

Assessing the effectiveness of two supplementation programs for Atlantic salmon recovery in
Nova Scotia

by

Natalie Koopman

Submitted in partial fulfilment of the requirements
for the degree of Master of Science

at

Dalhousie University
Halifax, Nova Scotia
August, 2025

Dalhousie University is located in Mi'kma'ki, the ancestral and unceded territory of the
Mi'kmaq. We are all Treaty people.

© Copyright by Natalie Koopman, 2025

Dedication

This thesis is dedicated to my family, my friends, and the salmon. Thank you for teaching me about resilience, each in your own way.

TABLE OF CONTENTS

LIST OF TABLES	vi
LIST OF FIGURES	vii
ABSTRACT	ix
LIST OF ABBREVIATIONS USED	x
ACKNOWLEDGEMENTS	xi
CHAPTER 1: GENERAL INTRODUCTION	1
1.1. Background	1
1.2. Objectives	7
CHAPTER 2: TRACKING BEHAVIOURAL DIFFERENCES AND PREDATION RISK BETWEEN HATCHERY AND WILD ATLANTIC SALMON SMOLTS DURING RIVER EXIT AND EARLY MARINE MIGRATION IN A NOVA SCOTIA RIVER	9
2.1 ABSTRACT	9
2.2 INTRODUCTION	10
2.3 METHODS	12
2.3.1 Study Site	12
2.3.2 Receiver deployment	13
2.3.3 Experimental design	15
2.3.4 Data analysis and modeling	16
2.4 RESULTS	18
2.4.1 Survival and predation	19
2.4.2 River movement and exit	22
2.4.3 Ocean detections	25

2.5 DISCUSSION	27
2.6 CONCLUSION	31
CHAPTER 3: A COMPARISON OF IN-RIVER SURVIVAL, MOVEMENT, AND MARINE MIGRATION BETWEEN WILD AND SMOLT-TO-ADULT SUPPLEMENTED (SAS) ATLANTIC SALMON IN NOVA SCOTIA	33
3.1 ABSTRACT	33
3.2 INTRODUCTION	34
3.3 METHODS	37
3.3.1 Study site	37
3.3.2 Receiver deployment	38
3.3.3 Experimental design	40
3.3.4 Data analysis and modeling	42
3.4 RESULTS	44
3.4.1 Survival	45
3.4.2 Acceleration	48
3.4.3 River movement	50
3.4.4 River exit	52
3.4.5 Ocean detections	53
3.5 DISCUSSION	56
3.6 CONCLUSION	64
CHAPTER 4: GENERAL DISCUSSION	66
4.1 Evaluation and Implications	66
4.2 Conclusion	74
REFERENCES	76

APPENDIX A – CHAPTER 3 SUPPLEMENTARY MATERIAL	94
APPENDIX B – CHAPTER 2 R CODE ANALYSIS	97
APPENDIX C – CHAPTER 3 R CODE ANALYSIS	100

LIST OF TABLES

Table 1. Number of smolts tagged and released on the LaHave River by release day, origin, means, and standard deviation for fork length and weight (range in parentheses).	18
Table 2. Summary of salmon tagged for Clyburn Brook and Chéticamp River including release year, sample size, origin (wild or SAS), SAS stage if applicable (SAS1=salmon spent one year in captivity, SAS2=salmon spent two years in captivity), mean fork length (mm) with standard deviation (\pm SD), and sex (female/male/unknown).	45

LIST OF FIGURES

Figure 1. Map of the LaHave River acoustic receiver deployment locations for April - June 2021, other than the three outer bay receivers that remained until the end of July.	14
Figure 2. Estimated cumulative survival by river section for hatchery and wild Atlantic salmon smolts in the LaHave River, NS based on a Cormack Jolly Seber survival model.	21
Figure 3. Map of predation events of hatchery and wild Atlantic salmon smolts on the LaHave River with size of point representing the number of salmon predated at the location and the colour representing the origin of Atlantic salmon smolts (hatchery or wild).	22
Figure 4. a) Boxplots of migration speed (body lengths per second) by river section of Atlantic salmon smolts from hatchery and wild origin. Boxes show interquartile range, and medians.	25
Figure 5. Map showing ocean detections of Atlantic salmon smolts tagged in the LaHave River, Nova Scotia, from hatchery (n=26) and wild (n=36) origins.	26
Figure 6. Map showing the broader Atlantic Canada region with a zoomed-in inset of Cape Breton Island, Nova Scotia, highlighting the two river systems included in this study: Clyburn Brook (SAS salmon) and Chéticamp River (wild salmon).	39
Figure 7. a) Map of the Clyburn Brook acoustic receiver deployment locations (red points) for 2023-2025.	40
Figure 8. a) Map of Clyburn Brook showing last detection locations of SAS salmon assigned mortalities.	48

Figure 9. Comparison of observed and predicted acceleration (m/s^2) of SAS and wild salmon over time in Clyburn Brook and Chéticamp River respectively.	50
Figure 10. a) Map of Clyburn Brook showing detection locations of SAS salmon three months post-release coloured by group.....	52
Figure 11. Cumulative proportion and timing of river exit for all SAS salmon (S) from Clyburn Brook (n=21; SAS1 n = 4, SAS2 n=17), wild salmon (W) from the Chéticamp River (n=17).	53
Figure 12. a) Map of individual detections in the ocean, faceted by most active months, of tagged Atlantic salmon from smolt-to-adult supplementation (SAS; n=12; red) and wild salmon (n=14; blue) origin.	56
Figure 13. Graph portraying the river movement of smolt-to-adult supplemented (SAS) salmon that spent 1 year in captivity at the Aquatron Laboratory (SAS1) before being released into the Clyburn Brook in October 2023 (n=15).	94
Figure 14. a) Graph portraying the river movement of smolt-to-adult supplemented (SAS) salmon that spent 2 years in captivity at the Aquatron Laboratory (SAS2) before being released into the Clyburn Brook in October 2023 (n=15).	96
Figure 15. Comparison of raw acceleration detections (m/s^2) of SAS and wild salmon from October 2023 to May 2024 in Clyburn Brook and Chéticamp River respectively.	96

ABSTRACT

Atlantic salmon (*Salmo salar*) populations have experienced severe declines across their range, prompting the use of hatchery-based supplementation strategies to support recovery efforts. To inform conservation practices, this thesis evaluates the post-release performance of two supplementation strategies used in Nova Scotia: traditional hatchery smolt releases and smolt-to-adult supplementation (SAS). Using acoustic telemetry, Chapter 1 compared hatchery-reared and wild smolts in the LaHave River with acoustic telemetry, revealing lower survival among hatchery smolts driven largely by predation in lake habitats during outmigration. Hatchery smolts had slower migration speeds in upstream reaches compared to wild smolts, but comparable river exit timing and early marine migration routes. Chapter 2 assessed the survival, behaviour, and migration patterns of SAS and wild adult salmon in Cape Breton rivers using acoustic telemetry. SAS adults exhibited significantly lower freshwater survival, higher acceleration levels, atypical river movements, premature river exit, and altered marine migration routes, with captivity duration influencing both survival and potential spawning behaviour. Collectively, these findings demonstrate that captivity imposes behavioural and likely physiological changes that reduce fitness in the wild, with different post-release challenges arising across life stages and supplementation programs. Effective supplementation will require life-stage-specific strategies, including optimizing smolt releases below known predation hot-spots, reducing captivity duration for SAS adults, and modifying SAS release practices (such as gradually decreasing feeding pre-release to replicate the fasting state of wild returning adult salmon and staggering releases across known spawning grounds). Without improvements to post-release performance, supplementation programs may likely fail to achieve their intended conservation goals.

LIST OF ABBREVIATIONS USED

AIC	Akaike's Information Criterion
CJS	Cormack-Jolly-Seber
DFO	Fisheries and Oceans Canada
DU	Designatable Unit
ECB	Eastern Cape Breton
GAM	Generalized Additive Model
GLMM	Generalized Linear Mixed effects Model
GSGSL	Gaspé-Southern Gulf of St. Lawrence
MCPs	Minimum Convex Polygons
MSW	Multi-Sea Winter
NASCO	North Atlantic Salmon Conservation Organization
OTN	Ocean Tracking Network
PIT	Passive Integrated Transponder
RMS	Root Mean Square
SABMPA	St. Anns Bank Marine Protected Area
SAS	Smolt-to-Adult Supplementation
SAS1	Smolt-to-Adult Supplementation salmon that spent 1 year captivity
SAS2	Smolt-to-Adult Supplementation salmon that spent 2 years captivity
SOBI	Strait Of Belle Isle
NSSU	Nova Scotia Southern Uplands
TMS	Tricane Methanesulfonate
1SW	One-Sea Winter

ACKNOWLEDGEMENTS

I am deeply grateful to my supervisors, Glenn Crossin and Robert Lennox, for their outstanding mentorship and support. Your generosity, insight, and encouragement have made a lasting impact. You two are an inspiration to this field.

To the Lennox Lab, it has been a privilege to work and learn alongside such a brilliant, kind, and supportive group of people. Thank you for all our unique field experiences, laughter, and discussions. I look forward to seeing you down the road.

A heartfelt thank you to Parks Canada, the Chéticamp River Salmon Association, and the many individuals who supported this work in the field including Marin, Catherine, Sarah, Ross, Fallon, René, Jillian, and many others. Your expertise, enthusiasm, and collaboration made this project both possible and deeply enjoyable.

Thank you to the Aquatron Staff including John, Nayla, Emily, and many others whose care and commitment to the fish and this research have been invaluable. Your attention to detail and dedication made all the difference.

Finally, to my family and friends, thank you for your humour, encouragement, and grounding across these 2 years.

I feel incredibly fortunate to have been part of this project working alongside amazing people and the Atlantic salmon. I will carry the experiences and lessons with me always.

CHAPTER 1: GENERAL INTRODUCTION

1.1. BACKGROUND

Freshwater biodiversity is declining at a faster rate than any other vertebrate group globally, with anadromous fishes, species that migrate between freshwater and marine habitats, experiencing particularly steep losses (Reid et al., 2018; Walsh et al., 2011; WWF, 2022). Observed decreases in anadromous populations are attributed to the challenges of surviving anthropogenic threats across multiple, distinct environments throughout their life history such as barriers to migration, habitat degradation, pollution, commercial harvest, and changing ocean conditions (Lehnert et al., 2019; NASCO, 2019; Vollset et al., 2022). Anadromous fishes must navigate these threats during migrations that are often energetically costly and tightly timed with environmental cues (Foldvik et al., 2024; Lennox et al., 2018). Salmonids, a well-known group of anadromous fishes, are vulnerable to population decreases from compounding anthropogenic threats due to their long-distance migrations and dependence on high-quality freshwater and marine habitats (Limburg & Waldman, 2009; Russell et al., 2012). Across the northern hemisphere, many salmonid populations have experienced dramatic declines in recent decades, raising concern for populations already experiencing low marine survival and limited freshwater productivity (Friedland et al., 2000; Limburg & Waldman, 2009; Thorstad et al., 2021).

