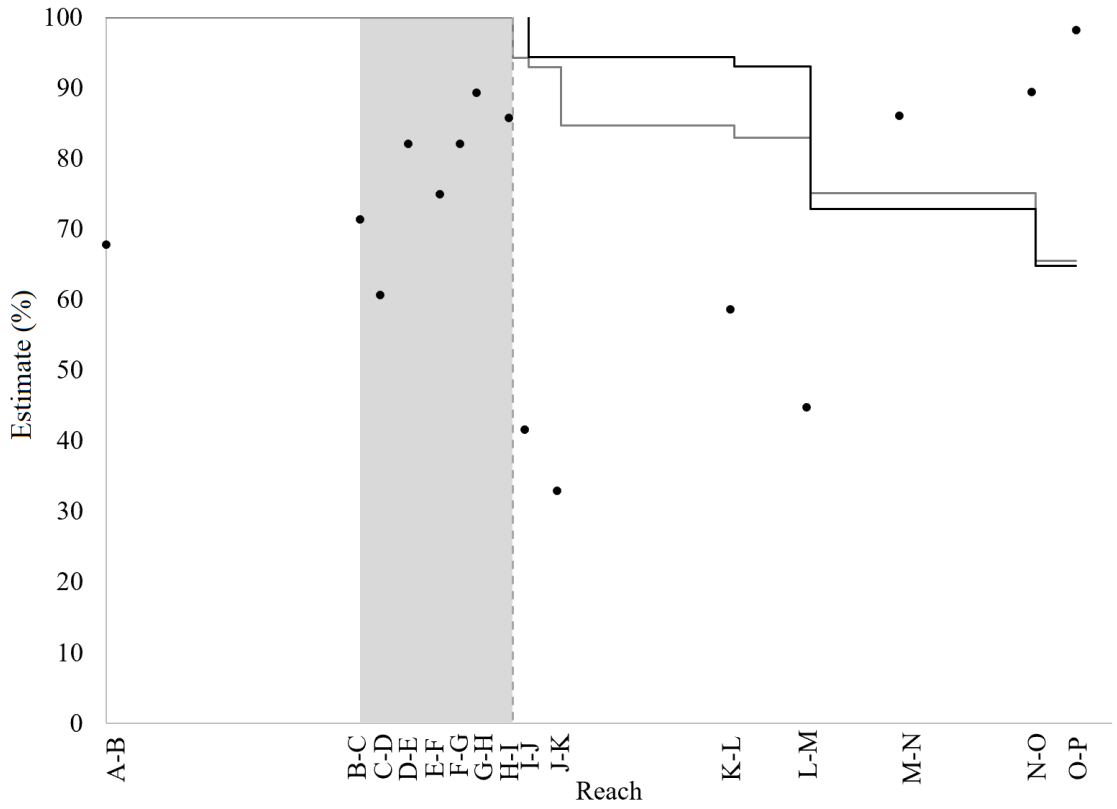


Figure 4.2. Cormack-Jolly-Seber encounter probability (p) by river reach (black dots) and cumulative apparent survival from φ estimates (%) during the spring migration of tagged (Free-Swim grey line, Trap-and-Haul black line) Atlantic salmon smolts in 15 river reaches (see Figure 4.1) in the Saint John River. The grey shaded area represents the Mactaquac reservoir and the dashed vertical line represents the location of the Mactaquac Generating Station.

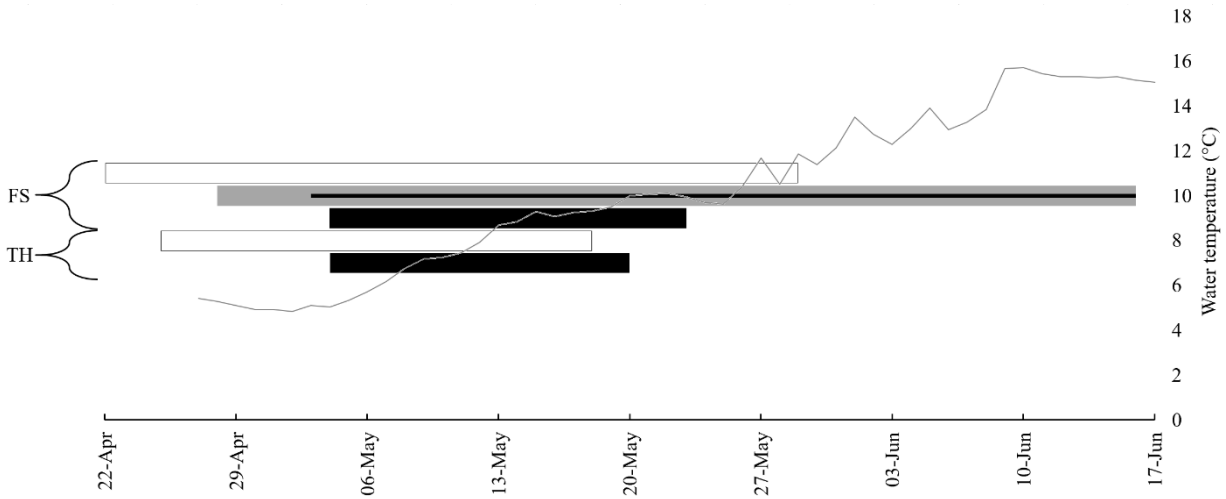


Figure 4.3. Migratory timing of Atlantic salmon tagged as pre-smolts (FS = Free-Swim, TH = Trap-and-Haul) initiation of migration (white bar), arrival at the Mactaquac Generating Station (MGS; grey bar) with closed spill (black line), and arrival at the lower Saint John River (SJR; black bar), and associated daily average water temperature in the mid-reservoir (grey line; reach G; Figure 4.1).

Chapter 5

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

A. B. Babin[a], T. Linnansaari[ab], M. Ndong[c], K. Haralampides[c], S. Peake[a], R. Jones[d], and R. A. Curry[ab]

Canadian Rivers Institute, Department of Biology[a], Faculty of Forestry and Environmental Management[b], and Department of Civil Engineering[c], University of New Brunswick, Bailey Hall, 10 Bailey Drive, P.O. Box 4400, Fredericton, New Brunswick, Canada, E3B 5A3

[d]Fisheries and Oceans Canada, Maritimes Region, 343 Université Avenue, P.O. Box 5030, Moncton, New Brunswick, Canada, E1C 9B6

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5.1 Abstract

Little is known about the behavior and migration of post-spawned Atlantic salmon (kelts). Repeat spawning can be critical to sustain natural populations and thus interruptions of kelt migration in hydropower regulated rivers, *i.e.*, dam passage success and delays or mortalities associated with reservoir residence, may exacerbate the challenges of post-spawning migration including over winter survival which may in turn affect the probability of kelts surviving to become repeat spawners. This study tracked 47 post-spawned adult Atlantic salmon (*Salmo salar*) in a hydropower-regulated river through autumn, winter, and spring across two field seasons. Winter survival was 56 % and 75 % in the two study years, respectively, with higher mortality of males than females (50 % vs. 33 % and 100 % vs. 13 %, respectively). Survival after the initiation of migration in spring was 95 % and 82 % to the hydropower dam in the first and second study years, and decreased to 63 % and 60 %, respectively, after dam passage. There were no further losses in the downriver reach in the first year, with the second 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 = 4) and the only remaining passage option was restricted to the turbines. Migratory delay was estimated at approximately six days as migration rates were significantly slower in the reservoir (median ± SE: 8.5 ± 2.5 km d^{-1}) than up- (29.7 ± 5.0 km d^{-1}) or downriver (22.1 ± 3.1 km d^{-1}). The proportion of time (median 30 %) that kelts spent swimming upstream in the reservoir was a significant variable negatively affecting an

index of migration success. Minimizing the migration delay of kelts observed could aid population recovery.

5.2 Introduction

Adult Atlantic salmon (*Salmo salar*) spawn in rivers in the autumn and due to their iteroparous life history strategy, the surviving post-spawners 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 (Ruggles, 1980; Jonsson *et al.*, 1990). The post-spawners that overwinter in the river are known as kelts when they re-initiate their migration in the spring. 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). There is a general paucity of data regarding kelt behavior and movements in the freshwater environment (Bardonnet and Baglinière, 2000; Hubley *et al.*, 2008).

Kelts can become repeat spawners in the population if they survive their outward migration, time at sea, and return spawning migration. Atlantic salmon iteroparity could be a key factor in the recovery of declining populations (Saunders and Schom, 1985; Niemelä *et al.*, 2006). 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 (Jones, 1959; Halttunen, 2011). Larger females produce fewer but larger eggs per unit body size that can develop into larger-bodied juveniles than those from smaller eggs, providing a greater chance of survival (Beachum and Murray, 1993; Fleming, 1996). Genetic diversity is also increased by repeat spawners because they add multiple year-classes to the annual production of young (Saunders and Schom, 1985; Niemelä *et al.*, 2006).

While iteroparity may be an aspect that helps Atlantic salmon 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 Atlantic salmon 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 as has been observed for anadromous brown trout (*Salmo trutta*; Östergren and Rivinoja, 2008) and steelhead (*Oncorhynchus mykiss*; Wertheimer and Evans, 2005). 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;

Scruton *et al.*, 2008). Passage via turbines makes them susceptible to injury and death due to their large body size (Ruggles, 1980).

Many populations of Atlantic salmon are declining in Canada (Committee on the Status of Endangered Wildlife in Canada, 2011). Atlantic salmon returning to the Saint John River (SJR; New Brunswick, Canada) are part of the Outer Bay of Fundy (OBoF) 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 lifestage for population recovery (Saunders and Schom, 1985; Halttunen, 2011). The objective of this study was to explore the overwinter and migratory behaviour of Atlantic salmon kelts in relation to a large hydropower generating station (the Mactaquac Generating Station; MGS) and its associated reservoir. Specifically, this study aimed to quantify (1) post-spawned adult survival over winter, (2) migration timing in relation to environmental conditions and hydropower operations, (3) migration rates through lotic and lentic reaches to estimate potential migratory delay in the reservoir, and (4) survival rates in the spring as they navigated the reservoir and dam on their way to the river mouth.

5.3 Materials and Methods

Study area

The 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 1,100 m^3 s^{-1} (Cunjak and 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 Dec 2014 to 12 Apr 2015, and from 14 Jan to 21 Feb 2016, respectively (C. Côté, Environment Canada, personal communication).

The MGS (Figure 5.1) was completed in 1968. It is the largest dam in New Brunswick (1,100 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 (max discharge 2,294 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; migrating fish may either pass via two separate spillway structures when open (bottom spill at 17 m depth), or through one of the six Kaplan turbines (112 MW/112.5 rpm each) which have their intake at 8-23 m depth. 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 5.1). Average water velocity in this 37 rkm lake-like reach upstream of the MGS (reaches I to C; Figure 5.1) 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 labeled 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; BGS, rkm 285, and the Tobique-Narrows Generating Station; TNGS, rkm 315) along the main salmon migration route to

the Tobique River which is the main Atlantic salmon nursery habitat in the upper SJR (Marshall *et al.*, 2014).

The Mactaquac Biodiversity Facility (MBF) just downstream of the MGS is operated by the Department of Fisheries and Oceans Canada (DFO) to supplement Atlantic salmon production within the river (Jones *et al.*, 2004). The MBF 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 1,000-3,000 annually) are captured from the Tobique River or the BGS gatewells upon their seaward migration, captively reared to maturity, and released back to the wild as adults (387-1,450; Jones *et al.*, 2014) to spawn naturally.

Tagging and tracking

Post-spawned Atlantic salmon adults were acoustically tagged (Table 5.1) and tracked to determine overwintering behaviour, spring migration rates and success. Fish were sourced from the wild via rotary screw traps operated by DFO located at Three Brooks (46.86914 -67.42933), or by angling in pools at the Forks of Tobique River (47.24502 -67.15644) or the Barrier Pool (47.24033 -67.14208) 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, DFO, personal communication), and therefore these fish are termed Wild-Caught, Captive-Reared (WC-CR). The number of kelts tagged were also supplemented by kelts that were spawned at the MBF as part of a broodstock program, and these fish are termed

CR-Broodstock. Captive-reared fish would 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 the TNGS or BGS in order 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 mainstem of the SJR from the Tobique River or any 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 5.1) and tagged (Table 5.1). 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 5.1). 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 CR-Broodstock adults were also tagged on 24 November 2014 at the MBF

facility (Table 5.1). After tagging, the fish were treated in a 1:300 formaldehyde bath for 45 min then held at MBF for 2 d before being transported for 1.5 h and released at the same site.

Two sea-run adult Atlantic salmon that had been gastrically tagged as part of a study examining the upstream migration of wild adults through the MGS reservoir were also tracked (Babin *et al.*, unpublished). These two adult Atlantic salmon were captured at the MGS fishlift during their summer spawning migration (Table 5.1; WCS), tagged on 28 July 2014 and held for two 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 and tagged. One was angled at the Forks of Tobique River and nine were angled at the Barrier Pool on 13 November 2015, and eight were captured from the Barrier Pool on 20 November 2015. 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 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) 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 d, every 600 s for the next 100 d (over winter period), and every 60 s during the spring migration period. Battery life was estimated to last 1078 days for non-sensor 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 non-sensor tags, and 277 days for the sensor tags. The tag/body weight ratio averaged 0.51 % (SE = 0.05 %). Tagging was performed using 40-80 ppm clove oil anesthetic (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 either recovered in a 1000 L tank (wild-caught), or in 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 in 2015-2016 (Figure 5.1). A data partnership with the Ocean Tracking Network also provided detections from these tagged kelts as they exited the SJR and traveled 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*., unpublished).

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

Hydrodynamic model 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 two hours 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 5.1) and 233 (reach B; Figure 5.1) 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. Within the reservoir loggers were placed within the mid-water column, whereas the up- and downriver reaches where water depth is much shallower, they were placed near the riverbed.

Statistical analyses and definitions

A Kruskal-Wallis test was 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.

Given the relatively high detection probabilities throughout the study area (see encounter estimates below), the last detection of each tag was assumed to represent the area of mortality. 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 include tag loss due to expulsion of the tag (Kennedy *et al.*, 2018). Chi-square tests were used to compare proportions of winter survival between years and sexes.

Linear mixed effects models (LMEM) 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 d^{-1}) were examined by comparing overall values within the upriver (defined as reach B; Figure 5.1), reservoir (C-I; Figure 5.1), and downriver (J-O; Figure 5.1) 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 5.1); reservoir – from the last detection as they first entered the reservoir (reach C; Figure 5.1) to the first detection near the MGS (reach I; Figure 5.1); and downriver – from the last detection as they were first detected downstream of the MGS (reach J; Figure 5.1) 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 traveling upstream during winter, the reconditioning period (*i.e.*, a period prior to initiation of directed spring migration movements but when activity was apparent), 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 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 5.1), 1 = dam passage at MGS but no further migration (J; Figure 5.1), 2 = movement downstream of the MGS (K; Figure 5.1), 3 = halfway downriver (L; Figure 5.1), 4 = top of estuary (N; Figure 5.1), 5 = lower SJR (O; Figure 5.1), 6 = outside of SJR.

Cormack-Jolly-Seber (CJS; Lebreton *et al.*, 1992; Bowerman and Budy, 2012) models were used to estimate survival (Φ) and encounter (p) probabilities during the spring migration towards 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 (Lebreton *et al.*, 1992; Bowerman and Budy, 2012). Models assumptions included that *i)* tagged individuals alive in spring were representative of the population, *ii)* survival rates in spring (*i.e.*, > 3 months post-tagging) did not differ between tagged and untagged individuals, *iii)* each tagged individual had an equal but independent probability of survival and detection during spring migration, *iv)* no tags were lost in the spring and sampling was instantaneous, and *v)* movement during spring was generally unidirectional (*i.e.*, downstream with an *a priori* motivation of exiting the river). For the purposes of the CJS analysis, detections from receivers were pooled into spatial clusters 14 reaches for which Φ and p estimates were calculated (reaches; Figure 5.1). 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) of each reach. A null model whereby both survival and encounter probabilities were not allowed to vary by reach was constructed for comparison. To compare models with or without spatial variability, the relative support for each candidate model was assessed by calculating the differences in corrected Akaike's Information Criterion (AIC_c) between the best model and the *i*th model and further calculating model probabilities (ω_i; Hurvich and Tsai 1993; Burnham and Anderson, 2002). Chi-square tests were used wherever proportions were compared for significance, including apparent 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 and Burnham, 1999). Normality plots were analyzed where appropriate, and statistical significance was assumed when *p* was less than or equal to 0.05.

5.4 Results

Two tagged post-spawned adult Atlantic salmon were never detected downstream of the release site in 2014 and were potentially mortalities related to tagging and associated stress.

Winter movements and survival, and spring reconditioning period prior to migration

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 5.1) to the next receiver downstream (250 rkm; reach B; Figure 5.1) was considered the initiation period. The length of the initiation period in 2014 was 7.9 ± 2.8 d (median ± SE; n = 17; 2014) and 20.2 ± 5.9 d (n = 16; 2015), with WC-CR fish taking significantly longer (11.5 ± 6.0 d) than CR-Broodstock fish (7.9 ± 2.1 d; Kruskal-Wallis test, $\chi^2 = 5.96$, df=1, $p = 0.01$), but no significant differences between the sexes were detected (Kruskal-Wallis test, $\chi^2 = 1.44$, df=2, $p = 0.49$).

Winter survival including potential mortality related to tagging was 56 and 75 % for 2014 and 2015, respectively ($\chi^2 = 1.76$, df = 1, $p = 0.18$). The majority (n = 7/11, 64 %) of overwintering mortality occurred upriver (reach B; Figure 5.1) in 2014, and in the lower reaches of the reservoir in 2015 (n = 4/5, 80 %; reaches H-I; Figure 5.1). Winter survival was higher for females than males in both years (2014 67 % vs. 50 %, 2015 88 % vs. 0 %; $\chi^2 = 4.90$, df = 1, $p = 0.03$). Winter mortality was generally higher for small than large salmon in both years (2014 47 % vs. 30 %, 2015 44 % vs. 9 %) but these differences were not statistically significant ($\chi^2 = 3.54$, df = 1, $p = 0.06$).

Kelts exhibited non-directed movements prior to directed downstream movements that indicated the initiation of migration in the spring. This behavior 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 non-directed movements (Table 5.2) from 7 to 20 May (mean ± SE: 9 ± 1 d) with water temperatures of 9-15 °C, whereas in 2016 reconditioning movements were observed by some of the earliest migrants as well as later migrants (Table 5.2) from 21 February to 8 April (17 ± 6 d) in waters just above

freezing. In both years, all individuals displayed this behavior over an approximately 30 rkm reach spanning from upriver into the reservoir (B-C; Figure 5.1), with the exception of one kelt in 2016 that reconditioned and initiated migration from near the MGS.

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 5.1). In 2015, earlier migrants (19 Apr-4 May; Table 5.2) initiated their migration from the top of the reservoir (reach C; Figure 5.1), with later migrants (7 May-2 Jun; Table 5.2) beginning their migration from upriver (reach B; Figure 5.1). Five kelts initiated their migration while the spring freshet was increasing, with the timing being associated with peaks in discharge (Figure 5.2). One kelt initiated migration during the first peak in discharge and was ultimately successful in reaching the lower SJR (reach O; Figure 5.1), whereas two kelts that initiated their migration during the second peak in discharge were unsuccessful in passing the MGS. The highest recorded discharge (23 Apr 2015 0400 h, 5862 m^3 s^{-1}) was closely followed by two kelts initiating migration, with only one passing the MGS and reaching the lower SJR. 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 5.2). Two of these kelts were unsuccessful in dam passage and six reached the lower SJR. There were only three males in the first study year that initiated 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 5.2). 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 5.1; Table 5.2). Two kelts initiated migration before the onset of the spring freshet, with one ceasing detection shortly after MGS passage and the other being successful in reaching the lower SJR. There was a strong association of the initiation of migration with peak discharges; one kelt was prompted by the first increase in discharge and reached the lower SJR; four kelts moved with the second increase in discharge to reach the lower SJR; and three kelts initiated migration during the third and strongest peak in discharge when one kelt presumably died after MGS passage while the others reached the lower SJR (Figure 5.2; Table 5.2). The remaining four kelts initiated migration after the peak freshet with one being unsuccessful in finding a pass through the MGS, two ceasing detection shortly after MGS passage, and one reaching the lower SJR (Figure 5.2; Table 5.2). Similarly to 2015, water temperature did not appear to be a direct trigger of kelt migration. Overall, cumulative degree day (CDD) 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 either being unsuccessful or successful in passing through the dam. In 2015, 58 % were delayed from 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 5.2). In 2016, MGS passage primarily occurred at night (73 % vs. 27 %), approximately 11

days after migration initiation (Table 5.2). The median duration between the last detection upstream and the first detection downstream of the MGS was 81 minutes (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 5.2) and 56 % of which were successful in reaching the lower SJR (Table 5.2). Four kelts attempted passage when spillway gates were closed with all being successful in reaching the lower SJR (Table 5.2). 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 5.2), and 25 % of which presumably experienced delayed mortality because their last detections occurred within 4 rkm of the MGS (reach J; Figure 5.1; Table 5.2). Two kelts last encountered the MGS when spillway gates were closed, one of which presumably experienced delayed mortality (reach J; Figure 5.1; Table 5.2) while the other reached the lower SJR (Table 5.2). Overall, all of the kelts actively migrating in the spring (n = 28) reached the MGS, 82 % were able to pass the MGS, but four of those (17 %) experienced delayed dam passage mortality.

Spring migration rates, and temperature and depth of migration

Migration rates were significantly slower in the reservoir (8.5 ± 2.5 km d^{-1}) than up- (29.7 ± 5.0 km d^{-1}) or downriver (22.1 ± 3.1 km d^{-1}; LMEM, $p < 0.001$; Table 5.3a; Figure 5.3), with 11.7 % of the observed variation in overall migration rates attributable

to individual fish. If kelts would have had the ability to travel through the reservoir at the river rates (*i.e.*, reservoir in its natural river state prior to MGS construction), they would have covered this distance approximately 5-6 days sooner than was observed (median ± SE: upriver migration rate 5.4 ± 1.9 d, downriver migration rate 6.2 ± 2.1 d).

Migration rates were related to concurrent water temperature and velocity in a fine spatial scale by calculating rates between each receiver only as the fish were directed downstream. Downstream-directed, fine-scale migration rates did not differ by reach (*i.e.*, upriver, reservoir, downriver; LMEM, $p = 0.79$; Table 5.3b); however, greater water temperatures were found to be associated with higher downstream migration rates between receivers (LMEM, $p = 0.04$; Table 5.3b), and concurrent water velocity was negatively related to downstream migration rates between receivers (LMEM, $p = 0.04$; Table 5.3b).

After initiating their directed spring migration, tagged kelts were often observed swimming in the reverse direction to the main migratory direction (Figure 5.4). Overall, kelts covered a minimum of an additional 57-61 (± 20-23) extra rkm due to the reversals as compared to traveling 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 behavior was especially prevalent in the reservoir where 63 % and 73 % of the tagged kelts spent a median of 17 % and 33 % of their time prior to reaching the MGS swimming upstream during the spring migration in 2015 and 2016, respectively (Figure 5.4). The proportion of time spent in reverse direction in the reservoir was lower (pooled median 12 %; Figure 5.4) 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 5.4; 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 5.1 and 5.5), the middle of the reservoir (reaches G-I; Figures 5.1 and 5.5), within the reservoir in proximity to the MGS (Figure 5.5), and in the estuarine part of the river that is under the influence of high tidal action (reach O; Figure 5.1 and 5.5). The higher the proportion of time that fish spent traveling upstream, the lower their overall migration success (ORM, $p = 0.05$; Table 5.3c), and water temperature was positively correlated with migration success (ORM, $p = 0.03$; Table 5.3c). Tides (ORM, $p = 0.06$; Table 5.3c), water velocity (ORM, $p = 0.22$; Table 5.3c), and individual migration rates (ORM, $p = 0.66$; Table 5.3c) 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 5.3d), or by the maximum angle of the water from downstream (LMEM, $p = 0.94$; Table 5.3d).

The distance that kelts traveled during their spring migration was equally distributed between the day and night (2015 50 % day, 2016 52 % day). The percentage of distance traveled 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 nighttime movements in the reservoir after the kelts had encountered the MGS (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 5.6A). Temperature experienced by the tagged kelts was different during the reconditioning period between the two years,

with median temperatures of 10-11 °C experienced by the late reconditioning period in 2015 compared to < 1 °C experienced by those reconditioning over a wider time frame in 2016. During the spring migration period, median temperatures experienced in the reservoir ranged from just above zero 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 5.6B) 96 ± 6 % (median ± SE) of the time (including dam passage), with the exception one tagged kelt in the second study year that spent 60 % of the time between 30-40 m overwintering near the MGS. It moved between 23-34 m (99 % of activity) during its reconditioning period and was never observed above 10 m. This fish survived and exited the river where it was subsequently detected in the Gulf of Maine (Figure 5.7).

Spring survival

The most plausible CJS model in the candidate model set had > 99 % of support (Table 5.4) and included spatial variability in both survival (Φ) and encounter (p) estimates between the 14 reaches (Figure 5.1). Encounter estimates were always greater than 65 % (Figure 5.8). Apparent survival estimates in all reaches upstream of the MGS were generally high (94 % in 2015 and 82 % in 2016, reaches A-I; Figure 5.1) and similar between study years ($\chi^2 = 1.37$, df = 1, $p = 0.24$). The greatest declines in apparent survival occurred as the kelts passed the MGS in both years (32 % in 2015, 22 % in 2016; Figure 5.8; reach I-J; Figure 5.1), with the estimate for the first study year including delayed effects of dam passage on survival. The tagged kelts that survived

passage at the MGS (including delayed mortality) had generally high survival for the rest of the migration downriver (no losses in 2015, 7 % decrease in 2016; Figure 5.8; reaches L-O; Figure 5.1). Upon reaching the lower SJR (reach O; Figure 5.1), cumulative survival estimates were 63 % in 2015 and 53 % in 2016 which were not significantly different ($\chi^2 = 0.31$, df = 1, $p = 0.58$). Survival was similar between the sexes (2015 60 % males, 50 % females; 2016 no males remaining, 57 % females; pooled $\chi^2 = 0.05$, df = 1, $p = 0.82$) and between small and large kelts (2015 37 % small, 57 % large; 2016 80 % small, 40 % large; pooled $\chi^2 = 0.13$, df = 1, $p = 0.72$).

Five kelts were detected after leaving the SJR (Ocean Tracking Network; Figure 5.7). In 2015, four kelts were detected by receivers on the Halifax Line. On average, it took 16 ± 4 days for the kelts to travel from the SJR to the Halifax Line where they were detected over a two-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 ± 10 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, traveling from 0-22 m depth and experiencing temperatures of 10.4-11.1 °C.

5.5 Discussion

This study tracked Atlantic salmon post-spawners/kelts from upstream of and in a large hydropower reservoir, and then downstream of a hydropower generating station.

We observed that *i*) the reservoir appeared not to be a preferred overwintering area but was potentially used for reconditioning in the spring by some kelts; *ii*) migration rates were slower in the reservoir with frequent migration reversals leading to migratory delay; and *iii*) dam passage was associated with declines in apparent survival.

Winter survival of tagged post-spawned Atlantic salmon 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 lifestages of Atlantic salmon (Huusko *et al.*, 2007). 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), and 20-37 % in a Norwegian river (Halttunen, 2011). 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 (67-88 % vs. 50-0 %), and compared to other systems where females had higher survival rates than males (62-74 % vs. 43-62 %; Niemelä *et al.*, 2000; Halttunen *et al.*, 2013). 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. 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 Atlantic salmon kelts was assumed to be minimal since the tag burden averaged less than 0.5 % of fish weight and thus, 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.

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, Atlantic salmon kelts had relatively high survival in the MGS reservoir (82-95 %). Atlantic salmon 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 (Wertheimer and Evans, 2005; Colotelo *et al.*, 2014; Nyqvist, 2016), 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 (Muir *et al.*, 2001; Jones and Flanagan, 2007), especially for larger-bodied fish (Ruggles, 1980), although spillway passage is not free of risks (*e.g.*, gas bubble disease; Brown *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 Atlantic salmon kelts (Nyqvist, 2016; Nyqvist *et al.*, 2016). In our study, dam passage was associated with declines in apparent survival estimates (22-32 %), including four kelts that presumably experienced delayed dam passage mortality. 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 apparent survival rate of 23 % as kelts exited the hydropower-regulated Penobscot River (Maynard *et al.*, 2018), but could be slightly lower due to dam passage in comparison to the high rates found for Atlantic salmon in un-regulated rivers (63-80 %; Halttunen, 2011; 90 %; Hubley *et al.*, 2008).

Migratory timing can depend on biological as well as environmental conditions. In the current study, the two years differed in their 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 Canada, personal communication). Jonsson *et al.* (1990) reported that post-spawned Atlantic salmon activity is low when water temperatures are < 2 °C, and migration initiation is often reported when water temperature exceeds 4-6 °C (Östergren and Rivinoja, 2008). At the MGS, water temperatures began rising from near zero earlier in 2016 (12 April) than in 2015 (25 April), driving faster CDD 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 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 lower condition after spawning (Jonsson *et al.*, 1990; Fleming, 1996; 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 and therefore low statistical power. The first male initiated spring migration two weeks after the first female (2 May 2015 vs. 19 April 2015), and the kelt which migrated latest in either season was also a male (2 June 2015).

Kelts often begin directed downstream movements before smolts initiate their migration (Jonsson *et al.*, 1990). A concurrent study tagging pre-smolts in the autumn and tracking their movements through the SJR in the spring indicated that kelts entered the reservoir approximately one month before smolts (19 April vs. 14 May 2015, 22 March vs. 25 April 2016; Babin *et al.* unpublished). Similar patterns are observed in the nearby, free-flowing Miramichi River, New Brunswick, where Atlantic salmon kelts reportedly recondition and actively migrate in late April (Strøm *et al.*, 2017), while the

smolt migration typically peaks between mid-May to early June (Chaput *et al.*, 2016, 2018).

There is evidence of kelts beginning to recondition by feeding in the spring while emigrating to the ocean (Penney and Moffitt, 2014). Kelts from Hammond River in the lower SJR were found to spend 10-27 d in the estuary feeding and reconditioning before entering the ocean (Lacroix, 2013). Food items can include smolts, other small fish, and invertebrates (Penney and Moffitt, 2014). In the current study, some kelts from the Tobique River of the SJR displayed non-directed movements for 10-33 d 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. The fish could be increasing muscular functioning by obtaining nutrition before undertaking a long migration; however, unlike other salmon rivers, there are no smelt or alewife 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. Their position remained near the surface during dam passage, 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. The kelts also traveled 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 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 d^{-1}, reservoir 8.5 ± 2.5 km d^{-1}, downriver 22.1 ± 3.1 km d^{-1}). This was interpreted to result in an approximate 6 d 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 and Coleman, 1988); otherwise, the exacerbated depletion in energy reserves could decrease the likelihood of a kelt becoming a repeat spawner (Fleming, 1996; Wertheimer and Evans, 2005).

Migratory delay in the reservoir could be attributed to three separate aspects: 1) low water currents leading to reversed direction swimming during searching behavior; 2) time spent in dead-end tributaries; and 3) 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 modeled 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 hydrodynamic model variables were estimated for the surface 5 m of the water column where the fish were assumed to travel, but the actual location of the fish in 3D space could have caused a mismatch with concurrent hydrodynamic conditions. The directional cue of water flow could potentially be re-introduced through the use of a large-scale implementation of a Flow Velocity Enhancement System (FVES; 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 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 brown trout 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 pre-disposed direction. The highest proportion of reversals was observed during the 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 re-occur.

If Atlantic salmon are to become repeat spawners, they must survive their first spawning, overwintering, and kelt spring migration that may include passage of one or multiple dams such as in the current study. Atlantic salmon 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 lifestage as a repeat spawner. The programmed transmission rate of the V13 tags used in this study would have generally allowed re-detection 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 acoustically tagged kelts that were known to enter the Bay of Fundy during the two years of study, four were detected on the OTN'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 acoustically tagged kelts were detected re-entering the SJR as repeat spawners. While post-spawner survival may be relatively high elsewhere

(Halttunen, 2011; Chaput *et al.*, 2016) and the repeat spawners have become an increasingly large component of total returns in some Atlantic salmon populations (*e.g.*, Chaput, 2008; 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 (Mills, 1989; Fleming and Reynolds, 2004; Hubley and Gibson, 2011; Jones *et al.*, 2014; Maynard *et al.*, 2018). In the light of the Atlantic salmon 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 Atlantic salmon in the marine environment (Chaput and Jones, 2006; Benoit and Swain, 2008; Hubley and Gibson, 2011; Lacroix, 2014; Kelly *et al.*, 2019).

Hydropower managers should ensure that safe and efficient downstream migration routes are available for migrating Atlantic salmon 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 the largest decline in apparent 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 non-turbine egress route would be available throughout the whole kelt migration period. Although ensuring survival of even 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 and then subsequently improving their survival would be a necessary first step contributing to recovery of the Atlantic salmon population in the SJR.

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Table 5.1. Fork length (cm) and weight (kg; mean ± SE) of acoustically tagged adult Atlantic salmon in 2014 and 2015. The tagged Atlantic salmon included wild-caught captive-reared (WC-CR) and captive-reared broodstock[1] (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.

Year	Origin	Sex	N tagged	Fork length (cm)	Weight (kg)
2014	WCS	F	1	78.4	4.95
	WCS	M	1	56.8	2.05
	CR-Br.	F	4	63.7 ± 2.1	2.56 ± 0.29
	CR-Br.	M	7	66.1 ± 1.4	2.76 ± 0.19
	CR-Br.	All	11	65.2 ± 1.2	2.69 ± 0.16
	WC-CR	F	10	56.8 ± 5.2	1.75 ± 0.43
	WC-CR	M	2	43.2	1.45
	WC-CR	Unk.	2	59.9 ± 3.9	3.31 ± 0.49
	WC-CR	All	14	56.3 ± 3.9	2.10 ± 0.38
2015	CR-Br.	M	2	65.0 ± 5.0	3.45 ± 1.09
	WC-CR	F	15	64.6 ± 2.4	3.08 ± 0.29
	WC-CR	M	1	60.0[2]	1.41
	WC-CR	Unk.	2	62.9 ± 2.9	2.11 ± 0.75
	WC-CR	All	18	64.4 ± 2.0	2.87 ± 0.27

[1]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)
[2]Total length

Table 5.2. Location (reach, rkm) and timing of initiation of Atlantic salmon kelt (WC-CR=Wild-Caught, Captive-Reared; CR-Br.=Captive-Reared, Broodstock; WCS=Wild-Caught, Summer) spring migration, and timing of the first encounter and passage of the Mactaquac Generating Station (MGS) with availability for fish passage via spillway gates upon the date of last encounter. The reaches are indicated using the lettering corresponding to Figure 5.1.

Year	Tag[1]	Origin	Reach (rkm)	Inititation	MGS encounter	MGS Passage	Spillway
2015	12395/96	WC-CR	C (187)	19 Apr	23 Apr	23 Apr	Open
	12381/82	WC-CR	C (187)	20 Apr	22 Apr		Open
	12387/88	WC-CR	C (187)	20 Apr	27 Apr		Open
	12391/92	CR-Br.	C (187)	23 Apr	27 Apr	27 Apr	Open
	22746	CR-Br.	C (187)	23 Apr	27 Apr	27 Apr	Open
	12383/84	WC-CR	C (187)	24 Apr	29 Apr		Open
	22752	CR-Br.	E (175)	26 Apr	28 Apr		Open
	17154	WCS	G-H (160)	1 May	2 May	2 May	Open
	22757	WC-CR	C (187)	4 May	8 May	9 May	Open
	22750	CR-Br.	B (216)	7 May	14 May	15 May	Closed
	12377/78[2]	WC-CR	B (216)	20 May	22 May	26 May	Closed
	12379/80[2]	WC-CR	B (216)	20 May	22 May	22 May	Closed
	22743[2]	CR-Br.	B (216)	2 Jun	22 Jun	22 Jun	Closed
2016	2134/35	WC-CR	B (192)	21 Mar	9 Apr	9 Apr	Open
	39354[2]	WC-CR	B (216)	23 Mar	9 Apr	9 Apr	Open[3]
	39352	WC-CR	B (216)	29 Mar	8 Apr	8 Apr	Open
	2130/31[2]	WC-CR	B (216)	1 Apr	8 Apr	8 Apr	Open
	2124/25	WC-CR	B (216)	2 Apr	18 Apr	18 Apr	Open
	2128/29	WC-CR	B (216)	2 Apr	22 Apr	22 Apr	Open
	39356	WC-CR	B (216)	4 Apr	14 Apr	14 Apr	Open
	39350	WC-CR	B (216)	8 Apr	24 Apr	24 Apr	Open
	2132/33[2]	WC-CR	D (182)	8 Apr	16 Apr	17 Apr	Open[3]
	2126/27[2]	WC-CR	I (150)	8 Apr	8 Apr	8 Apr	Open
	2138/39	WC-CR	B (216)	9 Apr	15 Apr	15 Apr	Open[3]
	39355	WC-CR	B (216)	15 Apr	24 Apr	26 Apr	Open
	39351	WC-CR	E (175)	16 Apr	18 Apr		Open
	39349	WC-CR	B (216)	25 Apr	3 May	3 May	Closed[3]
	39357	WC-CR	B (233)	5 May	17 May	20 May	Closed

[1]Tags with two ID codes indicate transmitters with temperature/depth sensors
[2]Individuals which were observed to have a reconditioning period
[3]Presumed dam passage mortality

Table 5.3. Model type, formula, sample size, and coefficient estimates, standard errors (SE), z- (ordinal regression model; ORM) or t-values (linear mixed effects models; LMEM, and linear mixed effects (LME) logistic regression model), and *p*-values, assessing Atlantic salmon kelt migration rates, success, and fine-scale direction.

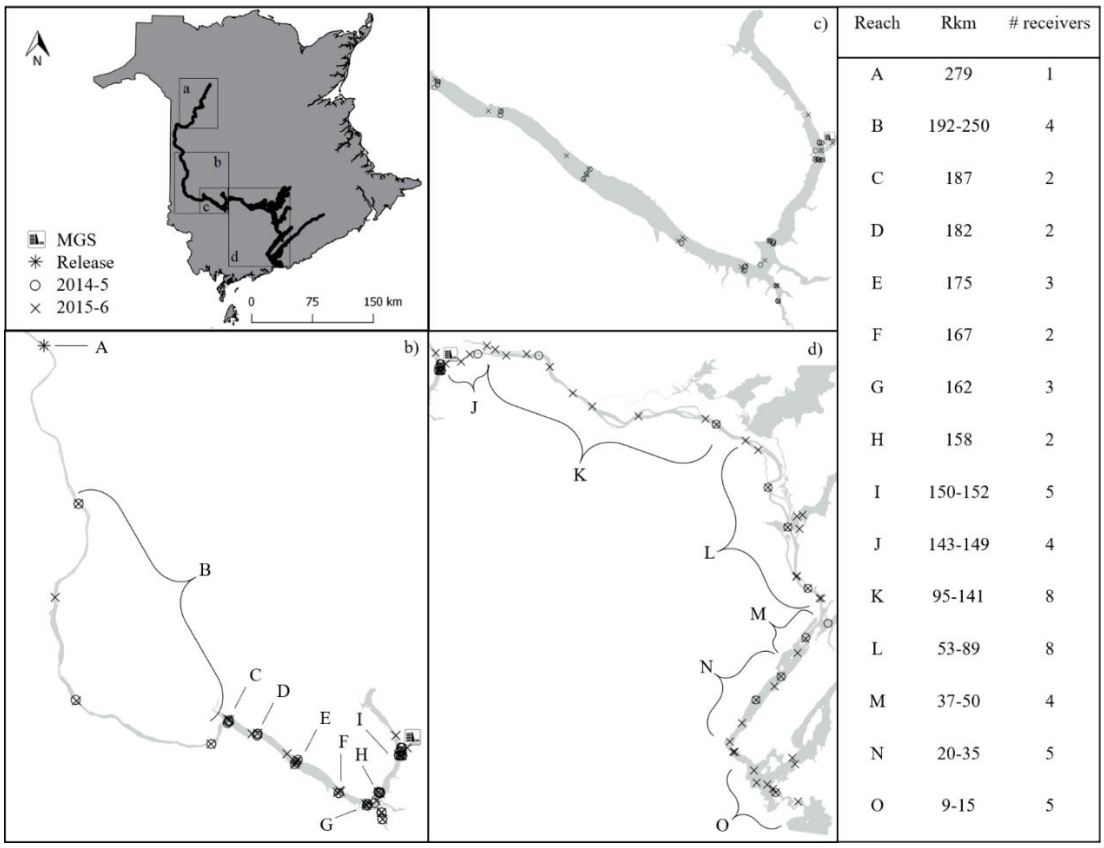
Coefficient	Estimate	SE	z/t	*p*
a) LMEM; fish_km_d ~ reach + (1|fish_id), n = 62 from 28 fish				
reach	12.527	2.798	4.478	<0.0001
b) LMEM; fish_km_d ~ reach * temperature_avg * water_velocity_avg + (1|fish_id)[1], n = 221 from 21 fish				
reach	-1.685	6.255	-0.269	0.79
temperature_avg	12.882	6.174	2.087	0.04
water_velocity_avg	-11.694	5.727	-2.042	0.04
c) ORM; success index ~ tides + temperature_avg + water_velocity_avg *fish_km_d * proportion_upstream[1], n = 28				
tides ebb vs. flood	0.1302	0.6514	0.200	0.84
tides overall	-10.8781	5.8090	-1.873	0.06
temperature_avg	3.0541	1.4320	2.133	0.03
water_velocity_avg	-2.2702	1.8478	-1.229	0.22
fish_km_d	-0.7135	1.6060	-0.444	0.66
proportion_upstream	-3.7164	1.8624	-1.996	0.05
d) LME logistic regression model; fish_direction ~ reach * water_angle + (1|fish_id)[1], n = 465 from 24 fish				
reach	0.12080	0.25537	0.473	0.64
water_angle	0.02912	0.38302	0.076	0.94

[1]Interactions (not shown) were non-significant

Table 5.4. Model selection of Cormack-Jolly-Seber apparent survival (Φ) and encounter (p) probabilities with (s) and without (.) spatial variability, Akaike Information Criteria corrected for small sample sizes (AIC_c), and model weight (w_i).