Atlantic salmon (*Salmo salar*) inhabit the North Atlantic Ocean ranging from North America to Russia and have an intricate life history with broad spatial coverage due to their anadromy (Thorstad et al., 2011). Atlantic salmon begin life in freshwater where juveniles typically rear for one to five years before migrating to sea as smolts (Chaput et al., 1998). Atlantic salmon smolts from the Canadian Maritime provinces migrate north to the Labrador Sea and the western coast of Greenland to forage and grow before migrating back to their natal rivers as mature adults for spawning after one winter at sea (i.e. one sea winter or 1SW) or multiple winters at sea (i.e. multi-sea winter or MSW), depending on the population (Chaput & Benoît, 2012; Dadswell et al., 2010; Rikardsen & Dempson, 2011). Atlantic salmon play an important ecological role in both freshwater and marine ecosystems, contributing to nutrient cycling and supporting biodiversity (Reimchen, 2018; Willson & Halupka, 1995). As indicators of ecosystem health, Atlantic salmon are often the focus of conservation efforts and freshwater habitat restoration (Pander & Geist, 2010; Soulsby et al., 2001; Vehanen et al., 2010a). For example, the presence

and abundance of juvenile salmon are used to assess habitat quality, as they require clean, cold, well-oxygenated water and complex stream structure to thrive (Soulsby et al., 2001). Declines in juvenile densities can signal ecological degradation, such as increased sedimentation or altered flow regimes. Similarly, Pander & Geist (2010) demonstrated that restoring river connectivity and spawning habitats led to measurable increases in Atlantic salmon recruitment, highlighting their value as a bioindicator species. Atlantic salmon have societal and economic importance, supporting commercial, recreational, and cultural fisheries across the North Atlantic (Butler et al., 2009; EUMOFA, 2019; Pokki et al., 2018).

Throughout their range, Atlantic salmon populations have been decreasing in number, with 43% of global populations designated as At Risk or Endangered by the International Union for Conservation of Nature and regional assessments conducted by organizations such as the North Atlantic Salmon Conservation Organization (NASCO) (Adams et al., 2022; Chaput et al., 2019; Dadswell et al., 2021; Mills et al., 2013; NASCO, 2018, 2019). Returns of 1SW adult salmon have decreased by 40%, while returns of MSW adult salmon decreased by 81% between 1971 and 2010 in NASCO's North American Commission area with record low abundances of returning adults continuing to be recorded across the North Atlantic (Chaput, 2012; ICES, 2025). The complexity of this life cycle exposes Atlantic salmon to a wide array of threats across both freshwater and marine environments, contributing to the decreases observed in many populations (Limburg & Waldman, 2009; Russell et al., 2012). Juvenile Atlantic salmon face localized threats such as pollution, habitat degradation (riparian zone loss, substrate composition, river channelization), human-made barriers, invasive species, acid rain, and warming water temperatures (Buddendorf et al., 2019; Forseth et al., 2017; ICES, 2020; Smialek et al., 2021; Waldman & Quinn, 2022; Watt, 1987). The freshwater juvenile stage of a salmon's life-history is largely recognized as a survival bottleneck, where only 2% survive to smolt and enter the sea (Chaput et al., 1998; Cunjak & Therrien, 1998). For the juveniles that survive and successfully reach the marine environment, migrating to distant feeding grounds introduces a new suite of threats. Across much of the Atlantic salmon's range, increasingly fewer adults have survived to complete the spawning migration and reproduce during the last three decades (ICES, 2020). Elevated mortality during the marine phase is believed to be driven by deteriorating ocean conditions linked to climate change, including warming sea surface temperatures, shifting ocean currents, and reduced prey availability (e.g., zooplankton and forage fish) (Adams et al., 2022; Chaput et al., 2019; Dadswell et al., 2021; Mills

et al., 2013). Understanding the drivers of marine mortality remains a critical research priority, particularly given that many populations continue to decline despite the moratorium on commercial fisheries (in place since 2000) and tight restrictions on recreational angling since the 1980s (DFO & MNRF, 2009; Levy & Gibson, 2014). The scale and persistence of Atlantic salmon declines have raised considerable concern, driving extensive conservation efforts globally (Lennox et al., 2021; Webb et al., 2007;).

Supplementation programs, where animals are reared in artificial conditions and released into the wild, have been used for centuries primarily to augment harvests and recreational fisheries (Young, 2017). More recently, these programs have been adopted for conservation purposes to support declining wild populations (Snyder et al., 1996). Naish et al., (2007) broadly defined supplementation as the intentional release of captively-reared animals to increase population abundance. For over 150 years, hatcheries (a type of supplementation program) have been a common management practice for salmonid populations whether the end goal is for economical, recreational, or conservational reasons (Maynard & Trial, 2014). Typically, wild adult salmon are captured for broodstock and their offspring are reared in captivity before the young are released back into rivers at a chosen juvenile stage (egg, fry, parr, or smolt) to increase recruitment (Fraser, 2016). Hatcheries offer a controlled environment with shelter, consistent feeding, and protection from predators, leading to much higher survival rates during early life stages compared to the wild, where egg-to-smolt survival often falls below 2% (Chaput et al., 1998; Cunjak & Therrien, 1998; Jonsson & Fleming, 1993; Reisenbichler et al., 2004). Thus, the underlying rationale of hatcheries is to offset high juvenile mortality in the wild by releasing greater numbers of young fish, with the goal of increasing population productivity.

Despite the proposed advantages of hatcheries, extensive research shows that captivity can alter fish behavior and physiology, lowering survival and reproductive success after release leading to potential ecological and genetic consequences (Araki et al., 2008; Fleming & Gross, 1993; Fleming & Petersson, 2001; Fraser, 2008; Jonsson, 1997). Captive rearing deprives juvenile salmon of wild natural experiences such as foraging, predator avoidance, and environmental variability, which are critical for survival in the wild (Jonsson, 1997). As a result, captive conditions may select for traits that are beneficial to survival in hatcheries but maladaptive in the wild environment leading to phenotypic divergence between hatchery and wild salmon. Released hatchery fish often exhibit lower survival (Araki et al., 2008; Jonsson et al., 2003), reduced

reproductive success (Fleming et al., 1996; Christie et al., 2014), elevated stress indicators (Bordeleau et al., 2018; Cogliati et al., 2019), and impaired migratory navigation (Larsson et al., 2012; Nilsen et al., 2023) in comparison to wild fish. Additionally, hatchery-origin juveniles often miss key environmental imprinting cues necessary for homing, leading to higher stray rates and reduced genetic contributions to wild populations (Jonsson et al., 2003; Quinn, 1993; Westley et al., 2013). If the goal of supplementation is to reduce juvenile mortality, increase recruitment, and ultimately enhance population productivity, then releasing fish that are behaviourally and genetically unsuited for the wild undercuts that objective (Carr et al., 2004). For supplementation to be effective, captive-reared fish must closely resemble their wild counterparts in behaviour, morphology, and physiology (Brown & Day, 2002; Salvanes & Braithwaite, 2006). To improve post-release outcomes, interventions such as predator exposure, environmental enrichment, and gradual acclimation to wild conditions have been proposed (Brown & Day, 2002). Nevertheless, conservation hatchery programs face widespread criticism due to their limited success in reversing population declines (Araki et al., 2008; Fraser, 2008). A recent review of 19 salmon stocking studies found only two reported success in producing self-sustaining wild populations (Lennox et al., 2023). This highlights ongoing concerns about the effectiveness of hatchery supplementation as a long-term conservation strategy (Almodóvar et al., 2020; Christie et al., 2012; Young, 2017).

Growing recognition that traditional hatchery programs may fail to support wild salmon conservation has led to the proposal of alternative approaches, including smolt-to-adult supplementation (hereafter SAS). In hopes of circumventing record-low adult returns of Atlantic salmon across the North Atlantic and the risks of early-life rearing in traditional hatcheries, some conservation programs have implemented the SAS approach. Unlike traditional hatcheries that rear salmon from eggs to smolts (or to some juvenile life stage), SAS involves capturing wild smolts (aged two to four years) during their downstream migration to the sea, raising them in captivity until they reach sexual maturity (typically one to two years duration), and then releasing them back into their natal rivers as adults (DFO, 2018). The goal of SAS is for these returning adults to survive and successfully spawn, increasing population numbers in the short term by bypassing the high mortality typically experienced during the marine phase. Thus, the SAS approach may be particularly valuable for populations in rivers with low marine return rates, because it ensures that at least some smolts reach adulthood to spawn (DFO, 2018). A key objective of SAS is to also retain genetic diversity by preserving natural selection during the juvenile stage.

Because smolts are collected from the wild, they are exposed to natural environmental cues that may mitigate some of the captivity-induced deficiencies commonly observed in traditional hatchery-reared fish (Araki et al., 2008; Jonsson, 1997; Naish et al., 2007). The SAS program limits captivity to one or two years during adulthood, and released individuals are allowed to mate and spawn naturally, avoiding the artificial mating practices typical of conventional hatchery programs (Fraser, 2016). Stark et al. (2014) evaluated habitat selection, courtship, and spawn timing in SAS-reared Chinook salmon (*Oncorhynchus tshawytscha*) and Atlantic salmon. They found that SAS-reared and wild salmon displayed similar habitat selection and spawning behaviours, although some differences in spawn timing were observed. Additionally, successful spawning of SAS-reared salmon was confirmed via evaluation of egg and fry production (Stark et al., 2014). Dempson et al. (1999) captured outmigrating wild smolts from Conne River, Newfoundland, reared them in sea-cages to 1SW adults, and released them 7 km from the river mouth in another example of a SAS program. Radio-telemetry comparisons with wild salmon demonstrated that 80% of SAS salmon were able to home back to the natal Conne River system and were able to navigate and distribute through the watershed similar to the wild salmon (Dempson et al., 1999). Taken together, these findings suggest that SAS programs may hold promise as a conservation strategy, however, their long-term success likely depends on whether captivity-related effects can be minimized to ensure that released adults survive and spawn, contributing to population recovery.