Model	AIC_c	w_i	Evidence ratio
Φ(s)p(s)	425.7594	0.99998	103932
Φ(.)p(.)	430.2882	0.00002	10797
Φ(s)p(.)	448.8624	0.00000	1

Note: Evidence ratio describes how well the evidence supports the model



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 5.1. 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 Atlantic salmon. 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 2014-5 (o; n = 27) and 2015-6 (x; n = 65). These receivers were combined into 15 reaches (A-O, with corresponding river kilometers 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 location 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 Atlantic salmon in reach A is also marked (*).

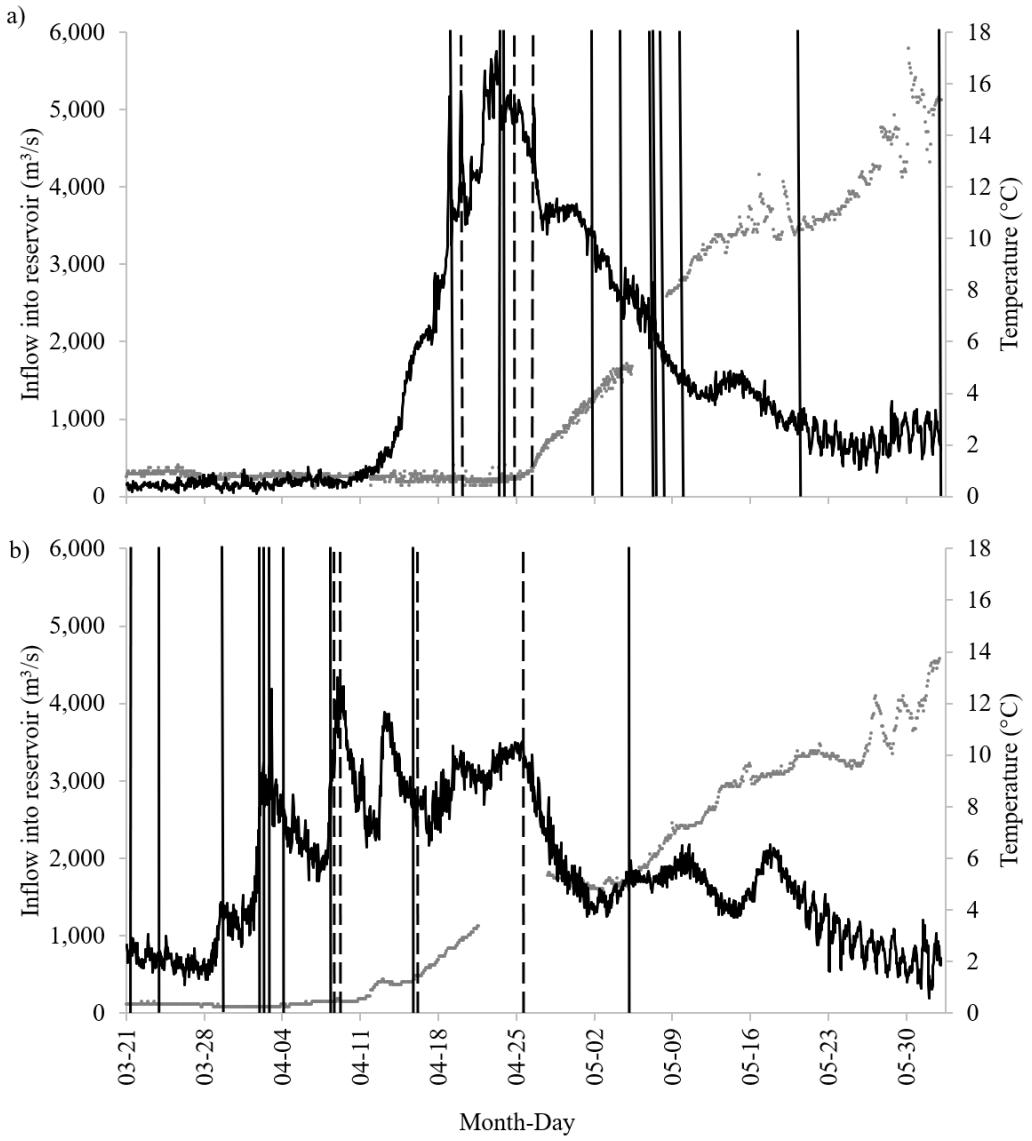


Figure 5.2. Initiation of Atlantic salmon kelt spring migration (vertical lines) in a) 2015 and b) 2016 and associated inflow (m^3 s^{-1}, black line) into the Mactaquac Generating Station (MGS) reservoir and mid-water column water temperature (°C; grey circles) recorded near the MGS. Solid vertical 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).

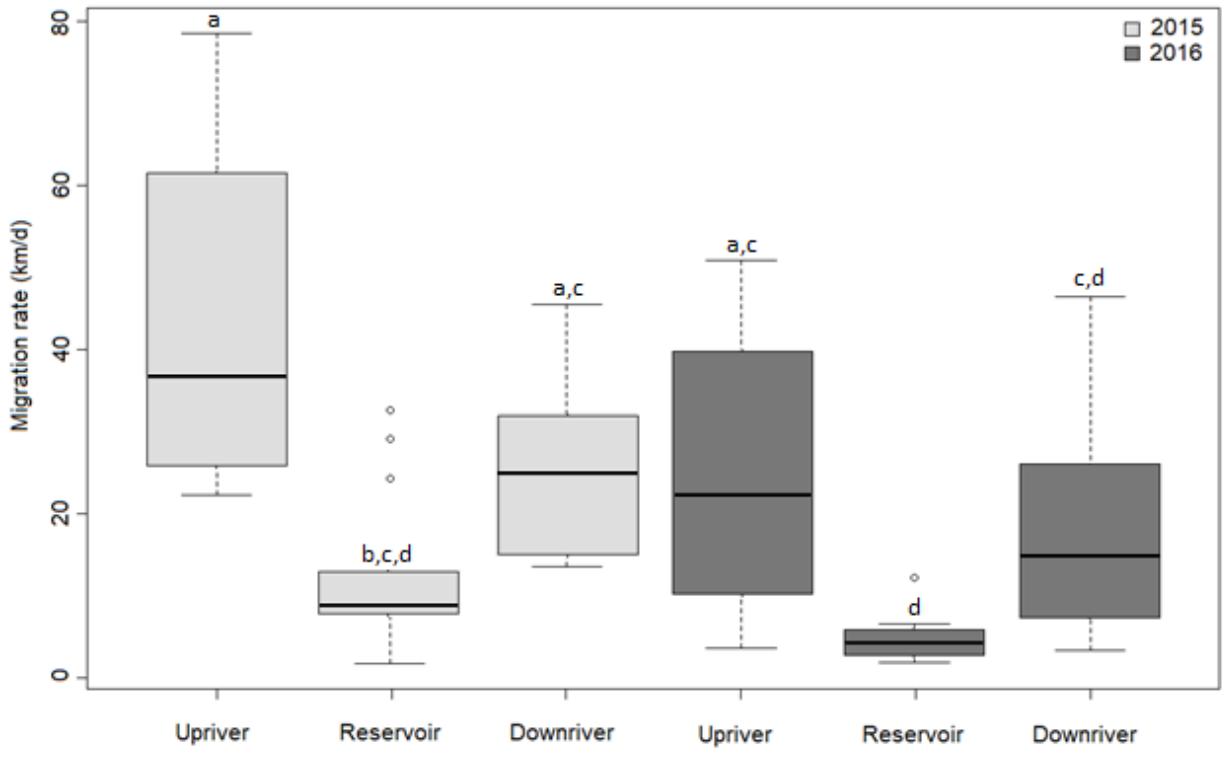


Figure 5.3. Migration rate (km d^{-1}) of Atlantic salmon kelts migrating through the upriver, reservoir of the Mactaquac Generating Station, and downriver reaches of the Saint John River in 2015 (light grey) and 2016 (dark grey). Letters represent significant differences.

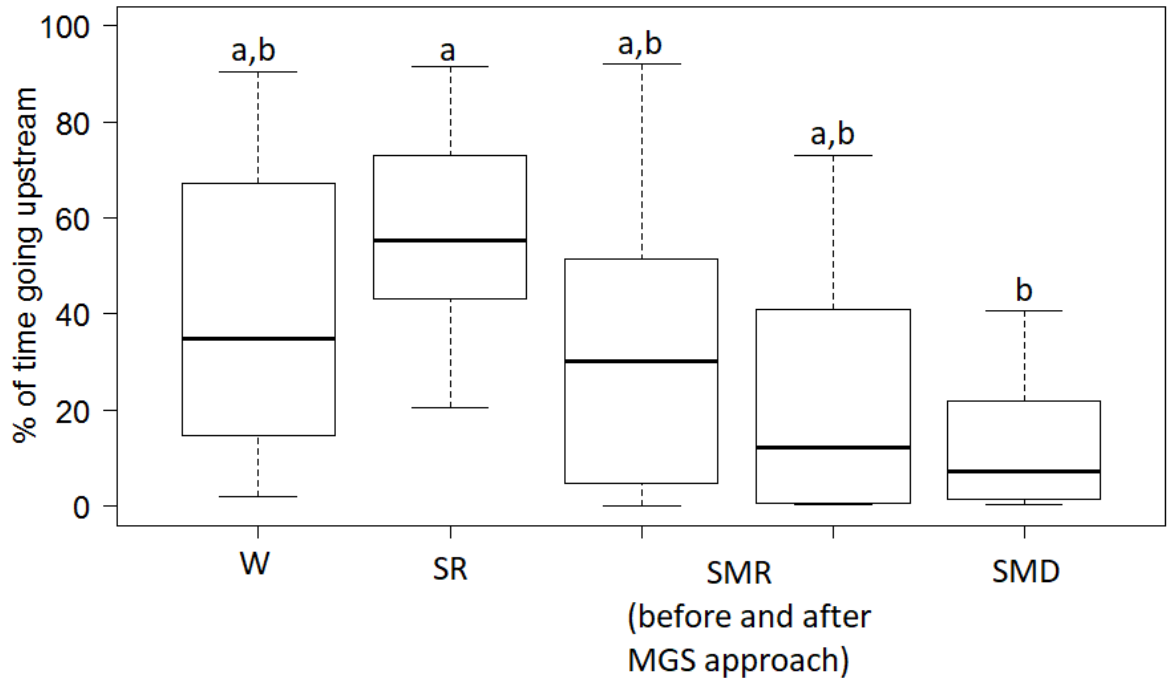


Figure 5.4. Percent of time tagged Atlantic salmon kelts spent moving upstream, in reverse of the main migration direction, during Winter (W), Spring Reconditioning (SR), Spring Migration in the Reservoir (SMR), and Spring Migration Downriver (SMD) of the Mactaquac Generating Station in the Saint John River. Letters represent significant differences.

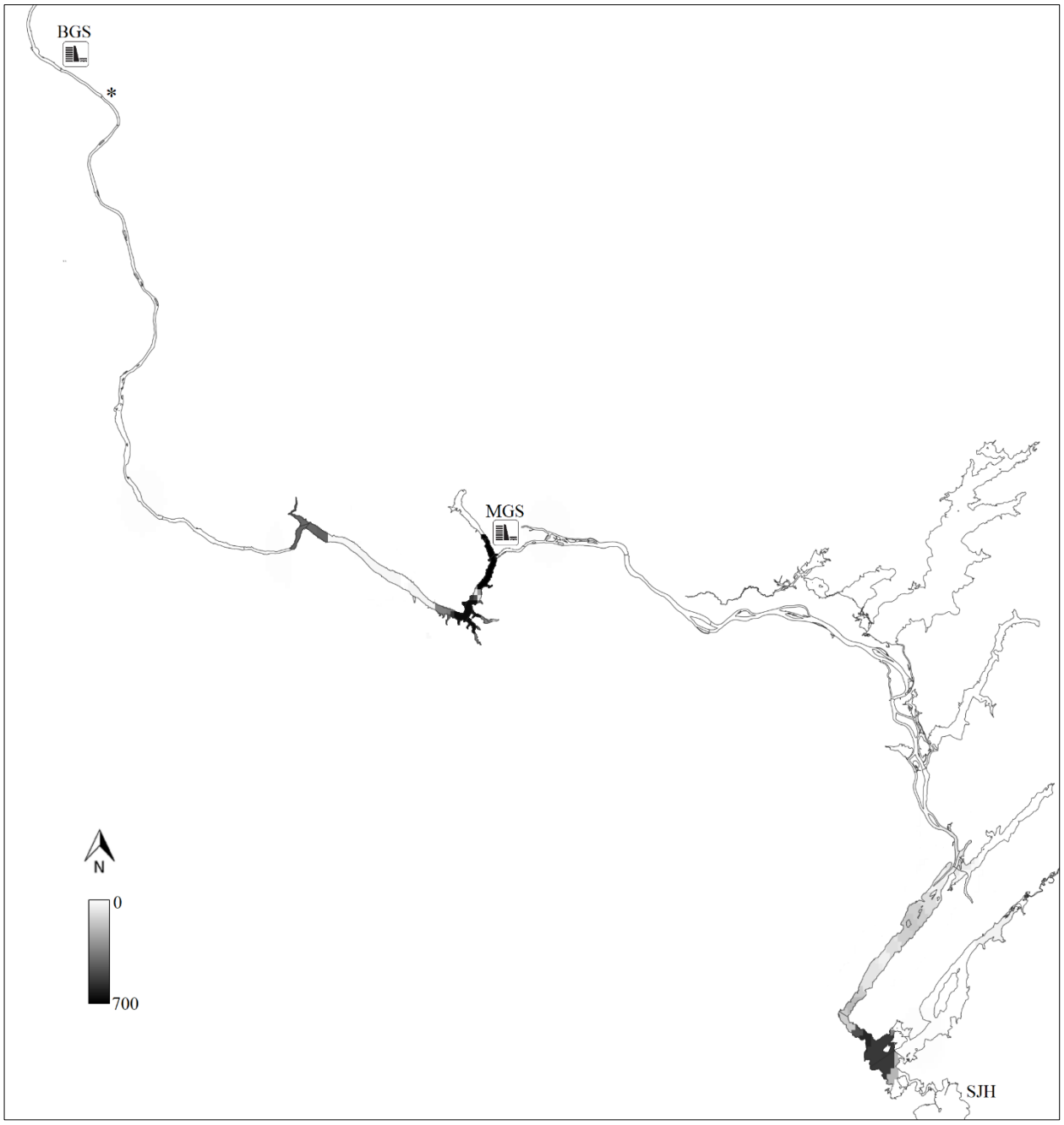


Figure 5.5. Heatmap of number of movement reversals by Atlantic salmon kelts in the Saint John River. Locations of release (*), the Beechwood Generating Station (BGS), the Mactaquac Generating Station (MGS), and the Saint John Harbour (SJH) are shown.

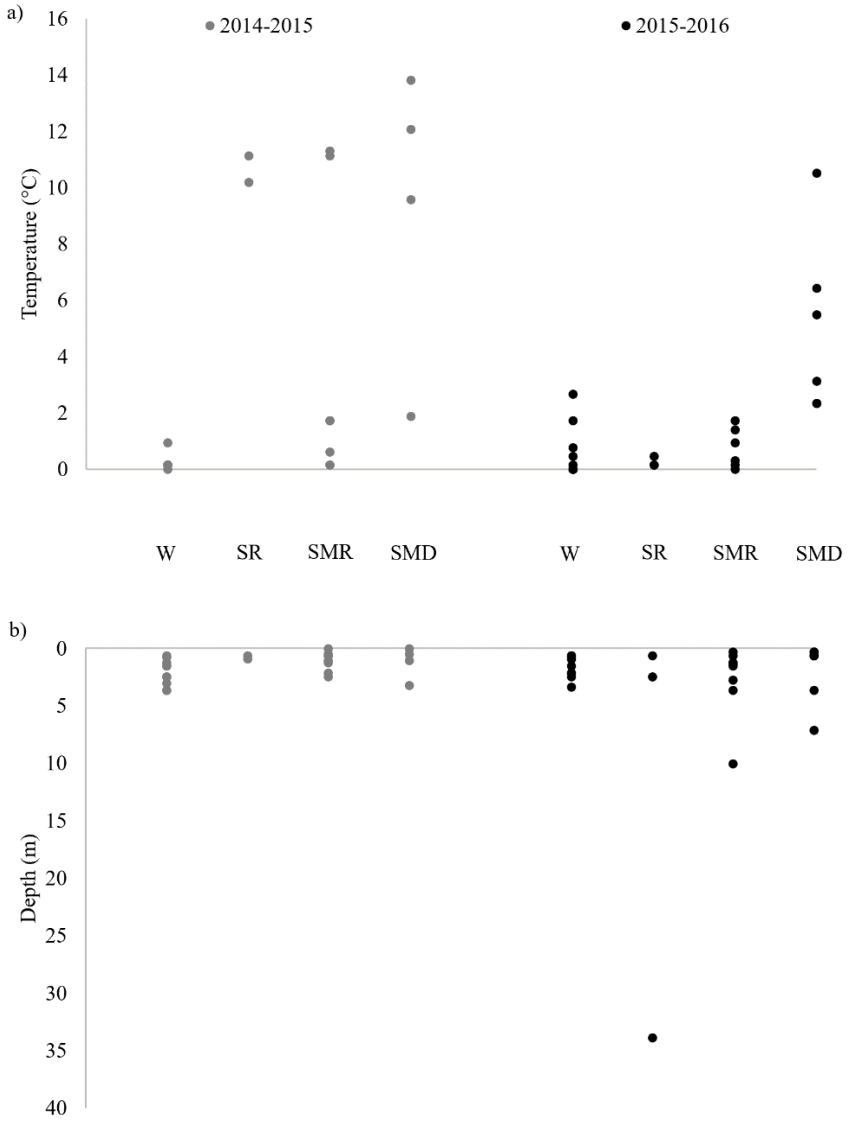


Figure 5.6. Medians of a) water temperature (°C) and b) depth (m) as experienced by individual Atlantic salmon kelts tagged with temperature/pressure sensor tags in 2014-2015 (grey) and 2015-2016 (black) during Winter (W), Spring Reconditioning (SR), Spring Migration in the Reservoir (SMR), and Spring Migration Downriver (SMD) of the Mactaquac Generating Station in the Saint John River.

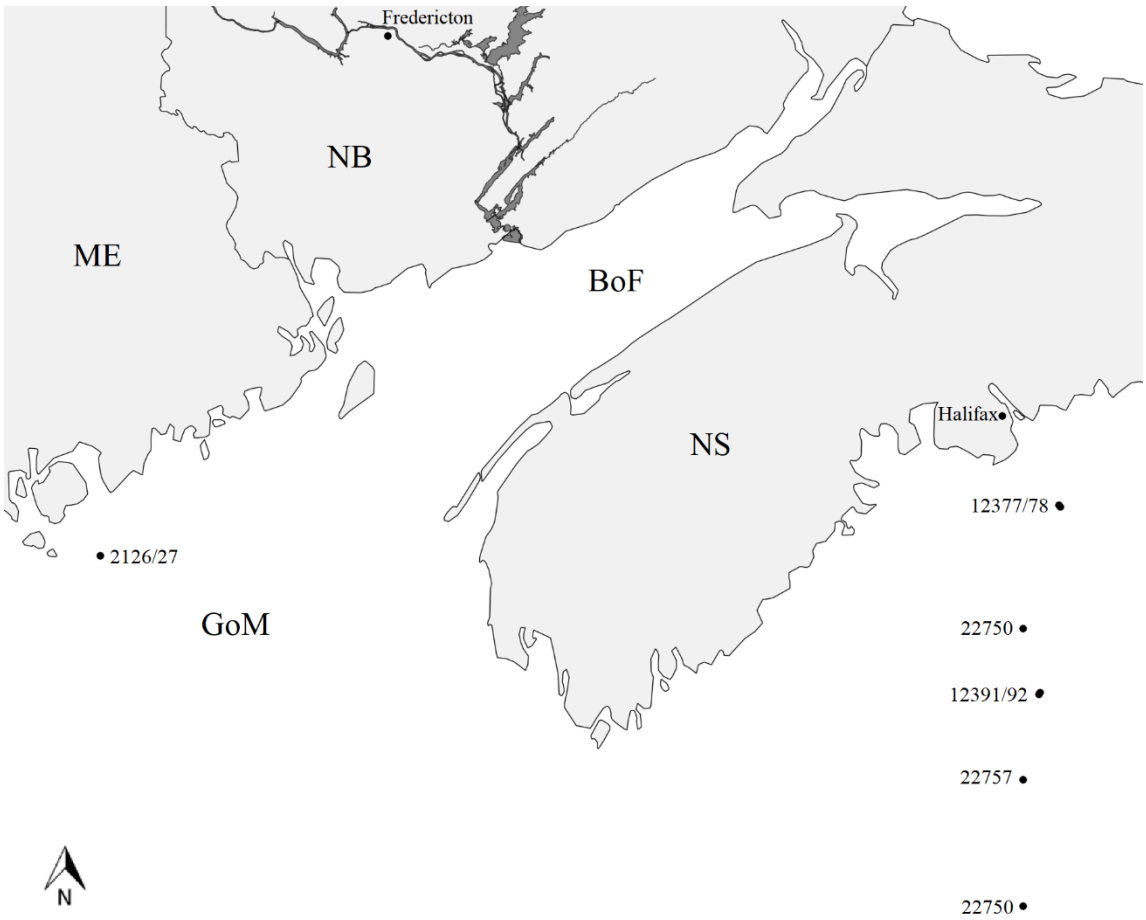


Figure 5.7. Locations of tagged Atlantic salmon kelt detections outside of the Saint John River in New Brunswick (NB), Canada, as they traveled through the Bay of Fundy (BoF), the Gulf of Maine (GoM) off Maine (ME), and the Atlantic Ocean near Halifax, Nova Scotia (NS). Tags with two ID codes indicate transmitters with temperature/depth sensors. Detections are from data sharing with the Ocean Tracking Network.

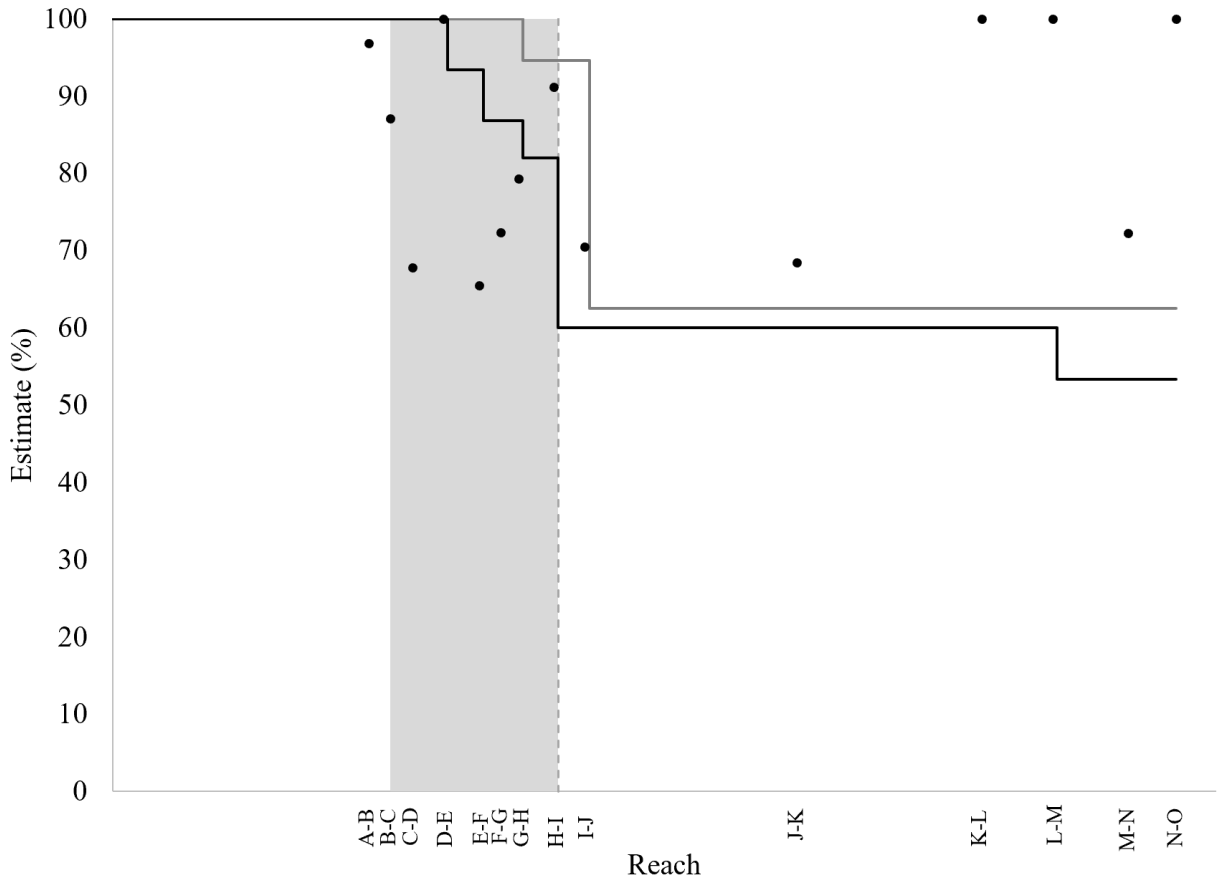


Figure 5.8. Cormack-Jolly-Seber p (black dots) and cumulative apparent survival from φ estimates (%) during the spring migration of tagged (2015 grey line, 2016 black line) Atlantic salmon kelts in 14 river reaches (see Figure 5.1) in the Saint John River. Shaded area represents the Mactaquac reservoir and the dashed vertical line represents the location of the Mactaquac Generating Station.

Chapter 6

Atlantic salmon (*Salmo salar*) upstream migration delay in a large hydropower reservoir

A. B. Babin[a], T. Linnansaari[ab], M. Ndong[c], K. Haralampides[c], S. Peake[a], R. Jones[d], and R. A. Curry[ab]

Canadian Rivers Institute, Department of Biology[a], Faculty of Forestry and Environmental Management[b], and Department of Civil Engineering[c], University of New Brunswick, Bailey Hall, 10 Bailey Drive, P.O. Box 4400, Fredericton, New Brunswick, Canada, E3B 5A3

[d]Fisheries and Oceans Canada, Maritimes Region, 343 Université Avenue, P.O. Box 5030, Moncton, New Brunswick, Canada, E1C 9B6

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6.1 Abstract

Atlantic salmon (*Salmo salar*) spawning success is challenged when the migratory routes to natal streams have been obstructed by hydropower generation stations and reservoirs which lack directional cues, potentially causing migratory delay. This study used 74 acoustically tagged adult Atlantic salmon during their spawning migrations to quantify migratory success, rates, and delay through the Mactaquac hydropower reservoir in the Saint John River, New Brunswick, Canada, during three separate migration seasons in 2014-2016. Tag loss or potential mortality was considerable such that the effective sample size was 34 successfully tracked adults. Of these, 41 % experienced fallback over the dam with all but one remaining within 20 rkm and the exception being detected in a tributary 36 rkm downstream, 12 % were unsuccessful in exiting the reservoir, and 47 % were successful in reaching upstream of the reservoir toward the next hydropower station on the way to the spawning grounds. Migration rates were significantly slower in the reservoir (9.3 ± 1.9 km d^{-1}; median ± SE) than upriver (39.0 ± 4.1 km d^{-1}), and the tagged Atlantic salmon spent 31-53 % of their time reversing direction and thus travelled longer distances (73 ± 58 rkm) than the minimum 37 rkm midline route through the reservoir. Traveling the distance of the reservoir at the upriver migration rate could have shortened their journey by a median of 3.8 days. Temperature and pressure (as a proxy of depth) sensor tags indicated that individual salmon experienced median temperatures of 10-20 °C (16.0 ± 0.03 °C; median ± SE) and migrated at depths of 5-35 m (23.4 ± 0.1 m) within the reservoir. Given that some of the energy needed for reproductive development and activities was likely appropriated by migratory delay, and that a moderate proportion (47 %) of adults

survived to reach the next hydropower generation station along the mainstem, volitional passage through the reservoir does not appear to be a preferred management strategy in the studied Mactaquac reservoir.

6.2 Introduction

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

Spawning migrations within unregulated rivers typically begin by alternating active swimming with periods of rest, followed by an apparent search pattern moving both up- and downstream, and finally a holding phase until spawning activities begin in a synchronized fashion (Hawkins and Smith 1986; Thorstad et al. 2008). Adult salmon expend tremendous amounts of energy without intaking feed as they migrate the long distance back to their natal stream and perform spawning activities (Fleming 1996; Hendry and Berg 1999; Mesa and Magie 2006). Migratory delay due to superfluous movements within reservoirs can reduce energy reserves and delay their arrival to the spawning grounds, causing sub-optimal or compromised egg production (Caudill et al.

2007). Within the Columbia River system, Chinook salmon (*Oncorhynchus tshawytscha*) adults used 6-17 % of their muscular energy density to migrate 510 rkm, with an additional 5-8 % attributed to migratory delay (Mesa and Magie 2006).

Reservoir delay can result in adult salmon being unsuccessful in finding the upstream exit of the reservoir and being unable to reach the spawning grounds (Caudill et al. 2007). Longer reservoir residence may expose coldwater salmonids migrating in spring and early summer to high water temperatures that could increase metabolic demands and affect sexual development and lead to pre-spawning mortality (Keefer et al. 2004). This is particularly concerning for river systems that accommodate multiple dam and reservoir passages where upstream migrants can accumulate migratory delay (Caudill et al. 2007).

Ensuring timely and successful migration of adult Atlantic salmon (*Salmo salar*) to their spawning grounds and back to the ocean for reconditioning is not only important for the immediate cohort but would also benefit future spawning events due to the iteroparous nature of the species. Repeat spawners can provide stability to small spawning populations such as the endangered Outer Bay of Fundy population (Saunders and Schom 1985; Committee on the Status of Endangered Wildlife in Canada 2011). After more time at sea, repeat spawners return to the river larger and with greater fecundity than maiden spawners (Ducharme 1969). When fish from multiple year classes are able to spawn across years, they increase genetic diversity that protects against inbreeding effects (Saunders and Schom 1985; Halttunen 2011).

To aid upstream migration of adult salmonids, fisheries managers may opt to deploy strategies that bypass the potentially problematic reservoir reaches by capturing

the migrating adults at a hydropower facility's fish passage/attraction structures, and subsequently transport them upstream of one or multiple reservoirs and hydropower dams. Such a strategy is referred to as trap-and-haul (TH) and is practiced in many hydropower regulated rivers (see Lusardi and Moyle 2017 for a recent review). While the TH strategy may bypass the potential negative effects caused by reservoir passage, it may introduce uncertainty regarding the correct upstream release locations for migrating adult salmonids homing to each of their natal streams.

Atlantic salmon ascending the Saint John River (SJR) encounter the first barrier at the Mactaquac Generating Station (MGS) where they are presumably attracted to fish collection facilities and transported to the Mactaquac Biodiversity Facility (MBF) for inspection and measurement, then further transported to upstream locations beyond the reservoir. The Tobique River is the largest habitat upstream of the MGS that is accessible and appropriate for salmon spawning (Marshall et al. 2014). Early migrants (May-June) are transported approximately 3 rkm downstream of the confluence with the Tobique River because they are thought to be homing to headwater tributaries (*i.e.*, Tobique or Aroostook rivers), whereas later migrants are transported to the upper end of the MGS reservoir at 230 rkm where they can home to their respective natal streams (Clarke et al. 2014).

The MGS is currently undergoing an assessment for its future due to alkali-aggregate reaction threatening its lifespan (Stantec Consulting Ltd. 2015). The hydropower owner and operator (New Brunswick Power) was considering multiple options for the future of the MGS, including rebuilding the dam on the opposite side of the river, maintaining the reservoir for water control without generating power,

removing the dam and allowing the SJR to flow freely in this reach, or attaining the intended lifetime of the dam via refurbishment (Stantec Consulting Ltd. 2015). While the dam removal option would have resolved any dam and reservoir passage issues in their entirety at the MGS (Linnansaari et al. 2015), the other options may allow for the replacement of the current TH strategy with volitional passage via a fish ladder or full height fishlift. However, before considering replacing the current TH strategy with a volitional passage option, the migration behavior and success of adult salmon through the MGS reservoir needed to be thoroughly assessed.

Previous studies examining adult Atlantic salmon behavior within the MGS reservoir suggested that migratory success was low (22.3 % of wild and 2.8 % of hatchery adults; Marshall 1975). There is no volitional fish passage at the MGS, and based on Marshall (1975), the managers implemented a TH that bypasses a free-swim through the MGS reservoir. Adults can be trucked over 300 rkm and such trucking could also have an impact on the population. However, the previous study utilized only external Carlin tags that do not allow for the assessment of movements and behavior within the reservoir, *i.e.*, the mechanism of the apparent mortality. Therefore, a reassessment of movement behavior using acoustic telemetry was desired to decipher potential migration bottlenecks, and link the behavior, movement rates, and migratory success to environmental variables within the reservoir, such that management advice can be based on the best possible technologies.

The overall purpose of this study was to explore the feasibility of reservoir transit of adult Atlantic salmon if the current passage structures at the MGS were modified to allow volitional passage. With uncertainty about the reservoir transit

impacts and the TH strategy, our objectives were to assess the migration success, behavior, and rates of adult Atlantic salmon during their spawning migration through the MGS hydropower reservoir.

6.3 Materials and Methods

Study site

The Saint John River is 700 km long with an average width of 750 m and an average depth of 2 m (Kidd et al. 2011). Discharge ranges from 280 $m^3 s^{-1}$ in the summer to 10,000 $m^3 s^{-1}$ during the spring freshet (Kidd et al. 2011). The MGS is the first hydropower facility encountered by adult salmon (rkm 150; Figure 6.1), followed by the Beechwood Generating Station (BGS rkm 285; Figure 6.1) on the mainstem and the Tobique-Narrows Generating Station (TNGS rkm 315; Figure 6.1) near the mouth of the Tobique River tributary which contains the majority of Atlantic salmon spawning habitat upstream of the MGS (Marshall et al. 2014). The MGS affects water flow for 100 rkm upstream, but it is the first 37 rkm, *i.e.*, from the MGS to the town of Nackawic (the "reservoir proper"; MGS to reach G; Figure 6.1), that has had the most drastic decline in water flow from an average of 0.52 m s^{-1} before impoundment to 0.06 m s^{-1} after dam construction (Stantec Consulting Ltd. 2015). The river upstream of this location (reach G) changes angle and narrows substantially in both width (750 m to 300 m) and depth (40 m to 18 m), becoming more lotic (4.0 cm s^{-1} to 14 cm s^{-1}; M. Ndong, University of New Brunswick, unpublished data). Therefore, this study considered reaches A-G (Figure 6.1) to be the 'reservoir' and reaches H-I (Figure 6.1) to be 'upriver'.

Fish Tagging and Tracking

Two sources of adult Atlantic salmon were used in this study; wild Atlantic salmon adults were acoustically tagged for the *in situ* tracking study, whereas captive-reared salmon (*i.e.*, Atlantic salmon that had been grown to adulthood from wild pre-smolts or smolts in a hatchery environment) were used as dummy-tagged control groups (in 2014 and 2016; Table 6.1) to assess tag retention and other tagging-related effects. The wild Atlantic salmon were captured from the fish collection facilities of the MGS and then transported an approximate 7 km to the Mactaquac Biodiversity Facility (MBF) for assessment and tagging (Table 6.1). Captive-reared salmon had been raised at the MBF and thus were already on site and were kept there for monitoring after dummy-tagging.

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

Due to the vulnerable population status of Atlantic salmon in the SJR, two different acoustic tagging methods were employed in this study. Specifically, gastric

tagging (in 2014) and external tagging (in 2015-2016) were used to avoid any potential impact of tagging on spawning success. Tagging was performed using 40 ppm clove oil anesthetic (eugenol as active ingredient; ethanol in 1:10 ratio used as carrier; 291 ± 103 s), except for in 2016 when flow-through water was used, and tagging lasted 178 ± 66 s.

In 2014, adult Atlantic salmon were gastrically tagged with either dummy tags (n = 12) or live tags (n = 20). For the gastric tagging, the V13 tags were modified by fixing a rubber o-ring to the middle of the tag using fusion tape to decrease the chances of regurgitation (Rivinoja et al. 2006). The control fish were tagged first to ensure the gastric tagging process resulted in reliable tag insertion and retention without complications; these fish fasted for 24 h prior to tagging. A long vinyl tube lubricated with glycerin was used to gently place the tag 18.8 ± 1.3 cm (32 %) into the body, and a thin wooden dowel was used to expel the tag from the tube and into the stomach. The tagged control fish were then observed on day 1, 2, and 7 post-tagging. As no tag expulsion, complications, or mortality had materialized, we proceeded to tag the wild sea-run Atlantic salmon using the same methods. The wild salmon were allowed to recover at the MBF for 48 h post-tagging where they were treated with a saltbath. Ten tagged salmon were then transported and released three rkm upstream of the MGS (Figure 6.1) on 30 July, nine on 31 July, and one on 1 August (Table 6.1). The monitoring of the control fish continued at the MBF, with one tag being found to be expelled after 17 d and an additional two tags being found to be expelled 23 d after tagging (total = 25 %), but no mortalities occurred among the control fish.

In 2015, the tagging method was changed to external tagging due to presumed low tag retention with the gastric method in the *in situ* fieldwork during field season

2014 (see results). The external tagging procedure involved preparation of the cylindrical acoustic tags by wrapping monofilament line over the tag casing, and then covering the monofilament wraps in epoxy such that approximately 10 cm of line remained at either end of the tag for external attachment. No controls were used in 2015, and only wild sea-run Atlantic salmon were tagged (n = 24, including n = 10 tags with sensors). During tagging, the fish were anesthetized and then placed upright on a V-trough where large-gauge hypodermic needles were inserted through the fish's dorsal musculature, monofilament lines were fed through the hollow needles, and a soft rubber barrier was inserted between the skin and the monofilament which was knotted to secure the tag. External anchor tags were also placed into the dorsal musculature to allow for identification at upstream dam passages and to assess the loss of acoustic tags when fish were re-sighted. All tagged fish were released on 9 July after a minimum recovery period of 1 h (max. 7 h), with the exception of one fish that was tagged and released after 30 minutes on 10 July (Table 6.1).

In 2016, external tagging was performed on n = 8 captive-reared control adult Atlantic salmon, and n = 30 wild fish using the same methods as in 2015. The wild fish were released to the same location as previous years after 24 h recovery (n = 7 on 28 June, n = 15 on 4 July, and n = 8 on 7 July; Table 6.1). The control group was monitored daily for 16 days, during which time one tag broke off, five tags were slightly loose, and two were in perfect condition, with no mortalities.

Adults were passively tracked through the Mactaquac reservoir and SJR upriver using n = 46 Vemco VR2W receivers in 2014, n = 44 in 2015, and n = 26 in 2016 (Figure 6.1). The fish were also actively tracked using a Vemco VR100 receiver and an

omnidirectional hydrophone, with a total effort of 77.8 h. Active tracking was restricted to daylight hours and wind speeds below 25 km h^{-1}.

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

Hydrodynamic model

Fish movements were examined in relation to water velocity and direction by modelling these variables through time and space. The numerical model Delft 3D (Delft3D-FLOW 4.01.00; Deltares 2013) used hourly inputs of tailrace discharge from the BGS, total discharge through the MGS, incoming tributary discharges, wind speed and direction, and bathymetric data to estimate surface (5 m) water velocities (cm s^{-1}, current angle from downstream) every two hours 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 6.1) and 233 (reach B; Figure 6.1) 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).

Definitions and statistical analyses

Fork length and weight of tagged adult Atlantic salmon were compared between groups (2014 control, 2014 experimental, 2015 experimental, 2016 control, and 2016 experimental) and sexes using two-way ANOVAs with Tukey's Honestly Significant Difference post-hoc tests.

The fate of each individual was determined based on the presence, duration, and location of detections. This was possible due to the extensive receiver network that was found to produce excellent encounter probabilities (> 99 %). These high probabilities, along with the known detection ranges from *in situ* range testing (537 ± 53 m near the MGS, 897 ± 227 m upriver; Babin et al. unpublished) confirming overlapping detection coverage between receivers in lines throughout the reservoir, allowed for reasonable determinations of both presence and absence throughout the study range. Four categories were defined: 1) Tag loss or mortality – adult salmon were presumed to have either lost their tag or to have died when detections were near continuous at a single receiver line for the duration of the battery life of the tag, or when detections ceased abruptly indicating that the tag or fish had been lost in an area outside the detection range of any receivers. This determination was further confirmed for fish carrying sensor tags when detections indicated that the tag was resting on the bottom. Tag loss or mortality could be attributed to natural causes, tagging effects, dam or reservoir related

impacts, or predation. In many cases, detections indicated active fish movements for a period of time before presumed tag loss. When appropriate, these data were included in the analyses. 2) Fallbacks – adult salmon were known to have fallen back over the MGS when their acoustic tags were detected by receiver(s) downstream of the dam, or when a fish entered the fish lift operations and were identified by a Carlin tag. Individuals were also presumed to have fallen back over the MGS when detections ceased abruptly within the vicinity of the MGS (< 3 rkm). 3) Unsuccessful migrants – adult salmon were considered to have been unsuccessful in migrating upstream of the reservoir when the last detection came from a receiver in or downstream of Nackawic (rkm 187; reach G; Figure 6.1). 4) Successful migrants – individuals were categorized as successfully exiting the reservoir when they were detected by receivers upstream of the reservoir or further upstream of the BGS toward the spawning grounds.