While several studies have examined aspects of SAS salmon performance post-release, the potential ecological and genetic consequences of this method remain poorly understood. Fisheries and Oceans Canada (DFO) has acknowledged that the use of SAS may pose risks to wild salmon populations and identified several areas that require investigation to understand its potential role in salmon recovery (DFO, 2018). One concern is how holding salmon in captivity during the period when they would normally undergo ocean migration may weaken natural selection at this life stage, potentially reducing their adaptation to marine environments. As a result, SAS-reared adult salmon could diverge from wild populations in important phenotypic traits, including growth, body size, predator avoidance, boldness, foraging ability, migratory timing, and fecundity (Fraser, 2016). Additionally, time spent in captivity has been linked to potential epigenetic changes that may negatively affect reproductive success and offspring fitness (Araki et al., 2008; Fraser, 2016; Milot et al., 2013). Because the success of SAS programs relies on released adults surviving,

reproducing, and behaving like wild salmon, it is essential to determine whether SAS salmon retain the behavioural traits required to contribute to wild populations.

To address the largely unknown behavioural uncertainties of post-release hatchery fish, movement ecology offers a valuable framework for assessing how supplementation affects individual performance in the wild. Movement ecology is the study of how and why animals move through space and time, shaped by their internal state, environmental conditions, navigation mechanisms, and physical capacity for movement (Nathan et al., 2008). This framework has growing relevance in aquatic conservation, as movement in fishes is essential for critical behaviours such as foraging, predator avoidance, habitat selection, migration, and reproduction, activities that can reveal fitness-limiting constraints in altered or managed environments (Cooke et al., 2022; Hays et al., 2019). For anadromous, long-distance migrants like Atlantic salmon, atypical movement patterns may compromise survival and reproductive success, making it essential to understand how supplementation programs may alter natural movement behaviours through the effects of artificial environments. Tools like acoustic telemetry and accelerometer transmitters are increasingly being used to study movement in conservation contexts, offering high-resolution data on activity, energy use, and migratory decision-making (Lennox et al., 2023; Matley et al., 2023). These technologies are especially relevant for assessing the performance of hatchery salmon in the wild, where divergence from expected movement patterns can indicate maladaptive outcomes of captivity and ineffective conservation strategy. By integrating movement ecology into supplementation research, conservation programs can evaluate whether captive-reared individuals behave similarly to their wild counterparts, and help determine whether current practices promote or impair the ecological success of released fish.

Canada supports a substantial portion of global Atlantic salmon populations, second only to Norway in the number of salmon rivers. Between 1970 and 2000, estimates report a reduction of Atlantic salmon for at least 75% for Canadian populations (WWF, 2001). While commercial salmon fisheries have been closed since the late 20th century and recreational fisheries are tightly regulated, many populations continue to decline (DFO & MNRF, 2009). Beginning in the 1860s, hatchery facilities were used in eastern Canada to augment production of salmon whether for commercial or recreational use (Naish et al., 2007). Within Canada, the maritime province of Nova Scotia is known historically to support salmon populations in 147 rivers (DFO & MNRF, 2008). These populations are divided into four major designatable units (DU's) including the endangered

inner Bay of Fundy, endangered Southern Uplands, endangered Eastern Cape Breton, and the Gaspé-Southern Gulf of St. Lawrence of special concern (COSEWIC, 2010). Historically, many rivers in these regions were stocked (DFO, 1997, 1998). Currently, the province of Nova Scotia owns and manages two hatcheries which traditionally rear and stock Atlantic salmon for five rivers to largely support the province's recreational sport fishery.

1.2. OBJECTIVES

This thesis focuses on rivers within two regions in Nova Scotia: the LaHave River in the endangered Southern Uplands DU and the Clyburn Brook in the Cape Breton Highlands endangered Eastern Cape Breton DU. The LaHave River has been monitored since 1970, documenting a steady decline in Atlantic salmon despite decades of hatchery intervention (DFO, 2010; Gibson & Hubley, 2011). Across the last three generations, adult returns have dropped by 83% and juvenile densities have declined up to 87% in the LaHave River (DFO, 2024). The hatchery program has released over three million juveniles into the river since the 1970s, yet returns of hatchery-origin adults have been negligible, with no confirmed returns after the last major stocking event in 2005 (Bowlby, 2013). These outcomes highlight the limited effectiveness of traditional hatchery recovery strategies for restoring self-sustaining populations in the LaHave River. The Clyburn Brook has been monitored by Parks Canada for 35 years and has similarly observed a steep 95% decline in adult spawners (Levy & Gibson, 2014).

The LaHave River and Clyburn Brook represent two valuable case studies for understanding Atlantic salmon recovery efforts in Nova Scotia. Wild and hatchery smolts in the LaHave River were acoustically tracked in 2021, with the goal of identifying factors contributing to low hatchery smolt survival and evaluating the potential influence of hatchery origin on outmigration success. In response to the near extirpation of the Clyburn Brook salmon population, Cape Breton Highlands National Park began a SAS program as part of a broader Parks Canada recovery initiative. Together, these population recovery efforts provide a unique opportunity to further assess the efficacy of different supplementation programs that target different Atlantic salmon regions, and life stages, in Nova Scotia.

This thesis investigates how captivity during different life stages influences the survival, behaviour, and migration of Atlantic salmon. Focusing on two supplementation programs, the

release of traditional hatchery-reared smolts in the LaHave River and implementation of a smolt-to-adult supplementation (SAS) program in the Clyburn Brook, this work evaluates whether the intended conservation benefits of these interventions are realized in the wild. Using acoustic telemetry, we tracked the movement of both wild and hatchery-origin salmon across freshwater and marine environments. This study provides important insights into the effects of captivity on post-release movement behaviour, and the broader implications for Atlantic salmon recovery efforts in critically endangered populations.

CHAPTER 2: TRACKING BEHAVIOURAL DIFFERENCES AND PREDATION RISK BETWEEN HATCHERY AND WILD ATLANTIC SALMON SMOLTS DURING RIVER EXIT AND EARLY MARINE MIGRATION IN A NOVA SCOTIA RIVER

2.1 ABSTRACT

Significant declines in Atlantic salmon (*Salmo salar*) populations across their range have prompted widespread use of hatchery supplementation programs to increase population abundance. However, concerns persist regarding the effectiveness of these programs, which remains uncertain due to limited understanding of how hatchery-reared smolts perform post-release in natural river systems compared to their wild counterparts. Here, this study compared the survival, predation risk, migration speed, river exit timing, and early ocean migration patterns of hatchery-reared and wild Atlantic salmon smolts in the LaHave River, Nova Scotia. Using acoustic telemetry, we tracked the movements of 100 smolts (50 hatchery origin, 50 wild origin) during their freshwater downstream migration and into the ocean. Hatchery smolts exhibited significantly lower survival during river outmigration, with predation being a large driver of this greater mortality. Migration speeds were significantly slower for hatchery smolts compared to wild smolts in upper river and lake habitats, although timing of river exit and early ocean migration routes were comparable. Both hatchery and wild smolts followed the expected marine migration path headed east along the southern coast of Nova Scotia. Taken together, these results suggest that hatchery smolts face heightened predation risk and potentially reduced swimming performance compared to wild smolts, likely due to inadequate antipredator conditioning and captive rearing conditions, but retain similar river exit timing and marine migration decisions. Improving future hatchery practices should include conditioning smolts to recognize local predator cues, releasing them downstream of high predation areas, and providing structurally enriched rearing environments to enhance post-release survival and increase the number of smolts that successfully reach the ocean. Incorporating these strategies could help address the specific post-release challenges identified in this study, potentially increasing return rates of stocked salmon and contributing to the recovery of Atlantic salmon populations in Nova Scotia and beyond.

2.2 INTRODUCTION

Steep declines in Atlantic salmon (*Salmo salar*) populations have been documented across much of their native range over the past several decades (Fraser, 2016; ICES, 2020; Pardo et al., 2021). Although climate-driven changes in the marine ecosystem are a major factor in declining adult salmon returns (Dadswell et al., 2022; Thorstad et al., 2021), freshwater habitats are also a large driver of these declines (Gillis et al., 2023; Todd et al., 2011). Warmer water temperatures (Gillis et al., 2023), habitat loss, acidification, migration barriers (Forseth et al., 2017; ICES, 2020; Thorstad et al., 2021), and the spread of invasive species (Bean, 2020; Kennedy et al., 2018) are all documented threats for Atlantic salmon during their freshwater life stages. Within Atlantic Canada, several salmon populations have experienced severe declines, particularly those in the Nova Scotia Southern Uplands Designatable Unit (NSSU DU) of Nova Scotia (DFO, 2024). In 2010, populations in the NSSU DU were assessed as Endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2010).

In response to declining populations, hatchery programs have been used as a management tool to restore freshwater fish populations, including salmon (IUCN, 2024; Leber et al., 2005; McMillan, 2023). Hatcheries typically capture wild adult salmon as broodstock, spawn the adults in captivity, then rear their offspring in captivity until releasing the juveniles back into the river (at some juvenile stage: egg, fry, parr, or smolt) to increase recruitment (Fraser, 2016; Lennox et al., 2021). Hatcheries have played a large role in salmonid management for over 150 years, serving economical (commercial fisheries support), recreational (stocking for more angling opportunities), and conservation purposes (population recovery and supplementation; Bordeleau et al., 2018; Maynard & Trial, 2014). In theory, hatcheries aim to reduce juvenile mortality and boost population productivity. In the wild, fewer than 2% of salmon typically survive from egg to smolt (Chaput et al., 1998; Cunjak & Therrien, 1998). By providing a controlled environment with a reliable feeding regime and predator protection, hatcheries greatly improve early survival rates allowing more juveniles to be released than would naturally occur.

Despite hatcheries intended benefits, it is well-documented that captive conditions deprive fish of natural experiences and environmental cues such as foraging and learned predator-avoidance which are critical for survival in the wild. As a result, hatchery-reared fish often exhibit altered behaviour and physiology compared to their wild counterparts, thus resulting in reduced

post-release performance (Araki et al., 2008; Fleming & Gross, 1993; Fleming & Petersson, 2001; Fraser, 2008; Jonsson, 1997). Extensive research has found that hatchery smolts display less effective foraging abilities and antipredator behaviour, which can contribute to higher mortality during outmigration (Järvi & Uglem, 1993; Sabal et al., 2020; Vilhunen, 2006). Additionally, hatchery-reared salmon often exhibit higher mortality (Araki et al., 2008; Jonsson et al., 2003), limited reproductive success (Christie et al., 2014; Fleming et al., 1996), heightened stress (Cogliati et al., 2019), and impaired navigation and migration abilities (Larsson et al., 2012; Nilsen et al., 2023; Thorstad et al., 2011) compared to wild salmon. Observed differences between hatchery and wild salmon likely derives from captive conditions selecting for phenotypes that are behaviourally and genetically better suited for life in captivity than for life in the wild (Carr et al., 2004). These outcomes raise concerns about the effectiveness of hatchery programs, especially if released individuals are not behaviourally and physiologically similar to the wild population and thus not suited to survive and reproduce in the natural environment (Brown & Day, 2002; Carr et al., 2004; Salvanes & Braithwaite, 2006). Lennox et al. (2023) conducted a review of 19 supplementation studies and found only two programs reported success in increasing fish numbers and creating a self-sustaining population. Efforts such as predator conditioning, environmental enrichment, and life-skills training have been proposed as management solutions, yet the long-term success of these interventions remains uncertain. As a result, many conservation hatchery programs continue to face criticism for their limited success in reversing population declines (Araki et al., 2008; Fraser, 2008). It is clear that there are many serious questions about the efficacy of hatchery stocking programs, particularly when used as a long-term recovery strategy (Almodóvar et al., 2020; Christie et al., 2012; Young et al., 2017).