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

The first model compared overall migration rates (km d^{-1}) within the reservoir and upriver reaches. These rates were calculated as: reservoir – from the first detection upon release to the first detection at the exit of the reservoir (reach G; Figure 6.1), and upriver – from the last detection at the Nackawic receivers to the first detection at the last receiver they were observed at upriver. Migration rates were further examined by only considering upstream movements between receivers within the reservoir and

upriver reaches, then relating these movements to concurrent water temperatures and velocities through a second LMEM. Water temperature values were taken from sensor tag detections when available, or from temperature loggers deployed at mid-column alongside the receivers. A small proportion (5 %) of fish movements could not be directly linked with concurrent water temperatures, in which case temperature values were interpolated based on the closest spatial and temporal locations.

The proportion of time that tagged adults spent traveling in the reversed direction to their upstream spawning migration, and the extra rkm that they minimally migrated as a consequence, was calculated and compared to a situation where the movement would have been unidirectional, *i.e.*, tagged fish moved uniformly in the upstream direction. Fish direction (upstream or downstream) between receivers was examined in relation to the associated maximum water angle from downstream in the reservoir and upriver reaches using a LME logistic regression model.

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

Dam passage delay was estimated by examining the amount of time adults spent around a receiver five rkm downstream of the BGS after first being detected in the area, and how long it took before being detected at a receiver three rkm upstream of the BGS.

Due to lost equipment, it was only possible to estimate dam passage delay for the 2014 adults.

Water temperatures and depths of individual fish with sensor tags were visualized with boxplots and kernel density plots (violin plots), without any data after presumed tag loss or mortality (*i.e.*, after a tag was observed to reside at the bottom of the reservoir/river without any further movements detected throughout the study).

Analyses were done in R (Version 1.1.423 © 2009-2018 RStudio, Inc. Packages car, lme4, lmerTest) with the exception of CJS analyses that were carried out in Program MARK (Version 8.2; White and Burnham 1999). Normality plots were analyzed where appropriate, and statistical significance was assumed when p was less than or equal to 0.05.

6.4 Results

Weight was different between groups (two-way ANOVA, $F_{4,85} = 2.81$, $p = 0.03$) but post-hoc testing only identified one borderline difference between the 2014 and 2015 experimental groups (TukeyHSD $p = 0.06$). Fork length was also different between groups (two-way ANOVA, $F_{4,85} = 5.56$, $p < 0.001$), namely between the 2015 experimental group and both control groups (TukeyHSD 2014 $p = 0.001$, 2016 $p = 0.006$). Females (all but two of 28 were large salmon > 63 cm) were heavier (two-way ANOVA, $F_{2,85} = 45.67$, $p < 0.05$) and longer (two-way ANOVA, $F_{2,85} = 64.49$, $p < 0.05$) than males (all but three of 47 were small salmon <= 63 cm.

Migration success

Fish were determined to have the following fates: tag loss/mortality, fallback, unsuccessful migrants out of the reservoir, and successful migrants that reached upriver toward the spawning grounds. The total number of fish that were determined to have each of these fates for each study year are given in Table 6.2.

Although controls for both tagging methods were largely successful with few tag losses and no mortalities, releasing wild fish in the reservoir produced lower than expected proportions of tagged fish successfully retaining the tags throughout the study. Some fish were determined to have lost their tag or experienced mortality between the release site and the MGS within three days of being released (2014 n = 2/20, 2015 n = 4/24, 2016 n = 2/30; Table 6.2), but more often the fish were detected moving upstream approximately 5 rkm (reach B; Figure 6.1; Table 6.2) before tag or fish loss typically within a week but up to 68 d post-release (2014 n = 4, 2015 n = 7, 2016 n = 3; Table 6.2), with others venturing upstream of the large bend within the reservoir up to 14 rkm from the release site and having a longer record of movements typically lasting over a week and up to 106 d before tag/fish loss (2014 n = 2, 2015 n = 5, 2016 n = 6; reaches C-D; Figure 6.1; Table 6.2). Included in these groups were two tagged adults that were determined to have lost their tags or experienced mortality after 3 and 4 d within the Mactaquac Arm (reach A; Figure 6.1; Table 6.2), a dead-end tributary east of the MGS. Lastly, a few tagged adults had reached the upstream exit of the reservoir before experiencing tag loss or mortality in the upper reservoir 2 d after release, or after returning back toward the MGS with tracked movements for 43 d post-release (2014 n = 1, 2016 n = 2; reach G; Figure 6.1; Table 6.2).

In 2015, ten fish had temperature and pressure tags from which tag loss or mortality could be confirmed when depths suddenly reached and remained near the bottom. These determinations are included in the number of tag losses or mortalities tallied above. Four sensor tags indicated tag loss or mortality after within a week with one additional loss after approximately two weeks. Eventually, four more sensor tags fell off after a longer period (1.5-3.5 months) during which data were still obtained. These tags indicated that 75 % of adult detections were within 13 and 29 m in the reservoir with temperatures of 12-18.5 °C (Figure 6.2). Only two fish with sensor tags migrated upriver. These fish remained within the surface 8 m with minimum temperatures near 20 °C reflecting the general habitat conditions in the upriver reach (Figure 6.2).

Many (n = 14; 41 %) tagged adult Atlantic salmon experienced fallback over the MGS (Table 6.2), mostly within the first week after their release three rkm upstream of the MGS (2014 n = 2, 2015 n = 1, 2016 n = 7;), with additional tagged salmon descending downstream of the MGS after 11-31 days after release (2014 n = 1, 2015 n = 2, 2016 n = 1). These fish only traveled upstream from the release site as far as the dead-end tributary (Longs Creek) at the large bend within the reservoir (between reaches B and C in Figure 6.1). There were also many instances where a tagged fish had likely fallen back and experienced tag loss or mortality based on abruptly ceased detections within the vicinity of the MGS (but no detections by downriver receivers, indicating loss at the MGS) within the first week (2015 n = 1, 2016 n = 4) or 11-74 days after release (2015 n = 2, 2016 n = 4). Three of these likely fallbacks also had contained their movements between the release site and the MGS, seven fish ventured up to 14 rkm

upstream of the release site before returning, and one fish made it all the way to the reservoir exit before returning back to the MGS.

Four tagged adults (12 %) were determined to have been unsuccessful migrants (2014 n = 3, 2015 n = 1; Table 6.2), most often moving back-and-forth between the large bend in the reservoir (reaches B-D; Figure 6.1) and the MGS, with the exception of one fish that reached the upstream exit of the reservoir (reach G; Figure 6.1) before returning back to the mid-reservoir (reach G; Figure 6.1).

Sixteen tagged adults (47 %) successfully exited the reservoir (2014 n = 5, 2015 n = 3, 2016 n = 8; Table 6.2) during mean water temperatures of 19.7 (± 3.1 °C, SD), with half of the successful migrants being last detected at the first receiver within reach H (Figure 6.1), and two of which were detected downstream of the BGS (reach I; Figure 6.1) in 2014, the only year when that particular receiver was successfully retrieved. Both of these latter fish continued to be tracked after 20 and 30 d in the area as they moved downstream as kelts in a concurrent study (Babin et al. unpublished).

Six tagged adults were successful in finding upstream passage over the BGS (2014 n = 2, 2015 n = 1, 2016 n = 3), with one adult tagged in 2014 being actively tracked at rkm 374 which could be the fish's spawning grounds. The single migrant that reached upstream of the BGS in 2015 had a sensor tag that indicated it was traveling within the surface 1 m where water temperature was near 20 °C.

Migration rate and delay

Migration rates in the reservoir were significantly suppressed when compared to rates in the upriver reach (LMEM $p < 0.05$; Table 6.3a). Overall, pooled median migration rates were 9.3 ± 1.9 km d^{-1} in the reservoir and 39.0 ± 4.1 km d^{-1} upriver,

reaching 65.2 km d^{-1} ± 12.5 upstream of the BGS (2016 only; Figure 6.3). Individual fish accounted for 40.8 % of the variance between migration rates. All but two tagged fish (both in 2014) traveled 2-17 times faster in the upriver reach than in the reservoir. The median delay within the reservoir (37 rkm) associated with the slower migration rates (as opposed to migrating in the pre-reservoir condition at the upriver rate) was 3.8 d (range 11 h to 19 d; Table 6.4).

Migration rates between each receiver line only as the fish were moving upstream were tested to determine dependence on concurrent water velocities. Individual fish accounted for 8.5 % of the variance between upstream migration rates. When only upstream movements between receivers were considered, there was no effect of reach (LMEM, $p = 0.075$; Table 6.2b), indicating that the rate of movements between receiver lines was not different within each reach but rather the back-and-forth movements or reversals (see below) led to decreased migration rates within the reservoir as a whole. There were also no relationships found between upstream migration rates and concurrent water velocities (LMEM, $p = 0.73$; Table 6.2b) or average water temperatures (LMEM, $p = 0.17$; Table 6.2b).

Adult salmon spawning migrations typically include a holding phase thought to time spawning activities in a synchronized fashion. The duration of time that adults remained nearby any one receiver or line of receivers was examined to explore whether the reservoir was used as holding habitat. Successful migrants never remained in a single area of the reservoir for longer than 1.1 d, whereas the unsuccessful migrants tended to have greater holding durations ranging from 1.1 d to 25.5 d.

Many fish (36 % of all adults tracked) entered Longs Creek, a dead-end tributary located at a large bend of the MGS reservoir (between reaches B and C; Figure 6.1). Time spent in Longs Creek had an important contribution to their overall delay within the reservoir, with tagged salmon spending a median of 5.2 h, but up to 4.7 d in the creek over multiple visits (Table 6.4). Five tagged adults also searched for the reservoir exit in the Mactaquac Arm (reach A; Figure 6.1), a dead-end tributary to the east of the MGS. Four of these fish visited the arm only once, spending 0.5-2.6 d, whereas one individual visited three times for a total duration of 4.3 d.

Slow water currents removed directional cues, and this was evidenced by the large proportion of time adults spent reversing direction, thus swimming downstream rather than making progress upstream. This behavior is highlighted using an example acoustic track of a successful migrant (Figure 6.5), demonstrating typical but extensive reservoir reversal movements to find the upstream exit of the reservoir, adding a minimum of 760 rkm to traverse the reservoir. The majority of tagged adult salmon each year exhibited the reversal behaviour (2014; 20/20, 2015; 21/24, 2016; 29/30), and spent a median of 31-53 % of their active movement time in the reservoir reversing direction (Figure 6.4). Fish direction was not detectably affected by the maximum angle of the water from downstream (LME logistic regression model, $p = 0.97$; Table 6.2c) but upstream movements were more common in the reservoir than upriver (LME logistic regression model, $p < 0.001$; Table 6.2c). Compared to the minimum distance the fish would need to travel to exit the reservoir (37 rkm), reversed-direction swimming added a median of 73 ± 58 rkm (Figure 6.4). Once the fish exited the reservoir, no time was spent swimming downstream by fish tagged in 2015 and 2016, and only two tagged fish

reversed direction in 2014 (with 3.7 % and 24.3 % of time upriver spent swimming in the reverse direction).

Adults that were successful in finding the upstream exit of the reservoir did not immediately leave after they were first detected in the reservoir exit area but continued searching before migrating upstream. This delay in exiting the reservoir took a median of 1.1 ± 5.5 d (range 27 min to 88 d).

Additional migratory delay occurred during dam passage at the BGS. This was estimated for four adults tagged in 2014 that were detected on a receiver just downstream of the BGS but could not be detected for the other two study years due to equipment loss. Delay was short for one fish that was downstream of the BGS for only 49 min before being detected upstream after 7.7 d, whereas another waited 13 d downstream and took 14.5 d to reach the upstream receiver. Two fish were unable to find a way upstream and were detected downstream of the BGS for 20 and 30 d before moving back downstream.

6.5 Discussion

The owner and operator of the MGS is currently considering options for improving fish passage, including the possibility of allowing volitional upstream passage to Atlantic salmon adults during their spawning migration. The current TH strategy removes the obstacle of reservoir passage, whereas volitional passage from the MGS would include navigation of the associated reservoir. This would be a new management strategy and therefore, the migratory success, rates, and behaviour of adult Atlantic salmon in the MGS reservoir needed to be assessed to inform the decision. It

was found that, of the fish successfully tracked, 47 % were successful in finding the upstream exit and traveling upriver toward the spawning grounds and 12 % were unsuccessful in exiting the reservoir. A high proportion (41 %) of adults experienced fallback over the MGS when released 3 rkm upstream of the dam. Within the reservoir, adults spent three-quarters of their time between 13 and 29 m with associated water temperatures of 12-18.5 °C, but they did not use the reservoir as holding habitat. Migration rates were suppressed within the reservoir (medians of 9.3 km d^{-1} vs. 39.0 km d^{-1} upriver) such that successful migrants would have been expected to traverse the 37 rkm of the reservoir 3.8 d faster on average (range 11 h to 19 d) if they were traveling at their upriver migration rate. Migratory behavior displayed within the reservoir included numerous reversals in direction, whereby 31-53 % of time within the reservoir was spent swimming downstream rather than upstream toward the spawning grounds. Adults also spent time searching for the upstream exit within dead-end tributaries. These reversals led to fish traveling a minimum of 73 ± 58 rkm over and above what was necessary to exit the reservoir.

The assessment of migratory success was hampered by presumed tag losses or fish mortalities (54 % of all adults tagged). However, because no mortalities were observed among control fish, and because one of the fallbacks was recaptured in the MGS fishlift without their acoustic transmitter but were identifiable through an external (Carlin) tag, we suspect that tag loss was a more likely fate than mortality. Reasons for the discrepancy in tagging success between control and experimental fish could include the difference in their environment, such as the much greater depths (40 m) that the adults were exposed to upon release in comparison to the depths experienced at the

MBF. Greater water temperatures at the surface (up to 23 °C) could also have been a factor upon release since the MBF used cooler water drawn at depth from the reservoir when holding fish. Therefore, migration success was not quantified through the use of models to avoid confounding factors, but rather is discussed in general terms which is justified by the high encounter estimates produced by a substantial receiver network throughout the reservoir.

Many (41 %) tagged adults were known to have fallen back over the MGS based on subsequent detections downstream of the dam. A substantial proportion (27.5 %) of adults determined to have experienced tag loss or mortality could potentially be attributed to fallback over the MGS based on abruptly ceased detections within the vicinity of the MGS. These results contrast with an earlier Carlin tag study that placed adult salmon less than 1 km upstream from the MGS and only observed only a 5.8-6.6 % fallback rate of wild fish (Marshall 1975). However, the same study observed much larger fallback rates of 12.5-54.2 % for hatchery fish. For Chinook salmon and steelhead (*Oncorhynchus mykiss*) in the Columbia River system, fallback has been reported to occur to 15-22 % of fish (Boggs et al. 2004). Fallbacks can incur injuries, especially when the fallback route is via turbines (Dauble and Mueller 2000). Fallback via turbine would be the only route available to adults at the MGS in the summer since the only other downstream migration route option are the spillways which are typically only available during the spring freshet. Such a high proportion of fallbacks was observed despite careful timing of release in coordination with dam operators to avoid entrainment. The timing of descending downstream over the MGS most commonly occurred in the first week but extended up to a month after release, with the adults not

attempting to travel very far upstream in search of the reservoir exit; therefore, one motivation for fallback could be a case of mistaken homing locations by fish that had intended to enter tributaries just downstream of the MGS (*i.e.*, Nashwaak River, located approximately 20 rkm downstream of the MGS) rather than spawning grounds upstream of the MGS (Marshall et al. 2000).

Only four tagged adults were determined to have been unsuccessful in navigating the reservoir as determined by continued movements in the reservoir throughout the autumn spawning migration season. Three of these fish had not traveled further than 14 rkm upstream of the release site whereas one found the reservoir exit before returning back to the mid-reservoir. All but one of these fish searched for the exit within a dead-end tributary (Longs Creek), visiting 1-7 times for a total duration of 3.5-19.4 h, adding to their migratory delay that could have contributed to their unsuccessful migration.

For the endangered Outer Bay of Fundy Atlantic salmon population, every adult's contribution (especially females) to recruitment is critical to work toward population recovery (O'Connell et al. 1997). The previous Carlin tag study done in the 1970s on 1,355 adults released in the MGS reservoir resulted in low proportions of fish reaching the BGS (22.3 % wild, 2.8 % captive-reared; Marshall 1975). Stemming from this, managers employed a TH strategy to aid their survival along the migratory route to their spawning grounds. The current strategy is that adult Atlantic salmon that return to the MGS are released upstream of the MGS reservoir, with the majority being released at the upper end of the MGS reservoir (Clarke et al. 2014). Migration success of the adults through the reservoir (47 %) and to the BGS (29 %) in the current study resulted

in greater rates than reported by Marshall (1975); however, the comparably high rate (41 %) of fallback with the potential risk of mortality in the absence of a bypass, leads to the conclusion volitional passage may not be advisable unless a safe downstream route (*e.g.*, a surface bypass with prevention of adult entry to turbines) for fallback salmon is installed and its efficiency is further proven.

Atlantic salmon cease feeding during their spawning migration; as a consequence, their energy reserves can be greatly impacted by reduced migration rates influencing their efficiency in reaching the spawning grounds (Salinger and Anderson 2006). Migration rates tend to be faster earlier in the migration and slow as they reach the spawning grounds (Thorstad et al. 2008). In this study, median migration rates were significantly lower early in the migration within the reservoir (9.3 km d^{-1}) and were faster as they moved upriver (39.0 km d^{-1}) and upstream of the BGS (65.2 km d^{-1}). The slower migration rate in the reservoir was assessed to result in a moderate migratory delay of 3.8 d and may be associated with the apparent lack of water current. Previous studies in the SJR have found adult migration rates to range from 5.5-6.2 km d^{-1} from the MGS to the BGS, with slower rates when released closer to the BGS (2.9 km d^{-1}; Marshall 1975). Reported rates of salmonids moving through free-flowing rivers are variable (0.7-65 km d^{-1}; Babin et al. unpublished), and investigations of salmonids moving through reservoirs are mostly limited to Pacific salmon of the Columbia River System. Chinook and steelhead have been reported to move through multiple reservoirs fairly quickly (22-77 km d^{-1}), with faster movements associated with greater water temperatures (Keefer et al. 2004).

While up- and downstream movements are typically seen as adult Atlantic salmon search for appropriate spawning grounds (Thorstad et al. 2008), this does not explain the reversals observed within the MGS reservoir since the impoundment is a minimum of 285 rkm downstream from their assumed spawning habitat. Instead, these reversals could be influenced by handling (Bernard et al. 1999), or by fish searching for the upstream exit of the reservoir with minimal directional cues from flowing water. This study did not detect a relationship between fish direction and water flow direction. The hydrodynamic model variables were estimated for the surface 5 m of the water column where the fish were assumed to travel, but the actual location of the fish in 3D space could have caused a mismatch with concurrent hydrodynamic conditions. In the reservoir, 95 % of the adults spent 31-53 % of their time swimming downstream rather than upstream, covering distances much greater than was needed to reach the upstream exit. Even the migrant that ascended furthest toward the spawning grounds in the Tobique River exhibited extensive movements to search for the exit of the MGS reservoir, visiting Longs Creek 22 times, approaching the exit 8 times, and spending approximately 30 % of the time within the reservoir swimming downstream covering a minimum of 760 extra rkm. Migratory delay accumulated between slower migration rates, searching in dead-end tributaries for up to 4.7 d (median 5.2 h) over multiple visits, and continued searching behaviour for a considerable period of time ranging from 12 h to 13 d after the fish were detected at the upstream exit before continuing their migration upriver. This could have been because the salmon could seek preferred water temperatures in the thermally stratified reservoir, whereas in the shallow upriver reach temperatures could have exceeded their preferred range. Lastly, delay was experienced

by fish as they attempted to pass the BGS, waiting for inconsistent periods of time. Overall, these sources of delay added approximately 4 to 30 d to their migration to the spawning grounds. These sources of delay within the lentic MGS reservoir is likely to result in reduced energy stores typically reserved for spawning activities.