The Atlantic salmon population within the LaHave River, NSSU DU has been monitored continuously since 1970, providing valuable long-term data that reveal drastic decreases in abundance (DFO, 2010; Hubley & Gibson, 2011). Despite decades of monitoring and extensive hatchery stocking, the population continues to decline. Over the last three generations, adult returns have decreased by 83%, while juvenile densities of all life stages have dropped by 73–87% (DFO, 2024). Since the 1970s, millions of hatchery-reared juveniles have been introduced into the system in an effort to bolster recruitment (DFO, 2024). However, despite sustained stocking efforts, smolt-to-adult return rates have remained below 1% since 2013, and no hatchery-origin adults returned following the last major stocking event in 2005 (Bowlby et al., 2013).

Compounding the challenges faced by smolts in this system, invasive aquatic predators such as smallmouth bass (*Micropterus dolomieu*) and chain pickerel (*Esox niger*) have been identified as predators of salmon smolts within the LaHave River (Feener, 2017). Given that predation is a major potential source of freshwater mortality during outmigration, these invasive species may represent an important selective pressure on smolt survival (Mensing et al., 2025). Understanding whether invasive species disproportionately affect hatchery versus wild smolts is therefore essential to evaluating the effectiveness of ongoing supplementation efforts in this system. Yet, there is limited understanding of how hatchery-reared fish perform after release, particularly in terms of river survival and predation risk during outmigration.

This study examines how survival, predation, river movement, river exit, and ocean migration differ between wild and hatchery-reared Atlantic salmon smolts during their seaward outmigration in the LaHave River, Nova Scotia. We hypothesized that hatchery-reared smolts would experience lower survival rates, higher predation risk, exhibit inefficient outmigration, including slower swimming speeds and delayed river exit, and deviate from the typical oceanic migration pathways compared to their wild counterparts. Differences between hatchery and wild smolts may arise from carryover effects of captivity, such as elevated stress or the lack of exposure to natural riverine conditions and environmental cues during early development. Using acoustic transmitters equipped with temperature and predation sensors, we tracked the downstream migration of wild and hatchery-reared smolts through the LaHave River, estuary, and into the Atlantic Ocean. Our findings offer key insights into the challenges faced by hatchery-reared smolts upon release into the wild, and will inform future supplementation programs that intend to restore salmon populations.

2.3 METHODS

2.3.1 STUDY SITE

Atlantic salmon smolts were tagged on the LaHave River, which is located on the southern shore of Nova Scotia within the NSSU DU (Figure 1). The headwaters originate in Annapolis County and flow 97 km before draining into the Atlantic Ocean, with a total drainage area of 1670 km² (Gray et al., 1989). The LaHave River Atlantic salmon population has been monitored since 1970, via electrofishing, mark-recapture studies, and fish ladder observations (Bowlby et al., 2013). The

majority of monitoring has taken place upstream of Morgan Falls, a hydroelectric power station located 45 km from the river mouth and equipped with a fish ladder. Fifty-one percent of the river's accessible habitat lies above Morgan Falls (DFO, 2024). Wentzells Lake, located 36 km upstream from the river mouth and 10 km downstream of Morgan Falls, is the only lake in the LaHave River system that smolts would have encountered during their migration (Figure 1). The lake is approximately 2 km long and 1 km wide, with shoreline housing and recreational boating activity.

In 2021, the LaHave River reported 176 individual adult salmon returns, comprising 157 who spent one year at sea (1SW) and 19 who spent at least two years at sea (MSW). Adult salmon returns counted at Morgan Falls and sampled juvenile densities have declined drastically in the last three generations (Bowlby et al., 2013). Population modeling has revealed a high probability of the LaHave River population becoming extirpated in the next 50 years if there are no changes in current survival rates (DFO, 2024).

Although stocking on LaHave River may have begun in the 1800's, the hatchery releases have been monitored since the 1970s. The releases of captive-reared juveniles have occurred above and below Morgan Falls from 1970s to 2005, with a break in the stocking until 2016. One of the most recent releases occurred in 2020, when over 270,000 fry, several hundred smolts, and 93 adults of native broodstock origin were released into LaHave River (DFO, 2024). Over these decades over 3.2 million hatchery juveniles largely from LaHave River broodstock (some other local NSSU DU river broodstock were used) were released in spring, however return rates for 1SW and MSW salmon peaked in the 1980's at 1.7% and has been falling since with only 0.5% returning in the 2000s (Bowlby et al., 2013), suggesting little success of population recovery.

2.3.2 RECEIVER DEPLOYMENT

Salmon were tracked using acoustic receivers deployed strategically throughout the LaHave River system (Figure 1). A total of 18 Innovasea VR2W-69kHz receivers (Innovasea, Bedford, Nova Scotia, Canada) were deployed throughout the freshwater, estuary, and bay of the LaHave River in April 2021 to track the outmigration of tagged smolts (Figure 1). The receivers were removed and data downloaded by July 2021.

Detection data from marine receiver arrays were sourced via the Ocean Tracking Network (OTN), which compiles acoustic telemetry data from coordinated deployments across

the Northwest Atlantic. Each array represents a spatially defined cluster of passive acoustic receivers positioned throughout the ocean to detect tagged animals as they travel through these monitored regions.

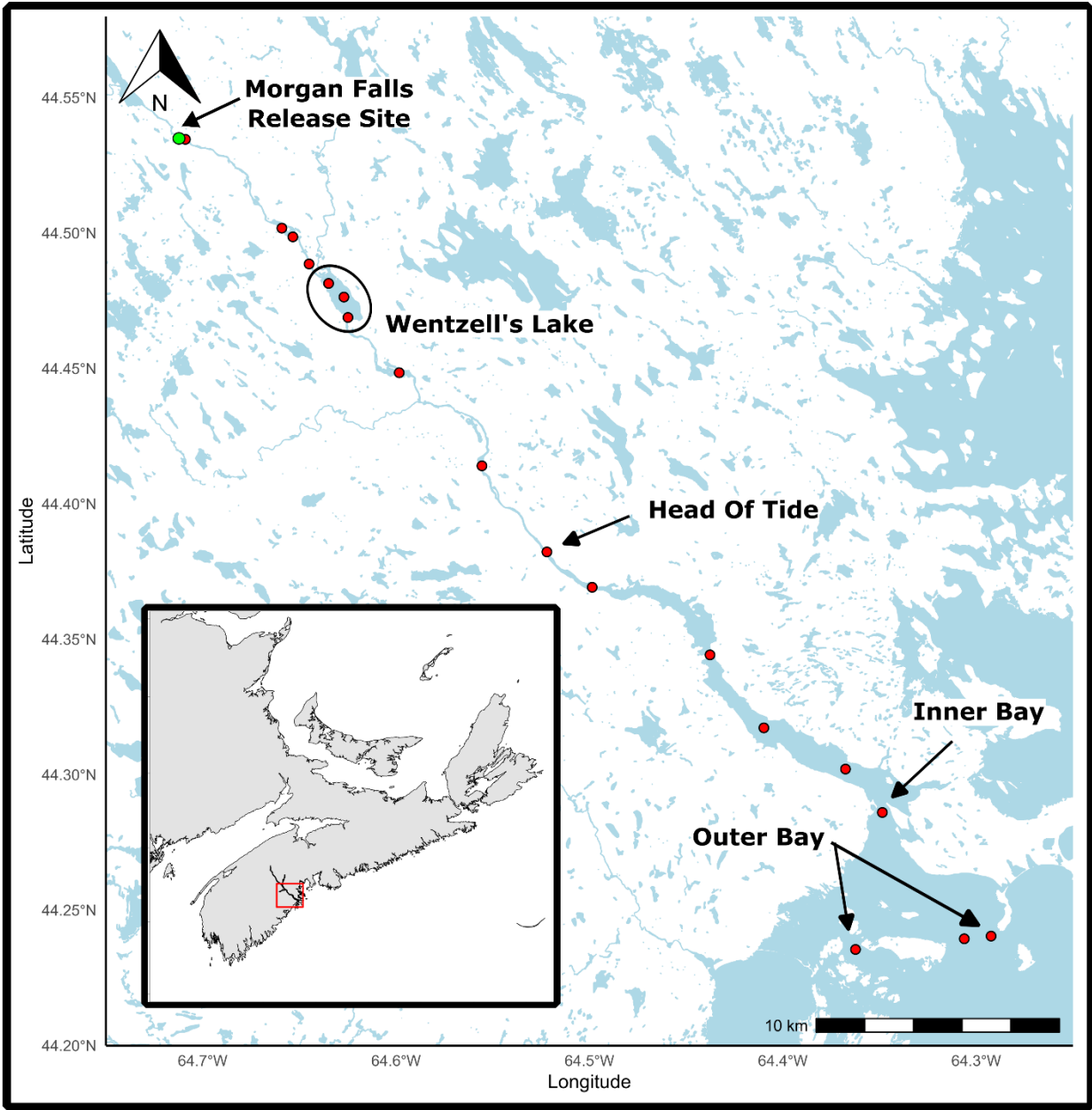


Figure 1. Map of the LaHave River acoustic receiver deployment locations for April - June 2021, other than the three outer bay receivers that remained until the end of July. The inset map with the red box indicates the location of the LaHave River in Nova Scotia, Canada. Important river locations such as Morgan Falls, Wentzell's Lake, the head of tide, inner bay exit receiver, and the outer bay array are labelled. Red points indicate receiver locations and the green point indicates the release site at Morgan Falls.

2.3.3 EXPERIMENTAL DESIGN

Study species

Salmon of both wild origin from LaHave River, and hatchery raised were used in this study. Salmon of hatchery origin were offspring from adult LaHave River broodstock salmon spawned in the fall of 2018 and reared at the Coldbrook Biodiversity Facility, Nova Scotia. Once the hatchery juveniles reached the smolt stage in the spring of 2021, they were transported to Morgan Falls in aerated tanks and placed in a circular holding tank supplied with water from the LaHave River. Smolts were fed every three days before tagging. Wild-origin smolts were captured at Morgan Falls power station fish trap, which was checked three times a week. Captured wild smolts were held in individual flow-through crates with water coming from the LaHave River and were separated by day of capture. The term “wild-origin” smolts is used to acknowledge that, although the fish were captured in the wild, the river has been subject to prolonged stocking, and the population may therefore not represent a wholly unstocked lineage.

Tagging procedure

A total of 100 smolts, 50 wild, and 50 hatchery, were tagged at a 1:1 ratio each day of tagging at the Morgan Falls power station (Table 1). Tagging occurred the spring of 2021 with Innovasea 69 KHz V7DT acoustic predation tags (7mm X 22mm, 1.7g in air, R64k protocol, 27 days of battery; Table 1). The V7DT tags provide a direct measurement of predation wherein the predator's stomach acids digest the tag's polymer, triggering a timer used to determine when the predation event occurred. Tags were also equipped with a temperature sensor with a range from 0-40°C to provide further information on what type of predator digested the smolts. As endotherms, birds (with body temperatures around 40°C) and mammals (ranging from 36°C to 39.5°C) maintain significantly higher and more distinguishable body temperatures, compared to aquatic ectothermic predators, whose body temperatures closely match the surrounding water.

Surgical tools and tags were disinfected in Betadine and rinsed in saline solution before each surgery. Smolts were anaesthetized in an aerated bucket with Tricane Methanesulfonate (TMS) until loss of equilibrium. Weight and fork length were taken before the fish was placed ventral side up on a moist sponge where gills were constantly irrigated with a maintenance dose of TMS. A small incision was then made on the mid-ventral line and the sterile acoustic transmitter placed intraperitoneally. The incision was closed with 2 interrupted sutures. The smolts were

immediately placed in a recovery holding tank until they regained equilibrium and swimming capacity. Once recovered, they were transferred to a flow-through crate, where all tagged smolts were held for a minimum of five hours before being released in the LaHave River later that same day.

2.3.4 DATA ANALYSIS AND MODELING

Data were processed using Rstudio 4.4.2 (R Core Team, 2024) and summary packages specific for acoustic telemetry including *actel* (Flávio & Baktoft, 2021) and *glatos* (Holbrook et al., 2024). Raw acoustic detection data were processed using the *actel* package function *migration* (Flávio & Baktoft, 2021). False detections were filtered by removing detections where apparent smolt movement speeds between receivers exceeded 3 m/s, which is a conservative threshold reflecting biologically plausible swim speeds (Remen et al., 2016), given the low flow rate of LaHave River (~1.01 m/s; COSEWIC, 2010).

Survival & Predation

To determine whether hatchery rearing affected survival, we used a Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965) using the *RMark* package (Laake, 2013). The CJS model is commonly used in mark-recapture studies to estimate the two key parameters of apparent survival (ϕ), the probability that a fish is alive and remains in the study area between detections, and detection probability (p), the probability a fish is detected if it is alive. The model uses a maximum likelihood method, meaning it determines the survival and detection values that best explain the observed data. Each fish's detection history was represented as a binary matrix, indicating presence (1) or absence (0) at each receiver location over time. Given the downstream, unidirectional migration of smolts, each survival interval corresponded to the section between two adjacent receiver arrays. We built candidate models using detection history as the response variable and included predictor variables expected to influence survival and detection, including fish origin (hatchery or wild), receiver location (array), release date, and fish weight. These models assume a binomial distribution for the detection histories. Model performance was evaluated using Akaike's Information Criterion corrected for small sample sizes (AICc), with the best-supported models having the lowest AICc values and highest model weights.

The CJS model addresses overall survival differences, but we expected that predation may be a large factor driving differences in survival between smolts of hatchery and wild origin. To assess the influence of origin on the risk of predation, we used a Cox proportional hazards model with time to predation event (in days since release) as the response variable via the `coxph()` function from the `survival` package (Therneau, 2024). Hazard (risk) of predation was modelled over time while including the explanatory variables origin (hatchery vs wild), weight, and release day as predictor variables.

River Movement & Exit

For all movement analyses, we used the final detection at a site to indicate when a fish departed (e.g., began migrating) and the first detection to indicate arrival, corresponding to downstream movements. A smolt's river movement during outmigration is assumed to be largely unidirectional towards the ocean, with some potential reverse movement at the head of tide for saltwater acclimation (Kocik et al., 2009; Halfyard et al., 2012). Based on this assumption, we calculated individual migration speed through four river sections (i.e., upper river, lake, lower river, bay) using the time elapsed between first detections at successive river sections. To standardize for smolt size, migration speed was expressed in body lengths per second (bl/s). For each fish, detections were arranged chronologically, and migration speed (m/s) was calculated by dividing the distance between detections (meters) by the time elapsed between detections (seconds). Migration speed in m/s was then divided by the individual's body length (in meters) to yield body lengths per second (bl/s). To compare outmigration of hatchery and wild smolts, a generalized linear mixed-effects model (GLMM) with a gamma distribution and log link was used, with migration speed (bl/s) as the response variable. Fixed effects included river section, origin, weight, release day, and the interaction between river section and origin. Fish ID was included as a random effect to account for repeated measures of migration speed across river sections for individual smolts.

River exit timing was assessed by extracting detection histories using `detection_events` summarizing functions from the `glatos` package (Holbrook et al., 2024). River entry was considered the date on which they were released into the river. River exit was defined as the date of final detection at the inner bay receiver, which reflects the last confirmed presence in the estuarine section of the river system. Exit dates were converted to Julian day. The duration of river

residence for each individual was calculated as the difference in days between their river entry/release and exit date.

Marine detection data from ocean arrays were obtained through OTN. To assess early marine migration, only detections occurring after river exit were retained, and 100% minimum convex polygons (MCPs) were generated around all ocean detections for hatchery and wild smolts. These MCPs illustrate the overall spatial extent of marine habitat use by each origin group.

2.4 RESULTS

A total of 100 Atlantic salmon smolts (50 hatchery, 50 wild) were tagged and released over a period of six days between April 29 and May 9, 2021, in the LaHave River (Table 1). On each day, equal numbers of wild and hatchery were released. Of those released, 98 individuals were subsequently detected. Two smolts (1 hatchery, 1 wild) were never detected and thus excluded from analyses. Amongst the 98 smolts, the glatos package aggregated 218,736 raw detections into 8,364 movements events, from April 29 to June 13, 2021. Events were defined as either a change in receiver location or a gap of more than one day between detections on the same receiver.

Table 1. Number of smolts tagged and released on the LaHave River by release day, origin, means, and standard deviation for fork length and weight (range in parentheses).

Release Day	Origin	n	Length (cm)			Weight (g)		
			Mean	SD	Range	Mean	SD	Range
April 29 2021	Hatchery	6	21.5 ± 1.9		(19-24.5)	95.3 ± 23.6		(63.8-128)
	Wild	6	19.9 ± 1.0		(18.6-21.2)	75.0 ± 13.0		(58.7-93)
May 1 2021	Hatchery	8	21.8 ± 1.5		(18.9-23.9)	101 ± 17.3		(72.8-133)
	Wild	8	22.0 ± 2.2		(22.0-26.5)	104 ± 35.2		(73.7-174)
May 3 2021	Hatchery	11	21.1 ± 2.3		(17.4-24)	90.4 ± 26.1		(55.4-123)
	Wild	11	20.1 ± 1.5		(17.9-22.8)	77.8 ± 18.1		(51.3-108)

Release Day	Origin	n	Length (cm)		Weight (g)	
			Mean	SD Range	Mean	SD Range
May 5 2021	Hatchery	11	21.7 ± 2.2	(17.6-24.8)	95.3 ± 30.9	(47-150)
	Wild	11	20.7 ± 2.6	(15.6-24.4)	87.8 ± 27.0	(42.5-129)
May 7 2021	Hatchery	8	21.0 ± 1.2	(19.3-22.4)	89.9 ± 14.9	(65.4-108)
	Wild	8	19.4 ± 1.4	(17.4-21.3)	74.1 ± 20.1	(49.1-111)
May 9 2021	Hatchery	6	21.7 ± 1.0	(20.7-23.2)	92.9 ± 12.0	(80.3-112)
	Wild	6	21.6 ± 0.9	(20-22.7)	99.1 ± 10.2	(92-120)
Total	Hatchery	50	21.4 ± 1.8	(17.4-24.8)	93.8 ± 22.8	(47.0-149.7)
	Wild	50	20.6 ± 2.0	(15.6-26.5)	85.8 ± 25.1	(42.5-174.2)

2.4.1 SURVIVAL AND PREDATION

Among 98 smolts detected, 29% (n=28) died within the monitoring period. There were large disparities in mortality between the hatchery and wild smolts, with 40% (20 of 50) of hatchery smolts dying after release compared to 16% (8 of 50) of wild smolts. Hatchery smolts had a 61.2% estimated cumulative survival and wild smolts had a 85.7% estimated cumulative survival during outmigration. The largest differences in survival estimates between hatchery and wild smolts was in the upper reaches of the river to the end of the lake. An estimated 32.4% of hatchery smolts died before reaching the lower reaches of the river during outmigration compared to an estimated mortality 5.9% of wild smolts (Figure 2). The rest of the river had comparable survival estimates between wild and hatchery fish, demonstrating that upper LaHave river including Wentzells Lake was an area that drives survival differences between hatchery and wild smolts (Figure 2).

Among hatchery smolts, 20 died in-river, with 17 (85%) of these mortalities identified as a predation event based on triggered digestion sensors. In contrast, eight wild smolts died, with

four (50%) of these deaths determined as predation. All predation events occurred within the first 22 km downstream of the release site at Morgan Falls, with 11 events (52%) taking place in Wentzells Lake and an additional four occurring just upstream of the lake's entrance (Figure 3). The Cox proportional hazards model revealed that origin was a significant predictor of predation risk, with wild smolts found to be 81% less likely to be predated than hatchery smolts ($p=0.003$). Neither weight nor release date were significant predictors.

Seven smolts (three hatchery, four wild) were last detected within the river without a triggered digestion sensor. Given their last known locations and the absence of further detections, these cases could also have been attributable to predation, specifically avian predation. The receivers in the array (excluding the bay receivers) had high detection efficiencies, ranging from 83.8% to 100%, which minimizes the likelihood that these were false absences due to missed detections.