This study examined the migratory movements of adult Atlantic salmon within the large MGS reservoir to determine whether the option of volitional passage upstream of the MGS would be viable. The comparable proportions of adults that successfully navigated the reservoir (47 %) and those that fell back over the MGS (41 %) suggests that volitional passage may expose a large proportion of adult Atlantic salmon to risks that may increase adult mortality and energy expenditure during the searching behavior exhibited in the reservoir in comparison to the current TH management strategy. Therefore, it is recommended that adult Atlantic salmon continue to be hauled upstream of the MGS reservoir as opposed to being allowed to pass volitionally.

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Table 6.1. Weight (kg) and fork length (FL; cm) [mean ± SE] of wild (released in reservoir) and captive-reared (controls kept at Mactaquac Biodiversity Facility; CR) Atlantic salmon adults tagged in 2014-2016. The number (N) of tagged wild adult Atlantic salmon is further split into small (<= 63 cm) and large (>63 cm) females (A, B) and small and large males (C, D). N/A = data not available.

Origin	Year	Tagging date	Tagging method	N (A, B, C, D)	Weight (kg)	FL (cm)
CR	2014	21 Jul	Gastric	12 (sex N/A, 10, 2)	2.8 ± 0.2	59.3 ± 1.5
CR	2016	27 Jun	External	8 (sex N/A, 5, 3)	2.7 ± 0.4	59.1 ± 2.3
Wild	2014	28 Jul-1 Aug	Gastric	20 (0, 5, 15, 0)	2.7 ± 0.3	62.5 ± 2.1
Wild	2015	9-10 Jul	External	24 (1, 10, 11, 3)	3.6 ± 0.4	66.9 ± 2.4
Wild	2016	28 Jun-7 Jul	External	30 (1, 11, 18, 0)	3.2 ± 0.3	63.4 ± 1.8

Table 6.2. The number of adult salmon in each fate categorization within each study year.

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

Table 6.3. Model type (linear mixed effects models; LMEM, or linear mixed effects (LME) logistic regression model), formula, sample size, and coefficient estimates, standard errors (SE), t-values, and *p*-values, assessing adult Atlantic salmon migration rates and fine-scale direction.

Coefficient	Estimate	SE	z/t	*p*
a) LMEM; fish_km_d ~ reach + (1|fish_id), n = 37 from 21 fish				
reach	-12.568	1.591	-7.901	<0.0001
b) LMEM; fish_km_d ~ reach * temperature_avg * water_velocity_avg + (1|fish_id)[1], n = 664 from 36 fish				
reach	12.4359	6.9720	1.784	0.08
temperature_avg	11.0324	7.9503	1.388	0.17
water_velocity_avg	1.2932	3.8010	0.340	0.73
c) LME logistic regression model; fish_direction ~ reach * water_angle + (1|fish_id)[1], n = 1102 from 36 fish				
reach	0.0210	0.0052	4.001	<0.0001
water_angle	0.0023	0.0056	0.041	0.97

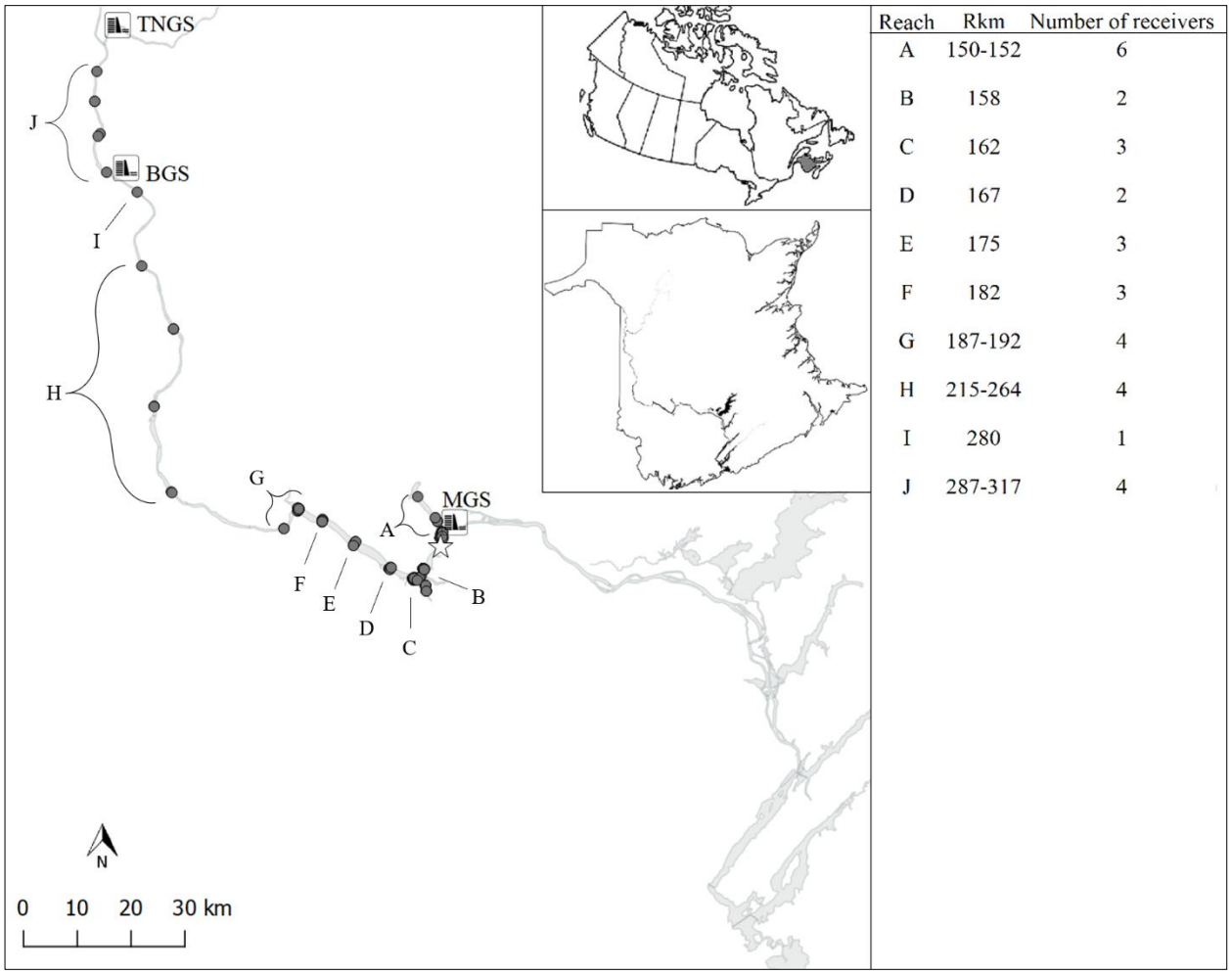
[1]Interactions (not shown) were non-significant

Table 6.4. Observed duration (d; mean ± SE) that adult groups spent traversing the MGS reservoir (37 rkm) versus the expected duration based on individual upriver migration rates (km d^{-1}).

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

Table 6.5. Number of Atlantic salmon adults that skipped or entered Longs Creek, number that entered upon their first encounter, and the median ± SE duration of time spent in the tributary.

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



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

Figure 6.1. A map of the Saint John River, New Brunswick, Canada, highlighting the locations of VR2W receivers (circles) and river reach groupings used in the Cormack-Jolly-Seber models. The location of fish release is indicated by a star, and the mainstem Generating Stations (Mactaquac MGS, Beechwood BGS, Tobique Narrows TNGS) are indicated by dam icons. Receivers downstream of the MGS are not shown.

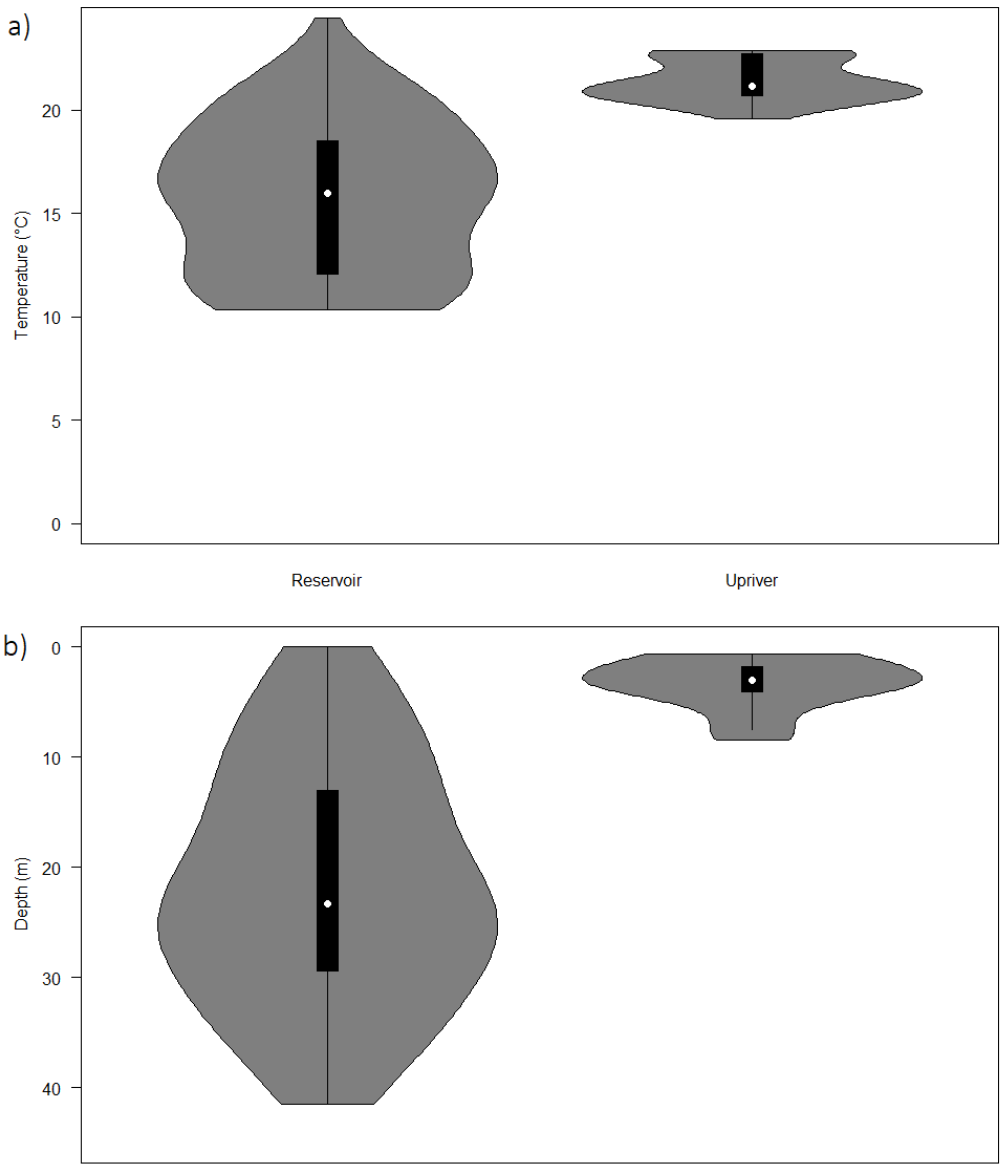


Figure 6.2. Violin plot of a) water temperature (°C) and b) depth (m) of adult Atlantic salmon with temperature/pressure sensor tags (Reservoir n = 10, Upriver n = 2). The black bars are boxplots with the white dot representing the median, the black bars representing the first and third quartiles, and the black lines representing the minimum and maximum. The grey areas are kernel density plots. Data after presumed tag loss or mortality are not included.

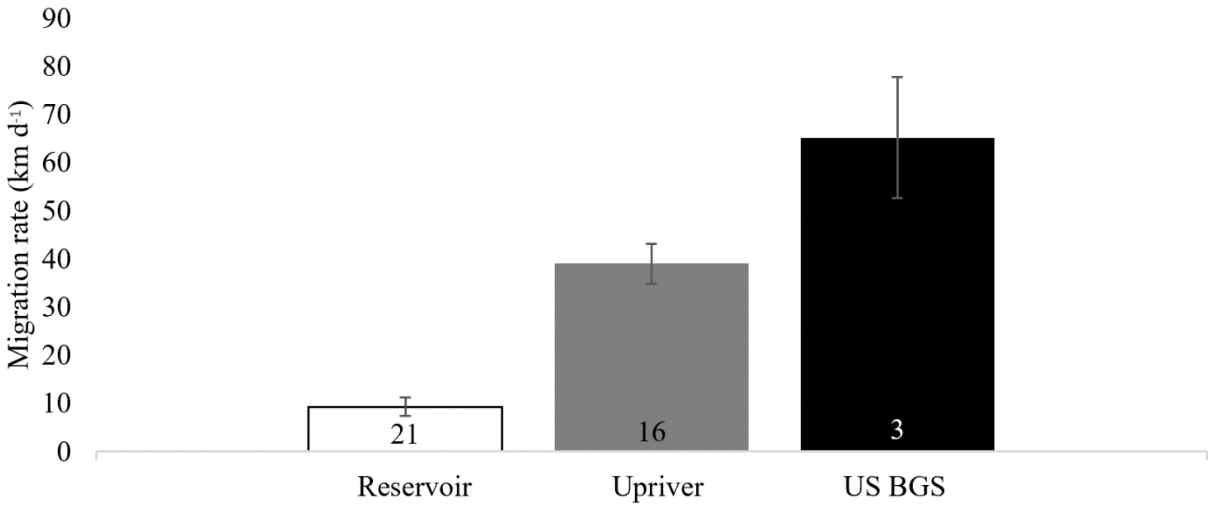


Figure 6.3. Median migration rate (km d^{-1}) of tagged (pooled 2014-2016) Atlantic salmon adults migrating through the MGS Reservoir, Upriver from Nackawic to the BGS, and upstream of the BGS (2016 only). Error bars represent standard error and sample sizes are in shown.

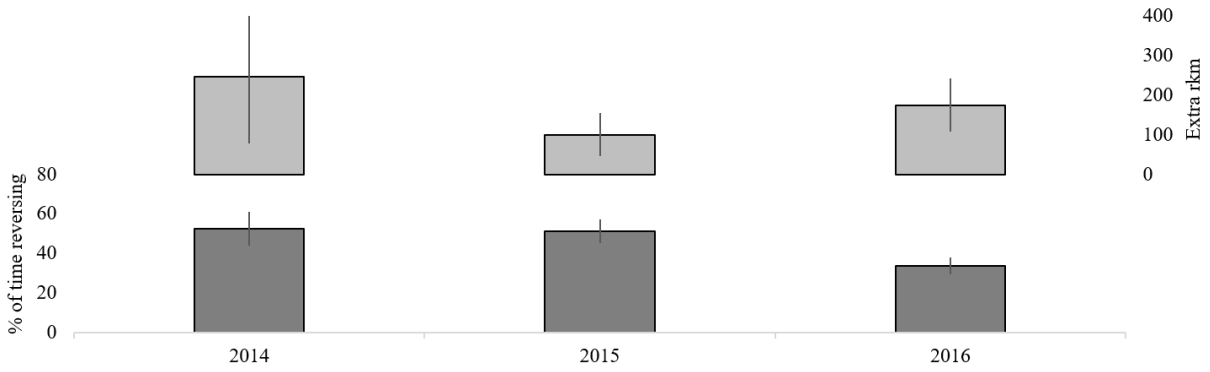


Figure 6.4. Percent of time tagged Atlantic salmon adults spent reversing (moving downstream) within the MGS reservoir in 2014-2016, and the minimum accompanying distance of extra rkm (additional to the 37 rkm of the reservoir); error bars represent standard error.

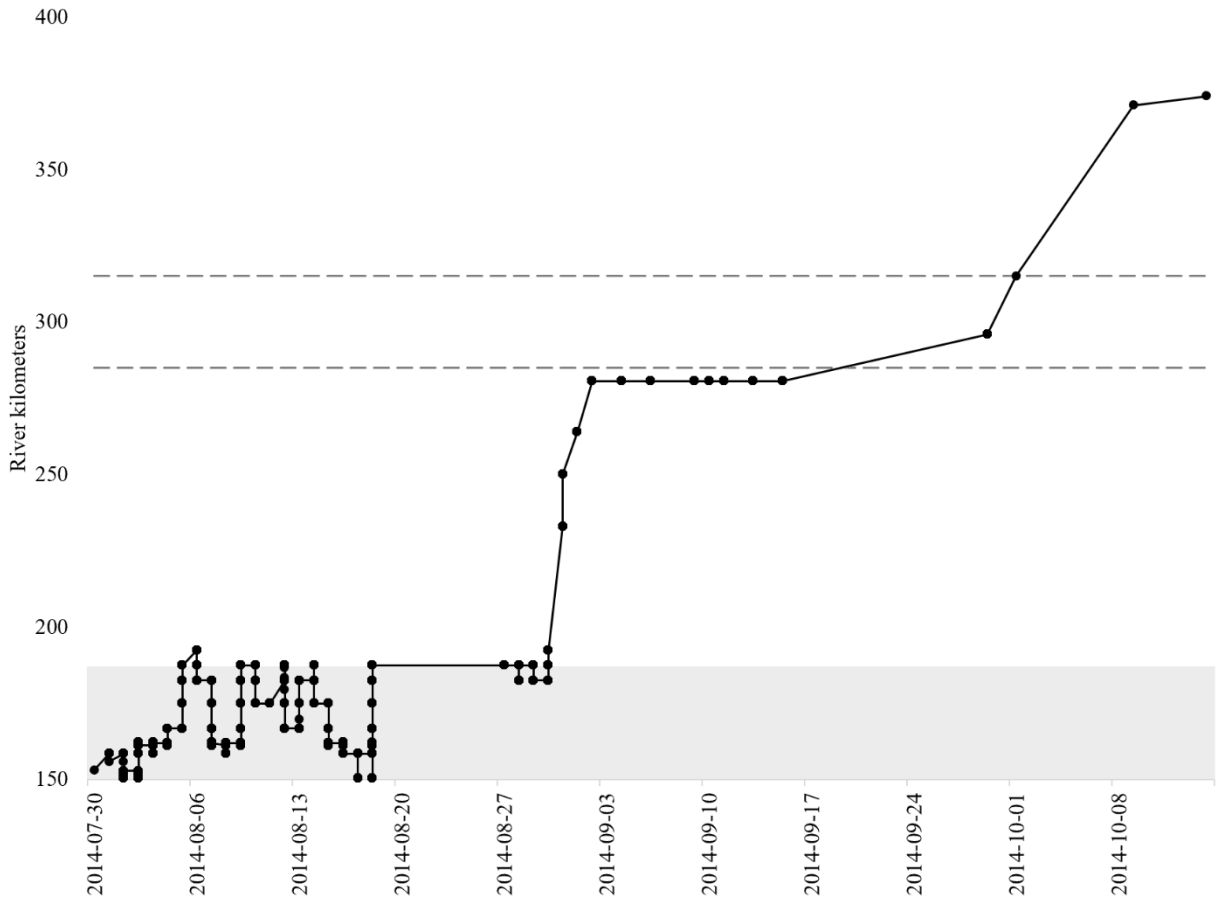


Figure 6.5. Location (river kilometers, rkm) of detections from an acoustically tagged adult Atlantic salmon released 3 rkm upstream of the Mactaquac Generating Station (MGS; rkm 150). The example acoustic track demonstrates the extensive reversals often observed within the MGS reservoir (light grey shading) before successfully exiting the reservoir and ceasing reversals in the upriver reaches as it passed the Beechwood Generating Station (rkm 285; dashed line) and Tobique-Narrows Generating Station (rkm 315; dashed line) on the way to the spawning grounds.

Chapter 7

General Discussion

7.1 Significance of dissertation: Improved understanding of the effects of a large hydropower reservoir on Atlantic salmon migrations

The main contribution of this dissertation is the improved understanding of the migratory delay experienced by all migratory lifestages of Atlantic salmon within the Mactaquac Generating Station (MGS) reservoir in relation to lotic reaches of the Saint John River (SJR). The most novel research contained herein is on the post-spawned adult (kelt), an often overlooked lifestage. Increased survival of kelts could support higher repeat spawning rates which could meaningfully contribute to population recovery. The most notable new findings presented in this dissertation are:

i. The MGS reservoir was not identified as overwintering habitat for juvenile migrants but was used by some kelts
ii. Winter survival of kelts was relatively high (56-75 %)
iii. There was evidence of kelts beginning to recondition in the SJR before migrating downstream earlier in the spring than smolts, coinciding with pulses of discharge during the spring freshet
iv. Kelts were generally found to remain in the surface 5 m, whereas adults during their spawning migration used the coolwater hypolimnion from 5-35 m
v. Smolt movements indicated active swimming both in the reservoir and upriver
vi. All lifestages displayed considerable movements in the reversed direction of their intended migration, increasing the distance traveled beyond the shortest route of 37 rkm of the reservoir: smolts 24-302 ± 14-217 rkm, kelts 57-61 ± 20-23 rkm, adults 73 ± 58 rkm

vii. The majority (50-100 %) of tagged Atlantic salmon of all lifestages experienced significant migratory delay within the MGS reservoir in comparison to river reaches: smolts 1.3-6.4 d, kelts 3.5-10.5 d, adults 3.8 d

viii. Spillways were open for fish passage for the majority (64-75 %) of attempts kelts made to pass the MGS, but were closed by the time all but three (0.04 %) smolts approached the MGS

ix. Migratory success to the lower SJR (downstream migrants) or the BGS (upstream migrants) was variable among lifestages: smolts 6-65 %, kelts 53-63 %, adults 47 %

x. Pre-smolts representing a trap-and-haul strategy from the Tobique-Narrows Generating Station presumably experienced high mortality partially attributable to predation, but timing to the lower SJR and survival rate curves in the downriver reach did not significantly differ from pre-smolts representing free-swim through a bypass

These conclusions are supported by the findings discussed below with relevant comparisons to related research, beginning with downstream migrants and followed by upstream migrants.

7.2 Downstream migrants

Downstream migrants through the SJR most often pass multiple reservoirs and dams (up to three) to reach the ocean. At the beginning of this study, there were no engineered downstream fish passage structures at any of these dams, which limited passage options to either the spillways when in operation (typically only during the

spring freshet), or the turbines. A downstream fish bypass was constructed at the Tobique-Narrows Generating Station (TNGS) and began operating in 2017. The new structure includes guidance and collection mechanisms along with a trap-and-haul facility. In order to determine whether downstream migrants should be allowed to swim freely through the bypass or be collected and transported downstream of the multiple dams, a separate study on their comparative success rates was conducted.

7.2.1 Pre-smolts and smolts

Pre-smolts that were released downstream of the Beechwood Generating Station (BGS) mainly overwintered in the upriver section, with only a few moving into the MGS reservoir in the winter. When released just downstream of the TNGS, a few fish overwintered in the BGS reservoir, but most moved down into the reach just upriver of the MGS reservoir. Therefore, the reservoirs do not seem to be the preferred overwintering habitat of pre-smolts, but rather they chose to use the more lotic reaches as they prepared for their spring migration.

Survival rates of juvenile salmonids moving through reservoirs are often reported to be lower than in free-flowing reaches (Connor *et al.* 2003; Beeman and Maule 2006; Monzyk *et al.* 2009). The later in the migratory season that fish remain in a reservoir has been found to decrease survival rates due to decreasing discharge and warming waters (45-76 % vs. <20 %; Smith *et al.* 2003). Apparent survival rates of smolts in this study were 95-100 % as they entered the MGS reservoir where survival remained relatively stable in most tagging years. Cumulative apparent survival to the lower SJR ranged from 6-65 %.

To attract fish movement toward the downstream exit and thus to improve migratory success, hydropower operators in other systems have strategically increased the discharge of water during biologically relevant timeframes, especially through spillways that typically have higher survival rates (Connor *et al.* 2005; Arnekleiv *et al.* 2007; Kraabøl *et al.* 2008). There was a limited timeframe of 4-6 d during which fish tagged as pre-smolts had the option of passing the MGS via the spillways, whereas those tagged as spring smolts did not encounter the MGS before the spillways were closed. Modelled water velocities within the MGS reservoir were not found to be related to an index of juvenile migration success. There were also no relationships found between a fish's migratory success and the proportion of time it spent traveling upstream rather than downstream, or its migration rate through the reservoir, but higher water temperatures were found to be correlated with greater migration rates. To provide directional cues to downstream migrants, the MGS operators could consider strategically increasing spill during as smolts and kelts approach the MGS in the spring during timeframes identified herein. However, increased spill is unlikely to be an economically feasible option; therefore, fish passage could be improved with the construction of a bypass at the MGS as was done at the TNGS.

Low-flow water bodies have been reported to cause juvenile salmonids to migrate 33-50 % slower than through free-flowing waters (Raymond 1968; Thorpe and Morgan 1978). Marschall *et al.* (2011) modeled Atlantic salmon smolt migration and found that migratory delay decreased survival beyond direct mortality from dam passage (86 % vs. 73 %). Migration rates of smolts in the SJR were 73 ± 4 % lower in the

reservoir (5.0-13.3 km d^{-1}) than up- (18.7-23.4 km d^{-1}) and downriver (15.4-29.3 km d^{-1}), regardless of smolt origin.

When migratory delay extends past the smolt window, juveniles are likely to desmoltify, reverting the physiological changes that had been made in order to tolerate salt water (Ruggles 1980; McCormick *et al.* 1998). These fish are thought to residualize in freshwater (Smith *et al.* 2003; Keefer *et al.* 2012), possibly going through the smoltification process again and continuing their downstream migration the following year, or becoming landlocked (Ruggles 1980). Migratory delay was quantified by comparing the observed duration of time it took smolts to traverse the reservoir to the durations that might be expected if they were traveling at their up- or downriver rates. Groups migrating in spring 2014 and 2015 took approximately 4.5 d to traverse the reservoir, whereas the groups migrating in spring 2016 took approximately 8 d. Over 50 % of all groups moved slower in the reservoir than would be expected, delaying their migration by 3.74 ± 0.94 d based on upriver migration rates or 3.54 ± 0.88 d based on downriver migration rates.

Juvenile salmonids are thought to use the river thalweg as a passive transport mechanism, especially earlier in the smolt migration window (Fried *et al.* 1978), although active swimming has also been observed in slow-moving waters (Thorpe and Morgan 1978; Thorstad *et al.* 2004). In this study, fish were found to move faster than the concurrent average water velocities throughout the study area, although significantly less upriver (68 %) than in the reservoir (93 %). This is indicative of a higher amount of passive reliance on flow for transport where the water flows are higher (upriver), but in

the reservoir the smolts had to engage in active swimming to make progress because the flows are so slow that they are not conductive for efficient migration.

Part of the delay was due to the amount of time (17-49 %) that smolts spent swimming upstream rather than downstream. Such counter-intuitive movements have been observed for Atlantic salmon smolts migrating through a lake which considerably increased the duration of their migration (Honkanen *et al.* 2018). Reversals were much less common upriver (3 %) than in the reservoir (35 %), such that they covered much more ground than was necessary to exit (24-302 ± 14-217 extra rkm). Reversals were also much less common downriver (11-41 ± 2-14 % of time; 7-64 ± 7-55 extra rkm).

Longs Creek was identified as an area of concern due to its position, whereby fish must make an approximate 90° left turn toward the MGS rather than heading straight into the dead-end tributary. Of the smolts that entered Longs Creek, the majority entered upon their first encounter as they moved downstream through the reservoir, and one smolt from each study year presumably died there. Searching this tributary contributed approximately 18 h-2.5 d to delay within the reservoir. This dead-end tributary was therefore identified as an obstacle to efficient migration causing delay and potential mortality. One option to help reconcile this issue would be a Flow Velocity Enhancement System (FVES) that could strategically increase flow during the spring migration toward the downstream exit to deter smolts from entering Longs Creek.

Dam passage was attempted by most smolts (71 %) only once, but others moved away from the dam and returned to attempt again up to seven times before passing. Average delay in the forebay area ranged from 30 min to 2.4 d, and dam passage was estimated to take an average of 8-9 h. Contrary to the literature (Aarestrup *et al.* 1999;

Ibbotson *et al.* 2006), most attempts (76 %) took place during daylight. Delayed dam passage mortality was presumably experienced by 1-3 fish in each tagging group.

Juvenile fish that are delayed in their migration are also at an increased risk of predation, compounding the enlarged risk already experienced during smoltification (Beamesderfer *et al.* 1990; Jepsen *et al.* 1998; Tiffan *et al.* 2006; Keefer *et al.* 2012). Predation may be increased within reservoirs due to high water transparency as compared to river reaches (Pelicice *et al.* 2014), along with increasing water temperatures as smolts are disoriented (Beamesderfer *et al.* 1990; Smith *et al.* 2003). While it was difficult to infer predation in the MGS reservoir due to the migratory behaviour of smolts including extensive reversals, it is known that predators such as smallmouth bass (*Micropterus dolomieu*), chain pickerel (*Esox niger*), and muskellunge (*Esox masquinongy*) are known to reside here (Ritter 2002; Clarke *et al.* 2014). Mortality by predation was inferred from detections in non-typical smolt areas downriver such as Grand Lake, Washademoak Lake, Belleisle Bay, and Kennebecasis River. Of the fish detected actively migrating downstream of the MGS in the spring, it was estimated that 12-46 % of mortalities could be attributed to predation. The tailrace area may also have been an area of increased predation risk, but mortality causes could not be distinguished between predation and delayed dam passage mortality, except for the pre-smolts transported just downstream of the MGS as a TH strategy. This group lost 77 % of individuals over the winter, some of which could be due to predation; however, some predators were found to have low proportions of Atlantic salmon smolts in their diets just downstream of the MGS (Curry *et al.* 2007; Andrews *et al.* 2018).

During three study years, both wild and hatchery smolts were tagged. Hatchery-origin fish have often been reported to be outperformed by their wild counterparts, having lower survival during their downstream migration and at sea, higher straying rates upon return, and lower spawning rates (Jonsson *et al.* 1991; Quinn 1993; Larsson *et al.* 2011). Stocking of hatchery-origin juveniles is controversial because the artificial environment does not allow for experience with predator avoidance and gaining skills for feeding (Carr 2001), which may account for their lower survival rates compared to wild fish (Ruggles 1980). Comparisons between wild and hatchery smolts in this study showed mixed results, with two study years having greater survival of hatchery smolts and one study year having greater survival of wild smolts. These results are compounded by the cumulative stress incurred by some wild fish being captured from the BGS gatewells before tagging. It is advisable to avoid sourcing the stressful smolt lifestage (Carey and McCormick 1998) from a stressful environment such as hydropower dam gatewells in future studies.

7.2.2 Free-swim versus trap-and-haul pre-smolts

The first engineered downstream fish passage structure at a hydropower generating station on the SJR began operating at the TNGS in 2017. The structure contains both guidance and collection mechanisms and a trap-and-haul (TH) facility, but whether a free-swim (FS) or TH passage strategy would be implemented following capture at the bypass was unknown before evaluating comparative survival rates. In autumn 2015, 50 tagged wild pre-smolts were released just downstream of the TNGS to represent a FS strategy, and another 50 fish were released just downstream of the MGS

to represent a TH strategy. Overwinter mortality and tag loss were estimated using 50 untagged pre-smolts and 50 dummy-tagged fish (both groups mostly CR fish) held at the Mactaquac Biodiversity Facility (MBF). The untagged group experienced a 4 % overwinter mortality rate, whereas the dummy-tagged group experienced a 22 % mortality rate with an additional 14 % experiencing tag loss without mortality.

Information from these groups on their migrations through the SJR and MGS reservoir were included within the larger juvenile study (Chapter 3 and section 7.2.1), while this study focused on comparative survival rates between passage strategies.

The FS group had the advantage of choosing their overwintering location from a greater variety of habitats than were available to the TH group. In the spring, fish in the FS group would imprint (Hasler *et al.* 1978) along the majority of the length of the river whereas those in the TH group would be unfamiliar with large reaches of river upon their return as adults. This could increase the straying rate of fish from the TH group (Buchanan *et al.* 2006).

The TH group presumably experienced high predation rates near the release site late in autumn based on low proportions of fish actively swimming in the spring, and concurrent telemetry studies that showed the presence of predators such as muskellunge (*Esox masquinongy*; K. Zelman, University of New Brunswick, personal communication) and striped bass (*Morone saxatilis*; Andrews *et al.* 2018) in the area.

Fish from both groups arrived at the lower SJR within similar time frames (FS 4-23 May 2016, TH 4-20 May 2016), and apparent spring survival rate curves in the downriver stretch were not significantly different (lower SJR: FS 65.5 %, TH 64.8 %). To avoid undue stress, predation risk, and to allow for the natural processes of

imprinting during long-distance movements, I recommend that the pre-smolts be allowed to swim freely to bypass the TNGS. The success of free-swimming individuals from the Tobique River throughout the SJR would be further facilitating by the installation of a bypass at the downstream BGS and MGS facilities.

7.2.3 Post-spawned adults

Individuals in relatively poor condition after spawning, typically males and larger-bodied fish, tend to leave the river quickly to recondition at sea, but those that are still in relatively good condition tend to overwinter in the river (Halttunen 2011; Nyqvist 2016). While overwintering, movements are thought to be minimal (Östergren and Rivinoja 2008). The motivation to recondition was assessed through the initial movements after tagging and release, and over the winter. It took kelts approximately 11 days in autumn 2014 and 25 days in autumn 2015 to move the initial 30 rkm to the first receiver downstream of the release site, with no difference between the sexes. There was evidence of kelts attempting to pass the MGS in the winter, presumably to recondition in the ocean, but none were detected downriver. Two males presumably died in the reservoir after being detected at the MGS. Some kelts (mostly large females) moved far into the reservoir but returned upriver to overwinter, whereas others overwintered in the reservoir without being detected at the MGS.

Overwinter mortality of kelts is underreported in the literature, but has been estimated as 30-46 % in a Nova Scotian river (Ruggles 1980), and was observed to be 63-80 % in a Norwegian river (Halttunen 2011). A study that transported kelts downstream to the SJR estuary in the autumn found that these fish moved upstream and

remained in the river until the spring (Huntsman 1931). Winter survival was generally high (56-75 %) in the SJR, with males incurring higher mortality rates than females (50-100 % vs. 13-33 %), and small salmon suffering more losses than large salmon (44-47 % vs. 9-30 %). Only three males survived to spring migration, with the first beginning movements on 24 April 2015, and the last on 2 June 2015 being the latest initiation of the kelts.

There is evidence of kelts beginning to recondition by feeding in the spring while emigrating to the ocean (Penney and Moffitt 2014). Food items can include smolts, other small fish, and invertebrates (Penney and Moffitt 2014). In this study, seven kelts displayed back-and-forth movements in the transition area from upriver to the reservoir before beginning directed downstream movements. This was interpreted as a reconditioning period that lasted 10-33 d.

Kelts have been observed to begin their outmigration just before the spring freshet (Hubley *et al.* 2008), with some fish extending their river residence for up to 2 months after peak discharge (Halttunen *et al.* 2013). Spring discharges in the SJR began approximately 2 weeks later in 2015 than 2016. Kelts appeared to respond to pulsed increases in discharge during the SJR spring freshet by initiating migratory movements. Temperatures also began rising later in the first study year, and the cumulative degree day (CDD) rate was slower. These inter-annual differences likely influenced the later initiation of kelt migrations in the first study year, which may have influenced the higher apparent survival rate (94.6 % vs. 81.9 % as kelts encountered the MGS, 62.5 % vs. 53.3 % once they reached the lower SJR). Water temperature was positively correlated with

migration success. Although the covariates of sex and body condition were not found to influence apparent survival rates, spring mortality was generally higher in females than males (33-38 % vs. 0-20 %) but was similar between small and large salmon in the first year (33 % vs. 30 %) and lower for small salmon in the second year (11 % vs. 55 %).

It has been postulated that kelts migrate downstream just before smolts, potentially aiding the navigation of the naïve juveniles (Jonsson *et al.* 1990). This was not corroborated by the research presented in my thesis; the temporal overlap of the kelt and smolt migrations was minimal, and generally there was an earlier migration of kelts in comparison to the smolts.

The larger-bodied kelts relative to smolts have a higher chance of incurring injury during turbine passage (Ruggles 1980; Franke *et al.* 1997). Spillway gates were closed after 15 May 2015 and 3 May 2016, forcing any migrants after these dates to pass via the turbines. In one instance, a fish was presumed dead due to dam passage when the only option available for fish passage was the turbines. Three other fish were also presumed to be dam passage mortalities, although the spillways were available as a passage option. Dam passage occurred mostly during the night (46-73 %; consistent with Scruton *et al.* 2008) and occurred approximately 5 days sooner relative to the initiation of migration in 2015 than 2016.

The downstream migration of kelts has been largely ignored (Ruggles 1980; Halttunen 2011), and information on Atlantic salmon specifically, or on this lifestage migrating through hydropower reservoirs, is non-existent. The majority of kelt reservoir migration literature comes from studying rainbow (steelhead) trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*). Steelhead kelts migrating through reservoirs in

the Columbia rivers system were found to travel significantly faster in the free-flowing stretches than the impounded stretches (medians 98.64-110.60 km d^{-1} vs. 9.84-64.04 km d^{-1}; Wertheimer and Evans 2005). This was also found for Atlantic salmon kelts in the SJR where migration rates were significantly slower in the reservoir (8.5 ± 2.5 km d^{-1}) than up- (29.7 ± 5.0 km d^{-1}) or downriver (22.1 ± 3.1 km d^{-1}). If fish had traveled through the reservoir at the river rates, they could have exited approximately 5-6 days sooner than was observed. Downstream migration rates between receivers were positively correlated with water temperatures and negatively correlated with concurrent water velocities. The seemingly contradictory relationship with water velocity seems to be driven by fast movements in especially low-flow areas such as the bend around Longs Creek.

Brown trout kelts migrating through a Norwegian reservoir displayed reversed direction swimming activity, but only after the fish had approached the dam and to a much lesser extent then observed in this study (Arnekleiv *et al.* 2007). In my dissertation data, only about one-third of the fish did not spend time reversing direction, whereas the majority spent approximately one-third of their time reversing direction during both the winter period and in the reservoir during spring. The proportion of time that fish spent traveling in the direction opposite to their downstream migration within the reservoir was found to impact overall migration success. Reversals were relatively rare once fish had passed through the MGS (7 %).

Ten kelts in each study year had temperature and pressure (as a proxy of depth) sensor tags. Jonsson *et al.* (1990) reported that post-spawned Atlantic salmon activity is

low when water temperatures have not exceeded 2 °C, and migration initiation is often reported to occur when water temperature exceeds 4-6 °C (Östergren and Rivinoja 2008). The reconditioning and migratory periods in 2015 increased from near zero in the winter to 10-12 °C, whereas temperatures were still near zero through the 2016 reconditioning period and reservoir migration, increasing to approximately 10 °C (maximum 23 °C) when downriver.

Kelts remained in the surface 5 m most of the time, with one notable exception. A 1SW female overwintered just upstream of the MGS, spending 60 % of the winter between 30-40 m and reconditioning at depths between 23-34 m. This kelt was ultimately successful in exiting the river and was detected in the Gulf of Maine in the summer.

7.3 Upstream migrants

Upstream migrants within the SJR that home to natal habitat upstream of the MGS must be successfully attracted to the MGS fishlift if they are to reach their desired spawning grounds. The current management strategy assumes that early migrants are homing to tributaries far upriver and are therefore transported just downstream of the Tobique River, whereas later migrants are released downstream of the BGS near Woodstock so they can home to their respective spawning grounds that are indistinguishable by managers. The current study evaluated the viability of allowing volitional passage through the MGS reservoir.

It is common for adult salmon to fallback over a dam (15-22 %; Boggs *et al.* 2004), incurring delay and potential injury especially when moving past turbines which

is the only possibility for summer migrants in the SJR (Dauble and Mueller 2000). A considerable proportion (41 %) of adults released three rkm upstream of the MGS fell back over the dam.

Migration rates tend to be faster earlier in the migration and slow as they reach the spawning grounds (Thorstad *et al.* 2008), but the opposite trend was seen in this study with migration rates being significantly lower in the reservoir (9.3 ± 1.9 km d^{-1}) than upriver (39.0 ± 4.1 km d^{-1}), and continuing to increase upstream of the BGS (65.2 km d^{-1}). If they traversed the reservoir at the upriver rate, it was estimated that they could have exited the reservoir approximately 3.8 d sooner.

Migratory delay can be detrimental for adult salmon that fast in freshwater as they migrate to the spawning grounds. Their constrained energy budget is adapted for reproductive tissue growth and spawning activities. When energy is lost (5-8 %; Mesa and Magie 2006) to searching for the exit of a reservoir, the risk of pre-spawning mortality can increase (Keefer *et al.* 2004), and they are less likely to be successful in reaching the spawning grounds (Caudill *et al.* 2007). Such searching within the MGS reservoir was seen by adults spending 31-53 % of their time in the reservoir swimming downstream rather than upstream, covering much more distance than was needed to exit the reservoir (73 ± 58 rkm). Once they moved upriver, only two fish spent time reversing (3.7 % and 24.3 %). Downstream movements were more common in the reservoir than upriver (45 % vs. 4 %). Most of the adults searched for the upstream exit of the reservoir within the dead-end tributary called Longs Creek, adding approximately 5.2 h to their delay over multiple visits. Once a fish was detected near the reservoir exit,

it often returned downstream before eventually exiting. This further added to their delay in exiting the reservoir by a variable amount ranging from 27 min to 15 d.

The surface waters of reservoirs are warmer than free-flowing rivers, and as the summer progresses these waters would continue to warm. The longer an adult remains within the reservoir, the more likely they will be exposed to increasing water temperatures that increase metabolic demands, further reducing energy stores (Keefer *et al.* 2004). Increasing water temperatures may become limiting for cool-water Atlantic salmon in the SJR with the progression of climate change (Dugdale *et al.* 2018). However, deep reservoirs such as the MGS reservoir thermally stratify, providing cooler water at depth. Water temperatures experienced by ten adults in the MGS reservoir ranged from 10-20 °C depending on the depth inhabited (5-35 m), which were not substantially greater than surface temperatures upriver (20 °C), indicating that adults were seeking cooler waters in the depths of the reservoir.