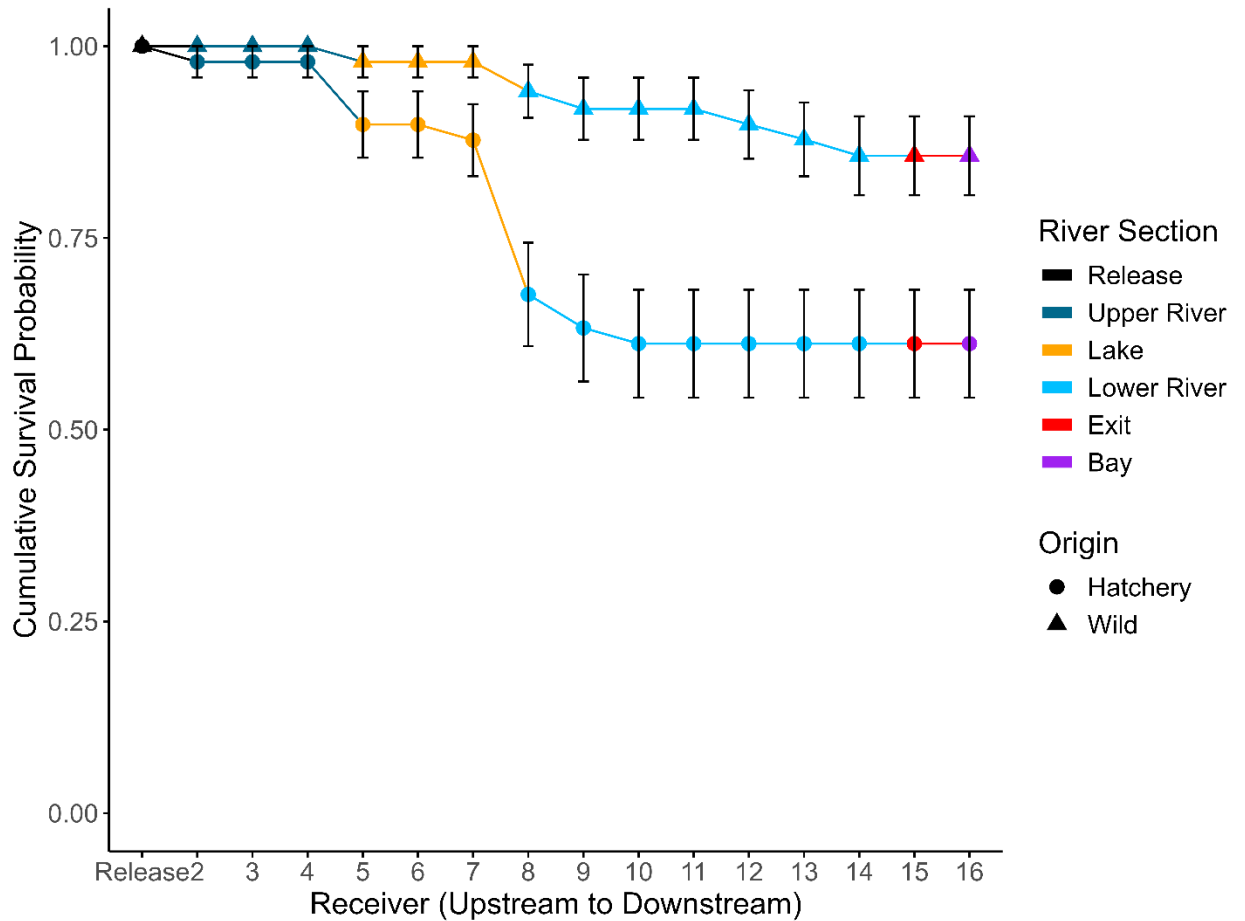


Figure 2. Estimated cumulative survival by river section for hatchery and wild Atlantic salmon smolts in the LaHave River, NS based on a Cormack Jolly Seber survival model. Error bars represent cumulative survival standard error.

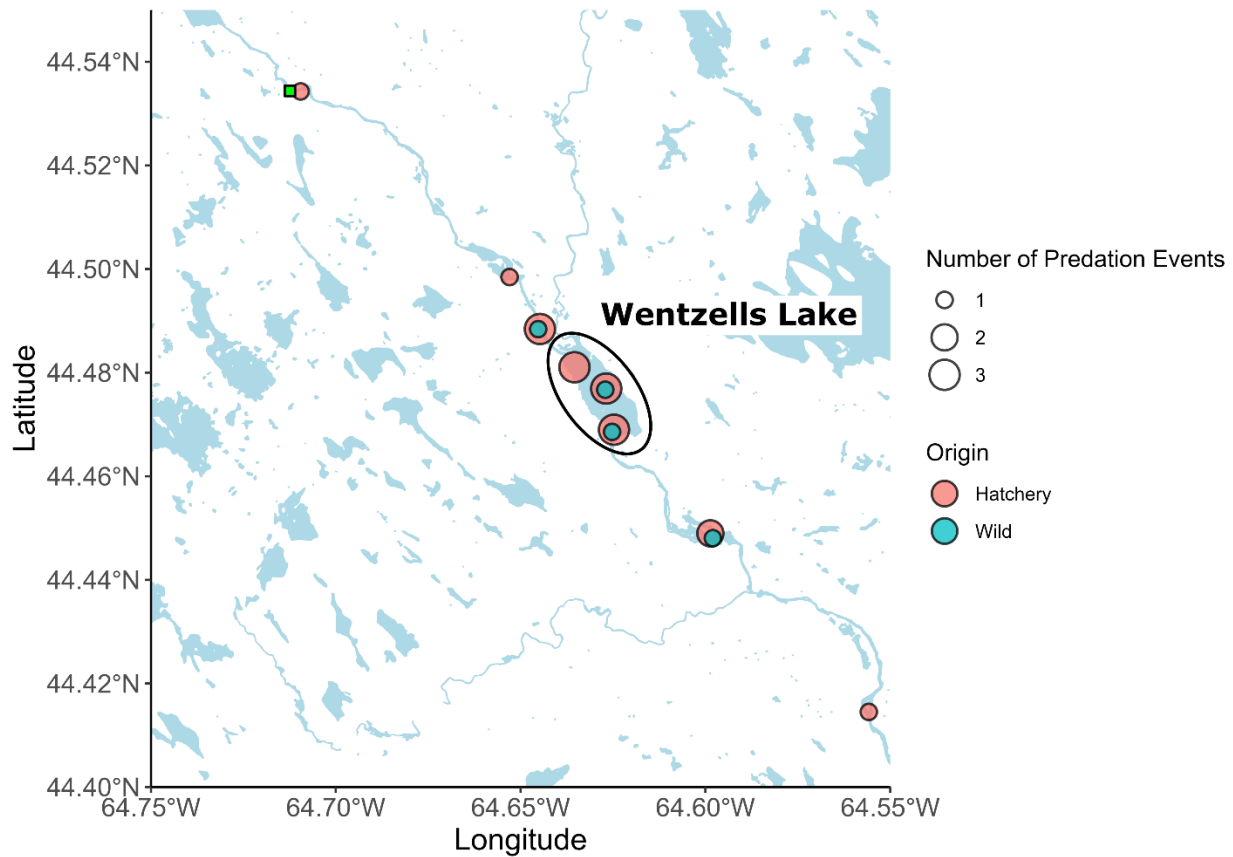


Figure 3. Map of predation events of hatchery and wild Atlantic salmon smolts on the LaHave River with size of point representing the number of salmon predated at the location and the colour representing the origin of Atlantic salmon smolts (hatchery or wild).

2.4.2 RIVER MOVEMENT AND EXIT

Migration speed varied significantly across river sections (GLMM, AIC=475.6). Both hatchery and wild smolts moved substantially faster in the lake (estimate= 2.12 ± 0.19 SE, $p < 0.001$) and upper river (estimate= 2.07 ± 0.19 SE, $p < 0.001$) compared to the bay, whereas speeds in the lower river did not differ significantly (estimate= 0.02 ± 0.20 SE, $p=0.92$; Figure 4a). Origin alone did not significantly affect migration speed (estimate= -0.25 ± 0.22 SE, $p=0.25$), but interaction terms showed that wild smolts moved approximately two times faster in the upper river (estimate= 0.81 ± 0.26 SE, $p=0.002$), the lake (estimate= 0.75 ± 0.26 SE, $p=0.004$), and the lower river (estimate= 0.86 ± 0.27 SE, $p=0.001$) compared to hatchery smolts. Release day and body weight

had little effect, although smolts released on May 3rd exhibited a moderate increase in speed (estimate=0.38 ± 0.14, p=0.009).

Although wild smolts exhibited faster migration speeds through freshwater sections, this did not translate into substantially earlier overall river exit, as our analysis of exit timing showed both groups emigrating over a comparable period (Figure 4b). Overall, 72 of 98 smolts (30 hatchery, 42 wild) successfully exited the river between May 12 to June 1. The majority of smolts exited between May 18 and May 26 with seemingly little difference between hatchery and wild smolts as determined by both origins largely exiting the river during the same time period (Figure 4b).

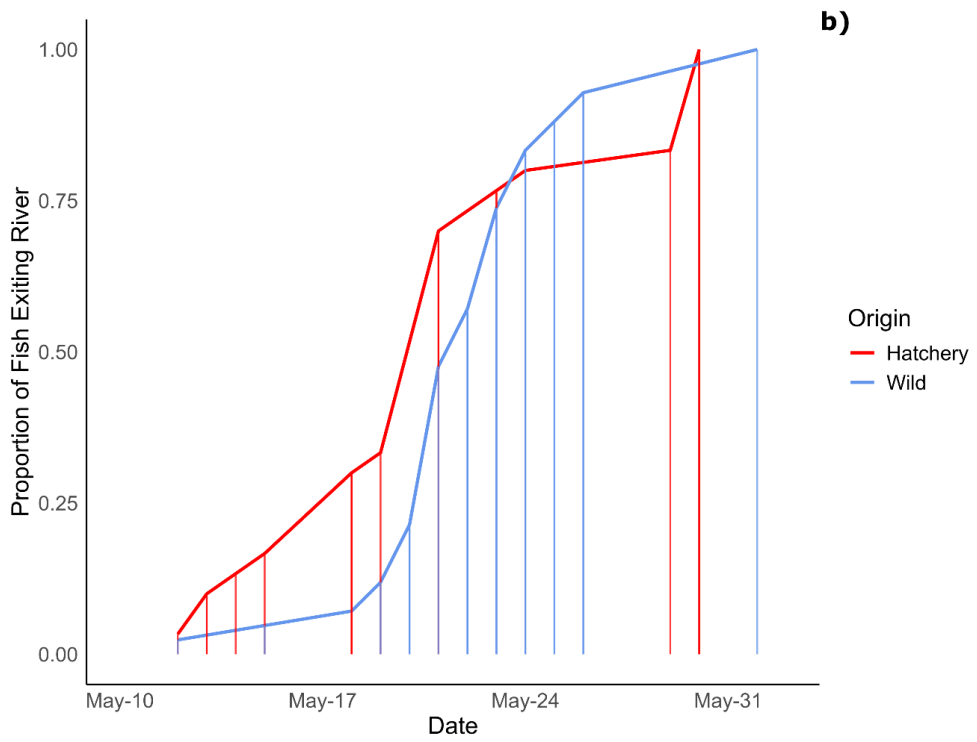
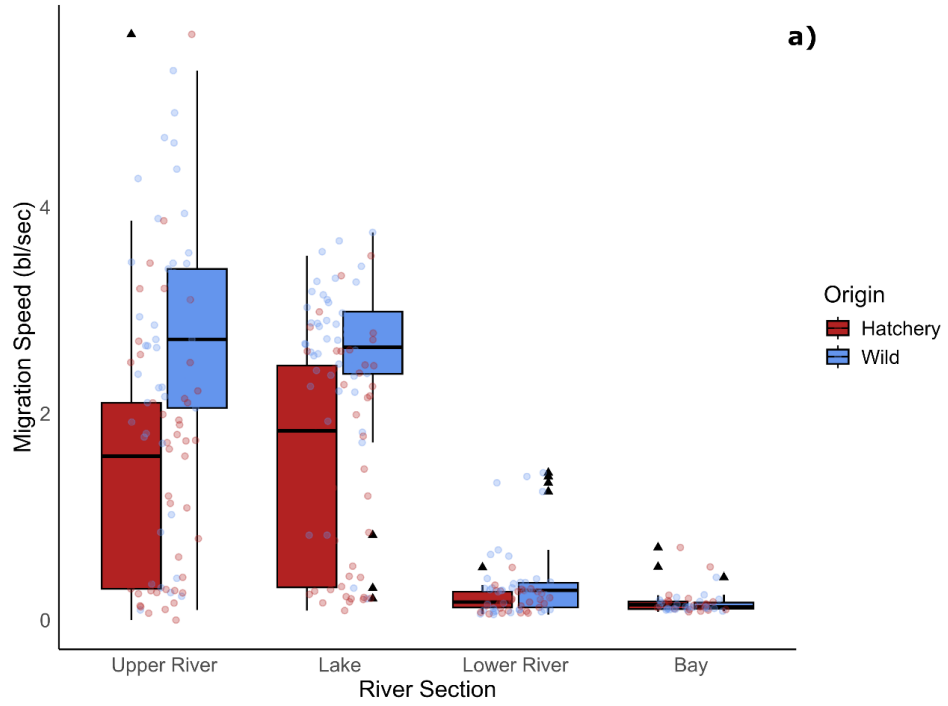


Figure 4. a) Boxplots of migration speed (body lengths per second) by river section of Atlantic salmon smolts from hatchery and wild origin. Boxes show interquartile range, and medians. The black triangles indicate outliers, and points coloured by origin show the raw data. b) Cumulative proportion and timing of LaHave River exit for hatchery (n=30) and wild (n=42) Atlantic salmon smolt. Each step in the line represents an individual smolt exiting the river, resulting in an increase in the cumulative proportion of fish that have left.

2.4.3 OCEAN DETECTIONS

A total of 26 hatchery and 36 wild smolts were detected on five marine acoustic receiver arrays between May 13 to June 11 2021. Smolts from both origins were detected at similar offshore sites, including the LaHave Islands, Halifax Line, and off the coast of Sable Island (Figure 5).

Hatchery and wild smolts exhibited similar offshore spatial ranges, as shown by 100% minimum convex polygons (Figure 5). Smolts were first detected within the LaHave islands on May 13 and were consistently detected there until June 1. Both hatchery (n=11) and wild (n=23) smolts were detected next on the Halifax line from May 21 to June 4 including the two that were detected on the southern reaches of the Halifax receiver line. Finally, hatchery (n=2) and wild smolts (n=4) were both detected approximately 50 km offshore of Sable Island.

Two smolts (hatchery n=1, wild n=1) were detected with triggered predation sensors on the Halifax Line and one near (hatchery-origin) Sable Island. The temperature sensors for the two predated salmon on the Halifax line detected post-predation events and recorded temperatures of 18.3°C and 23.9°C, while the Sable Island predation event did not record any temperature data.

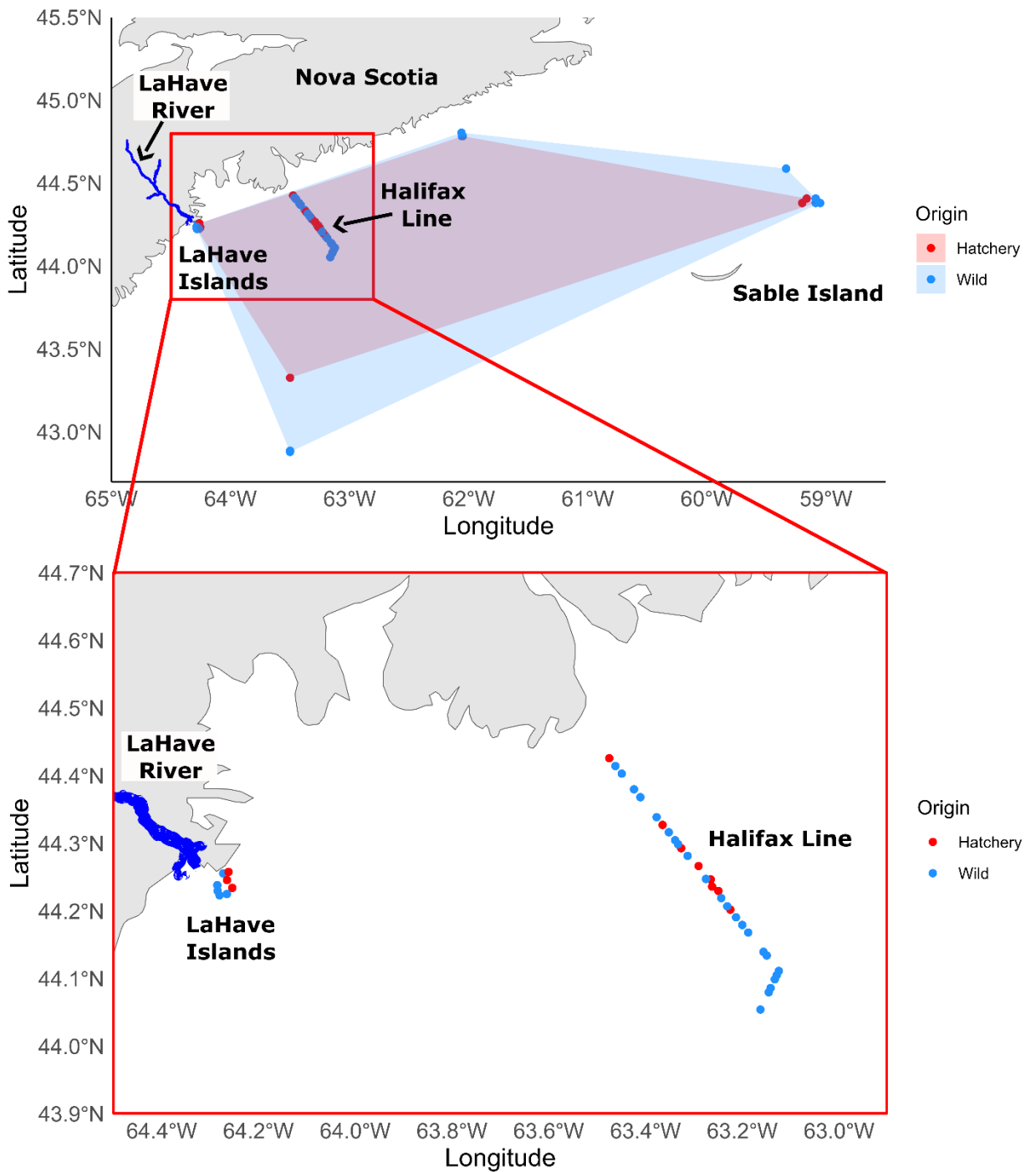


Figure 5. Map showing ocean detections of Atlantic salmon smolts tagged in the LaHave River, Nova Scotia, from hatchery (n=26) and wild (n=36) origins. Individual detections are represented by points, and 100% minimum convex polygons illustrate the spatial range of detections by origin group. Data span from May 13 to June 11, 2021. The inset highlights a closer view of smolt detections near the LaHave Islands and along the Halifax Line.

2.5 DISCUSSION

This study investigated the post-release behaviour of hatchery-reared and wild Atlantic salmon smolts in the LaHave River, Nova Scotia, by comparing survival, predation risk, river migration speed, river exit timing, and early ocean migration patterns. Acoustic telemetry revealed important differences between the two origin groups. In comparison to wild smolts, hatchery-reared individuals exhibited significantly greater mortality and predation rates during outmigration, and slower migration speeds across most river sections. These results point to a clear life-history consequence of hatchery rearing, which has relevance for management concerning the efficacy of current supplementation practices. Despite this, the timing of river exit (i.e. marine entry) was similar between the surviving hatchery and wild smolts, and both were subsequently detected in the same regions during the early stages of the marine migration.

Hatchery-reared smolts experienced significantly lower survival during outmigration compared to wild smolts. In total, 32.4% of hatchery smolts died before even reaching the lower river below Wentzell's lake. Most mortality occurred in the upper river and Wentzell's Lake, sections of the river smolts first encountered after release. Aquatic predation was the main cause of death according to temperature sensors, accounting for 75% of observed mortality events. We argue that most of the remaining, unaccounted deaths were also likely due to predation, specifically avian predators (Evans et al., 2016; Säterberg et al., 2023; Osterback et al., 2013). In these cases, the tag may have been removed from the detection range resulting in the salmon not being detected anymore. Given our high array efficiencies (83%-100%), it is unlikely that either a surviving smolt or a predator carrying a tag would have gone undetected. High hatchery smolt mortality due to predation aligns with previous salmonid research showing that hatchery smolts experience high mortality due to predation (Hyvärinen & Rodewald, 2013; Jepsen et al., 2000; Kekäläinen & Huuskonen, 2008; Melnychuk et al., 2014). In the LaHave River system, this mortality is likely to be driven by invasive species. There are established populations of invasive Chain pickerel and Smallmouth bass in the LaHave River watershed which are species recognized as major predators of juvenile Atlantic salmon (Feener, 2017; DFO, 2024; Mensinger et al., 2025). A study conducted in Wentzell's Lake found salmon smolts to be the most common prey item in the stomach contents of Chain pickerel (Feener, 2017). Smallmouth bass were also found to have ingested some salmon smolts (Feener, 2017). Furthermore, 85% of invasive predators that had consumed smolts were caught at the top of Wentzell's Lake, the same area where most predation occurred in our study.

This strongly suggests that the invasive species were the primary predators and reason of death for smolts in our study and likely extends to the LaHave River system.