The pooled survival estimate upon exiting the reservoir was 47 %. These results are greater then observed in a Carlin tag study done in the 1970s that found only 22.3 % of wild and 2.8 % of captive-reared adults released in the MGS reservoir reached the BGS (Marshall 1975). Two adults from this study presumably spawned after a 20-30 d residence downstream of the BGS, and their migratory information as kelts are reported in Chapter 5. Two other fish were able to pass the BGS after waiting variable periods of time (49 min-13 d).

7.4 Conclusions and recommendations

The overarching question of my dissertation was:

Does the MGS reservoir present a problem for Atlantic salmon migration?

This overarching question was broken down into two principal objectives, to:

(1) Quantify migration success, rates, and delay of downstream (smolts and kelts) and upstream (adults) migrants as they navigated through the SJR and the MGS reservoir, and to

(2) Relate smolt, kelt, and adult movements to hydrodynamic conditions that are impacted by MGS operations.

Objective (1) was achieved, and the results are summarized in Table 7.1. Overall migration success through the reservoir was higher for downstream (smolts > 81 %, kelts > 82 %) than upstream (adults 47 %) migrants. Migration rates through the reservoir were slightly faster for smolts (~5-13 km d^{-1}) than kelts (~4-9 km d^{-1}), or adults (~9 km d^{-1}). Migration delay was lowest for adults (~4 d), greatest for kelts (~4-11 d), and slightly less for smolts (~1-8 d).

Objective (2) was attempted by modeling the hydrodynamic outputs of water velocity and direction (angle from downstream) from inputs of hourly tailrace discharge from the BGS, total discharge through the MGS, tributary discharges, wind speed and direction, as well as bathymetry. Water velocity and direction was estimated at the same locations as the receivers in the upriver and reservoir stretches for every 2 h during the study period. Fish movements were examined in relation to hydrodynamic conditions through numerous models, including:

i. Migration rates of each downstream movement between receivers for downstream migrants, and of each upstream movement between receivers for upstream movements, were tested for their dependence on water velocities

ii. Water velocities were subtracted from the migration rates of each downstream movement between receivers for smolts to determine where they were traveling passively (water velocity > fish migration rate) or actively (fish migration rate > water velocity)

iii. Fish direction (upstream or downstream) during each movement between receivers was tested for its dependence on water direction (maximum angle from downstream)

iv. An index of migration success was tested for its dependence on average water velocity and the fish's migration rate through the reservoir

The only model in which hydrodynamic conditions were found to correlate with fish movements was from model (i); downstream movements of kelts were found to be negatively correlated with concurrent water velocities. This relationship was not expected since one would assume that higher water velocities would motivate greater migration rates. However, kelts are not dependent on water currents as a transport mechanism and may seek calmer waters to allow for feeding and reconditioning during their spring migration. Smolts that are thought to use water currents as a transport mechanism had later migration timing whereby most were restricted to passage after the spillway gates had closed. If the spillway gates were still open during the smolt migration, perhaps flow-migration relationships would be revealed.

Returning to the overarching question "Does the MGS reservoir present a problem for salmon migration?", the results of the studies within this dissertation provide multiple lines of evidence that the MGS reservoir does present a problem for salmon migration. The main findings for each lifestage are shown in Figure 7.1. The lentic waters of the reservoir have removed directional cues, causing all migratory lifestages to migrate slower through these waters than in free-flowing stretches that leads to migratory delay and reduced migration success. This is detrimental for smolts that are restricted in time to reach the ocean during physiologically and ecologically optimal conditions, for kelts that are attempting to reach the ocean to recondition after an energetically taxing spawning season, and for adults that are conserving energy for reproductive use at a time when they are not feeding. To aid the endangered Atlantic salmon within the SJR, the findings of this research have been applied to recommendations for the hydropower management of the MGS.

7.4.1 Implications for hydropower managers and fisheries management

Current operations at the MGS related to downstream migrants involve spilling during the spring freshet but no downstream fish passage structures are provided, and for upstream migrants a trap-and-haul strategy is practiced. The selection of the Option 4) Lifetime Achievement in the Mactaquac Project maintains this *status quo*.

Water velocities and directions modelled within the reservoir were very low (~0.04 cm s^{-1}) and erratic, especially at the bend near Longs Creek. The hydrodynamic model results could not be related to fish movements, and therefore recommendations regarding discharge magnitude in order to aid migrations cannot be made based on the

flow ranges studied herein. However, the spill timing was found to be too early for most downstream migrants in the spring, and unavailable to those attempting to pass in the autumn. Therefore, the first recommendation that could be implemented without any change to existing structures would be to consider changing the spill regime such that a greater proportion of the kelt migration, and perhaps the later smolt migration, could have the option of using the higher survival route of spillway passage. However, changes to the spill regime may not be compatible with power generation operations and the realities dictated by the spring freshet. There is another option that could improve survival rates beyond those of spillway passage, *i.e.*, a bypass installation.

The second recommendation is to improve downstream fish passage by constructing a bypass at the MGS as was done at the TNGS. Bypass passage has been found to have improved survival rates over spillway and turbine passage (Whitney *et al.* 1997; Buchanan *et al.* 2006). Such structures can include a collection facility where downstream migrants can be assessed. They can also be de-watered such that only a small volume is lost to the tailrace in order to prevent injury to the fish as they are passed downstream, with the remaining water volume being recovered and passed through a secondary turbine (Johnson and Dauble 2006). As with any passage structure, the efficacy of a bypass is dependent upon its success in attracting fish to the entrance. Mechanical guidance structures, such as bar racks, louvers, or floating-boom systems would likely need to be associated with the bypass to improve attraction. Another mechanism to aid in attraction, a Flow Velocity Enhancement System (FVES), could also be considered. A FVES is a hydraulic system that induces currents to guide fish through low-flow areas toward the direction of migration (Coutant 2001). Such systems

could be installed just upstream of the MGS to direct fish toward the entrance of the bypass and could also be considered in other problem areas such as the 90° bend in the reservoir near Longs Creek. This dead-end tributary was identified as an area where downstream migrants incurred delays, likely searching for the downstream exit, and smolts within each study year presumably died here. The bend in the reservoir also had especially low water velocities and erratic directions. Therefore, a strategically placed but necessarily large-scale FVES could prevent downstream migrants from entering the tributary, and instead induce them to take the left turn toward the MGS.

At the TNGS, migratory success and timing were not significantly different between groups of fish allowed to free-swim after being released downstream of the TNGS to represent a bypass scenario, and those released downstream of the MGS to represent a trap-and-haul strategy. To avoid undue stress, predation risk, and to allow for the natural processes of imprinting during long-distance movements, it is recommended that pre-smolts be allowed to free-swim to bypass the TNGS.

Upstream migrating adults are currently attracted to a fishlift at the MGS that places them into a truck for transport to the MBF for assessment of biological characteristics and stock determination (*e.g.* Serpentine stock). The adults are then transported and released either just downstream of the Tobique River or near the town of Woodstock. This study assessed the viability of allowing volitional upstream passage through the MGS reservoir. Adults were found to have low migration rates and success through the reservoir, and many individuals experienced fallback through the turbines. Therefore, it is recommended that the current trap-and-haul strategy is retained.

In summary, the following recommendations are given:

i. Explore changes to the spill regime to allow a greater proportion of downstream migrants the option of spillway passage
ii. Construct a downstream bypass facility at the MGS with associated guiding structures, potentially including a collection facility for non-invasive assessments of downstream migrants
iii. Allow downstream migrants to free-swim through the TNGS and potential future MGS bypasses rather than implementing a trap-and-haul strategy
iv. Continue trap-and-haul operations for upstream migrating adults

The Outer Bay of Fundy Atlantic salmon population is facing multiple threats that have led to severe population declines (Committee on the Status of Endangered Wildlife in Canada 2011; Clarke *et al.* 2014; Jones *et al.* 2014). The threat of most concern for this population is habitat fragmentation such as that introduced by the MGS (Clarke *et al.* 2014). In addition to the high mortality at sea and future changes caused by climate change (Condron *et al.* 2005) experienced by all Atlantic salmon populations, the fish returning to habitat upstream of the MGS are experiencing low production and high mortality due to reservoir and dam effects (Gibson *et al.* 2009). The only option that was under consideration that would remove these threats in entirety was the Option 3) Restoration of the river via dam removal.

Some hydropower projects worldwide have been considered for removal to avoid any adverse effects on fish and the ecosystem as a whole. Only two high-head

dams have been removed to date, the Elwha Dam and the Glines Canyon Dam, both on the Elwha River in Washington, U.S.A. (Gregory *et al.* 2002). Chinook salmon took advantage of the recovered habitat very soon after dam removal (McHenry *et al.* 2015). Many countries are also incorporating the lessons learned from hydropower impacts into frameworks of minimum environmental flow requirements to ensure the health of river ecosystems while allowing for anthropogenic use. Countries worldwide are initiating legal protection for segments of rivers or whole river basins from hydropower development (World Commission on Dams 2000). From the salmon's perspective, dam removal would be recommended to permanently restore river flows and reconnect habitats.

7.5 Future research

Lessons learned during the course of performing this research are applicable for future research ventures. The SJR has a large proportion of juveniles that begin downstream movements in the autumn as pre-smolts. Juveniles tagged as pre-smolts were allowed to acclimate to the tag throughout the winter before beginning their spring migration, whereas those tagged in the spring may have displayed some unnatural movements due to tagging effects despite keeping the tag burden to less than 2 % of body weight (Thorsteinsson 2002). Those tagged as pre-smolts began movements earlier in the spring than some of the release dates of the spring smolts, which allowed the former group the option of passing the MGS via the spillways. Due to the physiological sensitivity of tagging fish undergoing the smoltification process (Ruggles 1980; McCormick *et al.* 1998) and the potential mismatch in their release timing, the authors

advice future researchers to tag pre-smolts if available in their system to allow fish to acclimate to the tag and provide results more aligned with the natural behaviours of the untagged population.

The data partnership with the Ocean Tracking Network provided additional information on the movements of salmon once they had left the SJR. Two fish tagged as pre-smolts were detected off the Halifax Line, presumably on their way to feeding grounds in the Laborador Sea before returning as alternate spawners. Similarly, four kelts were detected off the Halifax Line in 2015. Another kelt was detected in the Gulf of Maine in 2016 that may have been staying closer to the coast to return as a consecutive spawner. Such information is valuable because it shows that these fish have survived their freshwater migration and have traveled a fair distance at sea and could provide insights into their respective life history strategies, especially when the battery life of the tag allows for detections upon return to the river. Any telemetry study conducted on migratory species worldwide are strongly recommended to take advantage of such a powerful data sharing platform.

In regard to future research on Atlantic salmon migrations within the SJR, continued monitoring should be conducted along with potential improvements to flow velocities and fish passage at all hydropower generating stations. Since population numbers are low, the relatively non-invasive strategy of assessment during downstream passage via a bypass collection facility and continued assessment of upstream migrants as it is currently conducted would be preferable. Due to the extensive inputs of captive-reared fish into the SJR, these individuals should also be assessed in relation to the wild counterparts.

7.6 References

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Table 7.1. Migration success (% apparent survival), rates (km d^{-1}; medians), and delay (observed – expected duration based on up- and downriver rates; medians) of downstream (smolts and kelts to the lower SJR) and upstream (adults to the Beechwood Generating Station BGS) migrating Atlantic salmon within the Saint John River from 2014-2016.

		Smolts	Kelts	Adults
Migration success (% apparent survival)	BGS			24
	Reservoir	81-100	82-94	47
	Lower SJR	6-65	53-63	
Migration rate (km d^{-1})	Upriver	18.8-23.4	22.4-36.8	39.0
	Reservoir	5.0-13.3	4.4-8.9	9.3
	Downriver	15.4-29.3	14.9-25.1	
Migration delay (d)	Reservoir vs. Upriver	2.2-6.4	4.2-5.5	3.8
	Reservoir vs. Downriver	1.3-5.7	3.5-10.5	

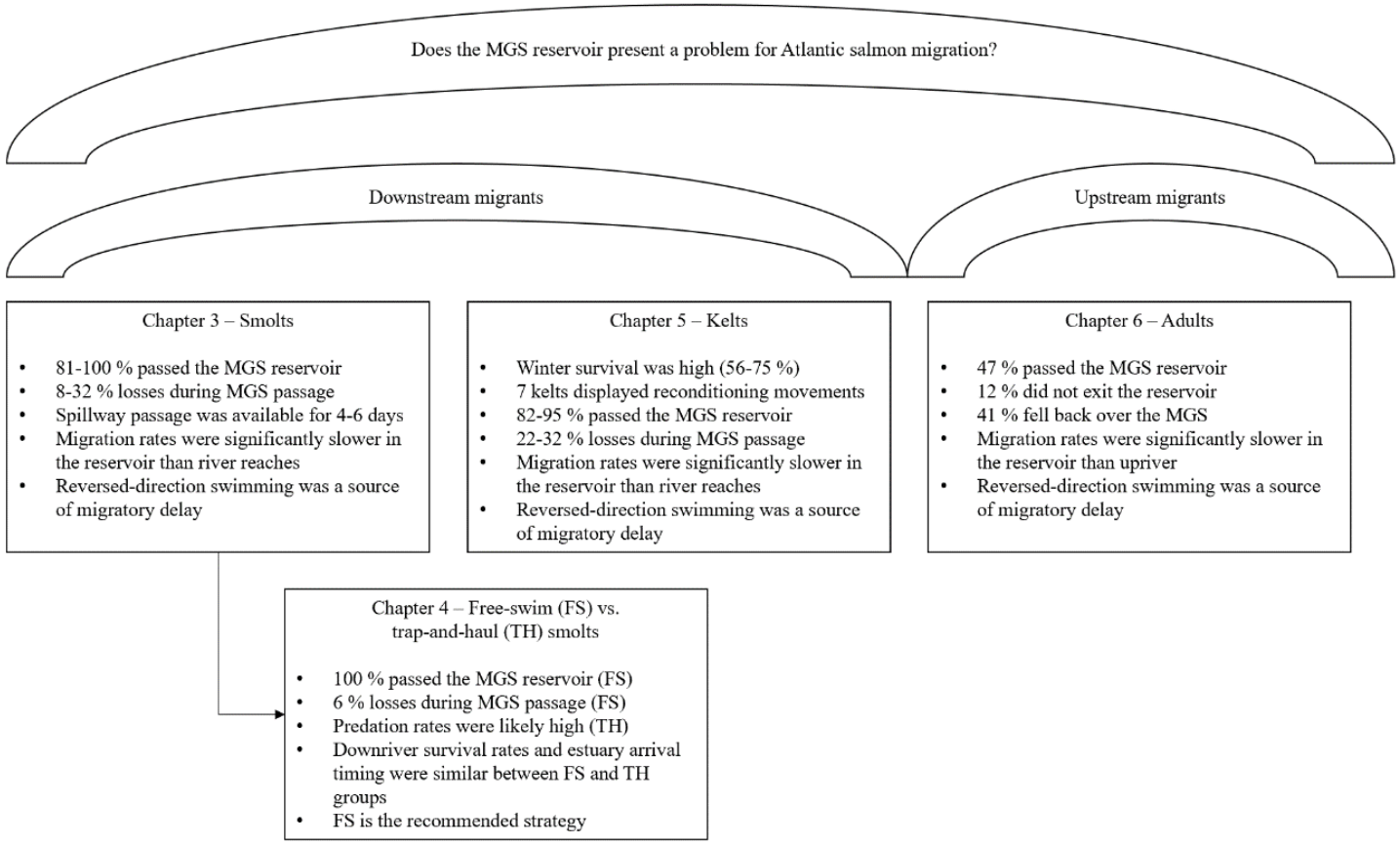

Figure 7.1. Diagram of the main findings on Atlantic salmon migrations within the Mactaquac Generating Station (MGS) reservoir and Saint John River.

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Appendix 1

Contribution of authors in Chapters 2 – 6

Chapter 2 [*Detection efficiency of acoustic receivers in a large hydropower reservoir*]

A. Babin designed the range testing study for the acoustic tag types used throughout the thesis, supervised the fieldwork and data analysis, and wrote the article. L. Fitzpatrick performed the majority of the fieldwork and initial data analysis. T. Linnansaari consulted on the study design and data analysis and was the primary editor on the article. R. A. Curry contributed in editing the article.

Chapter 3 [*Migration of Atlantic salmon (Salmo salar) smolts in a large hydropower reservoir*]

A. Babin performed the majority of the fieldwork including fish collection, tagging, active tracking, data management and analysis, and wrote the article. T. Linnansaari designed the study, supervised the fieldwork, and was the primary editor. M. Ndong created the hydrodynamic model under the supervision of K. Haralampides. S. Peake provided input on fieldwork and data analysis and contributed in editing the article. R. Jones was a partner in the field for fish collection and active tracking, supervised the use of captive-reared fish, provided input on fieldwork and data analysis, and contributed in editing the article. R. A. Curry helped to design the study, provided input on fieldwork and data analysis, and contributed in editing the article.

Chapter 4 [*Evaluation of downstream passage management strategies for Atlantic salmon Salmo salar smolts in a regulated river: free-swim versus trap-and-haul*]

A. Babin performed the fish tagging and helped with receiver deployment, and was also responsible for the data management and analysis, and writing of the article. S. Peake provided input on the fieldwork and contributed to editing the article. T. Linnansaari designed the study, supervised the fieldwork, and was the primary editor. R. A. Curry helped to design the study and contributed to editing the article. R. Jones was a partner in the field for fish collection, supervised the use of captive-reared control fish, and contributed in editing the article.

Chapter 5 [*Overwintering and migration behavior of post-spawned Atlantic salmon (Salmo salar) in a large hydropower-regulated river and reservoir*]

A. Babin performed the majority of the fieldwork including fish collection, tagging, active tracking, data management and analysis, and wrote the article. T. Linnansaari designed the study, supervised the fieldwork, and was the primary editor. M. Ndong created the hydrodynamic model under the supervision of K. Haralampides. S. Peake provided input on fieldwork and data analysis and contributed in editing the article. R. Jones supervised the use of captive-reared kelts, provided input on fieldwork and data analysis, and contributed in editing the article. R. A. Curry helped to design the study, provided input on fieldwork and data analysis, and contributed in editing the article.

Chapter 6 [*Atlantic salmon (Salmo salar) upstream migration delay in a large hydropower reservoir*]

A. Babin performed the majority of the fieldwork including fish tagging, active tracking, data management and analysis, and wrote the article. T. Linnansaari designed the study, supervised the fieldwork, and was the primary editor. M. Ndong created the hydrodynamic model under the supervision of K. Haralampides. S. Peake provided input on fieldwork and data analysis and contributed in editing the article. R. Jones supervised the use of captive-reared control fish, provided input on fieldwork and data analysis, and contributed in editing the article. R. A. Curry helped to design the study, provided input on fieldwork and data analysis, and contributed in editing the article.

Curriculum Vitae

Candidate's full name: Amanda Babin

Universities attended:

Master of Science, University of New Brunswick, 2013 (Biology)

Bachelor of Science, Mount Allison University, 2009 (Biology)

Publications:

Amanda Babin, Lauren Fitzpatrick, Tommi Linnansaari, and R. Allen Curry. 2019. Detection range of acoustic receivers in a large hydropower reservoir. Fishes, 4(4): 1-10.

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Conference Presentations:

Atlantic Salmon Ecosystems Forum, Quebec City, QC. 2019. Atlantic salmon (*Salmo salar*) pre-smolt and smolt movements in the Saint John River and Mactaquac reservoir.

Departmental Seminar, University of New Brunswick, Fredericton, NB. 2018. River to lake: Challenges for Atlantic salmon (*Salmo salar*) migrations in the Mactaquac Reservoir.

Mactaquac Biodiversity Facility update, Fredericton, NB. 2018. Atlantic salmon (*Salmo salar*) in the Wolastoq/Saint John River and Mactaquac Reservoir.

Saint John River Watershed International Cross-Boundary Summit, online webinar. 2018. Atlantic salmon (*Salmo salar*) migrations in the large reservoir of the Mactaquac Generating Station.

25th annual Graduate Research Conference, University of New Brunswick, Fredericton, NB. 2018. Atlantic salmon (*Salmo salar*) migrations in the large reservoir of the Mactaquac Generating Station.

Atlantic Salmon Ecosystems Forum, University of Marine, Orono, ME. 2018. Post-spawned Atlantic salmon overwinter behaviour and spring migration in relation to the large reservoir of the Mactaquac Generating Station.

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24th Annual Graduate Research Conference, Fredericton, NB. 2017. Atlantic salmon kelt overwintering behavoiur and spring migration through the Mactaquac Reservoir and Saint John River.

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41st Annual Atlantic International Chapter of the American Fisheries Society, Cap-Pelé, NB. 2015. Atlantic salmon movement within the Mactaquac Reservoir.

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