High post-release mortality of hatchery-reared smolts in the LaHave River system appears to be largely driven by predation, a pattern consistent with broader salmonid research. Captively raised smolts are known to exhibit poorer antipredator behaviours, which contribute to high post-release mortality due to predation (Olla et al., 1998). These antipredator behavioural deficiencies may include greater surface-feeding behaviour (Vincent, 1960), a reduced ability to escape predators (Woodward & Strange, 1987), increased movement and quicker return to foraging after exposure to predator alarm cues (Einum & Fleming, 2001; Jackson & Brown, 2011), or a lack of avoidance in the presence of predators (Johnsson et al., 1996). In natural environments, wild smolts are exposed to predators across their multiple juvenile years, where individuals that behave riskily are more likely to be selected against by predation, and survivors may learn predator avoidance through experience. Natural exposure contributes to density-dependent mortality, a process where survival rates decline as population density increases, due to intensified competition and predation (Gee et al., 1978; Grant & Kramer, 1990). Under these conditions, only the most fit individuals (i.e., those better able to detect, evade, or avoid predators) are likely to survive, shaping behaviour and improving the predator awareness of the surviving smolts (Falkegård et al., 2023; Laundré et al., 2014). In contrast, hatchery-reared smolts are raised in stable environments with low structural complexity, a lack of predators, and routine feedings which likely results in hatchery smolts ill-prepared for the wild environment, including evading predation, since they do not experience intense natural selective pressures like their wild counterparts (Larsson et al., 2012). As a result, traits important for survival in the wild such as predator recognition or cautious foraging behaviour are not developed in the hatchery setting due to the absence of natural selective pressures. Upon release, their inexperience and lack of conditioning, compounded by the likely stress of captivity handling and the introduction into a novel habitat, may reduce their ability to detect or appropriately respond to predators, increasing vulnerability and reducing survival.

Large disparities in freshwater predation between hatchery and wild smolts highlights the need for improved management strategies to enhance in-river smolt survival. Some studies have demonstrated methods for improving post-release outcomes, which could be implemented to decrease predation events. Vilhunen (2006) trained hatchery-reared Arctic charr (*Salvelinus alpinus*) to recognize the odour of a predator by repeated exposure. Fish that were conditioned

survived longer than predator-naive fish when later exposed to real predators. Similarly, salmon hatcheries could use predator odours, chemical cues, and visual stimuli, such as those from Chain pickerel and Smallmouth bass in the LaHave River, to help smolts develop anti-predator responses before release. Additionally, in many river systems, smolts must pass through lakes during their migration. While some studies have shown that smolts can traverse lakes quickly (up to 15.6 km/day; Bourgeois & O'Connell, 1988), others report significant delays and increased predation in lakes because they lack navigational cues due to slower water flow, offer fewer refuges, and contain higher predator densities (Hansen et al., 1984; Kennedy et al., 2018; Schwinn et al., 2019). Hanssen et al. (2022) found that 60% of tagged Atlantic salmon smolts died in lake habitats, with half of these deaths due to predation. Thus, to mitigate increased predation risk, hatchery programs should incorporate predator cue exposure to promote the development of anti-predator behaviours, and release smolts downstream of known predation hotspots, such as below lakes. Implementing such practices may significantly improve early in-river survival and increase the number of hatchery-reared salmon that successfully reach the sea.

We found significant variation in migration speeds within individual river sections, with wild smolts migrating faster than hatchery smolts in the upper river, lake, and lower river. The observed migration rate differences in most river sections suggest that behavioural responses to different habitats may vary between wild and hatchery smolts, even if their overall migration rates are comparable, which is reflected in the similar river exit timing observed between origins. Pedersen et al. (2008) found that wild salmon smolts performed significantly better than hatchery smolts in a swim flume, swimming 30% faster. Similarly, Gale et al. (2004) reported that hatchery-reared juvenile steelhead (*Oncorhynchus mykiss*) migrated more slowly than their wild counterparts. This indicates that reduced swimming ability, likely due to the lack of exercise and experience with different water flow regimes while reared in captivity, could be a driver in the slower migration speeds we observed in this study's hatchery-reared smolts. Disorientation and limited navigational skills after release into a novel wild environment may also contribute to the slower migration observed in hatchery smolts, especially in lake habitat (Olla et al., 1998). Additionally, the slower migration speeds observed in hatchery smolts may explain the high predation rates they experienced in Wentzell's Lake. Reduced swimming ability, combined with prolonged residence in a known predator hotspot, likely increases vulnerability to predation particularly when paired with likely poorer anti-predator responses. Despite these challenges,

previous studies have observed hatchery smolts match or even exceed wild smolts in outmigration speeds (Hansen et al., 1984; Urke et al., 2013). Hyvärinen & Rodewald (2013) demonstrated that hatchery smolts raised in enriched rearing environments (overhead cover, gravel substrate, and variable water flow) exhibited faster initial migration speeds than those raised in standard bare tanks. Future management practices could benefit from adopting such enriched rearing strategies. Adding structural complexity and variable flow regimes could provide physical exercise opportunities, improving smolt swimming performance and orientation during outmigration. Enhancing swimming ability could also increase survival, as smolts would be better able to avoid predators and move through predation hotspots like lakes more quickly.

Hatchery and wild smolt marine detections showed strong spatial and temporal overlap. Both hatchery and wild smolts followed the expected migration route, first being detected along the southern coast of Nova Scotia (including the Halifax Line) before moving offshore near Sable Island which is consistent with their anticipated path toward eastern offshore Newfoundland and ultimately the Labrador Sea (Bowlby et al., 2013; ESRF, 2023; Reddin & Lear, 1990). The comparable early marine migration between hatchery and wild smolts could indicate similar navigational decisions and responses to environmental cues in the marine environment, suggesting that captive-rearing did not affect marine migration phenotypes. Jonsson & Fleming (1993) previously reported that hatchery-reared smolts migrated to the same marine feeding areas as wild salmon, which could explain the hatchery and wild smolt detections near Sable Island, a biologically rich area within the Eastern Scotian Shelf Canyons known for its high species diversity and ecological importance (Bowlby et al., 2014). Interestingly, most smolts detected in the marine environment did not have their predation tags triggered, despite the high mortality rates typically associated with early marine migration for smolts (Lacroix & Knox, 2005; Thorstad et al., 2010, 2012). The lack of marine predation is especially surprising given that Sable Island is home to the largest breeding colony of grey seals (den Heyer & Bowen, 2018), a known predator of Atlantic salmon smolt (Baker et al., 2015; Lenky, 2011) that frequently forage throughout the Scotian Shelf, overlapping with areas where our smolts were detected (Breed et al., 2009; Nowak et al., 2020). Despite this overlap, only one of the six smolts detected off Sable Island had its predation tag triggered. While temperature sensors were included on transmitters in this study, several predation events were not accompanied by usable temperature data, limiting our ability to identify predator species involved in those specific cases. Future studies should continue to

incorporate temperature sensors with predation tags to distinguish between avian and piscine predators based on post-ingestion temperature profiles (English et al., 2024; Lennox et al., 2024). Identifying predator type using temperature-equipped predation tags could clarify whether hatchery and wild smolts face different predation pressures, as behavioural deficiencies may leave hatchery smolts more susceptible to certain predator types, improving understanding of survival outcomes in freshwater and early marine phases.

Modifying the location of hatchery smolt releases may offer a practical strategy to improve early marine migration. Research has shown that smolts released closer to the river mouth exhibit higher marine survival compared to those released further upstream (Thorstad et al., 2012). This supports recommendations to release hatchery smolts lower in the river, which could help them avoid freshwater mortality (predation) hotspots, such as Wentzell's Lake, and potentially enhance early marine survival. Although hatchery and wild smolts exhibited overlapping distributions during the first month of their marine migration, a limitation of this study is the lack of tracking data beyond this period, leaving the subsequent stages of their oceanic movements and survival unknown. Future studies should consider using tags with longer battery life or coded tags to track smolt movements beyond the Nova Scotia coast (Kennedy et al., 2023). Being able to track individuals for longer would help determine whether hatchery smolts successfully reach key areas along their marine migration such as Newfoundland's Grand Bank or the Labrador Sea. Smolts could also be double-tagged with passive integrated transponder (PIT) tags or physical tags (e.g., Floy tags) to monitor the return rates for hatchery and wild smolts. If returning smolts could be recaptured and measured, or if scale samples were collected, researchers could also gain valuable insights into growth rates and identify successful marine feeding grounds (Jensen et al., 2012; Thomas et al., 2019).

2.6 CONCLUSION

This study demonstrates that hatchery-reared Atlantic salmon smolts exhibited significantly reduced survival during river outmigration than their wild counterparts, primarily due to elevated predation risk. Hatchery smolts also migrated more slowly through the upper river and lake sections, although their river exit timing and early ocean migration patterns were comparable to wild smolts. These findings highlight the critical need to improve hatchery practices to enhance

smolt survival during early outmigration, ensuring more hatchery smolts successfully transition to the marine environment. Based on our results, we propose several practical recommendations to strengthen current management strategies. First, captive rearing environments should be modified to better mimic natural conditions by incorporating structural complexity, substrate, and variable water flow, which may improve swimming performance to provide comparable migration speeds to wild smolts. Second, conditioning hatchery smolts to recognize predator cues before release (visual and chemical cues), particularly those of Chain pickerel and Smallmouth bass in the LaHave River, could help reduce post-release predation by promoting antipredator behaviors such as increased vigilance, avoidance responses, and improved escape tactics. Third, strategic release locations should be implemented. Releasing smolts downstream of high-risk predation habitats like lakes may help avoid predation hotspots and improve early survival. Finally, long-term tagging and monitoring efforts, such as the use of coded tags for long-term tracking and the monitoring of smolt returns, should be expanded to better understand marine migration success and determine whether hatchery smolts reach key feeding areas or return to spawn. Despite facing greater mortality in freshwater, hatchery smolts that survived to the ocean showed similar spatial and temporal migration patterns to wild smolts, highlighting that hatchery programs may support long-distance migration if early freshwater survival challenges are addressed. Moving forward, hatchery rearing and release strategies that incorporate recommended improvements are essential to increasing the return rates of stocked salmon and supporting the long-term recovery of declining wild populations.

CHAPTER 3: A COMPARISON OF IN-RIVER SURVIVAL, MOVEMENT, AND MARINE MIGRATION BETWEEN WILD AND SMOLT-TO-ADULT SUPPLEMENTED (SAS) ATLANTIC SALMON IN NOVA SCOTIA

3.1 ABSTRACT

Atlantic salmon (*Salmo salar*) populations are declining across much of their range with fewer adults returning from their ocean migration to spawn, prompting the use of supplementation strategies such as smolt-to-adult supplementation (SAS) to enhance adult returns. However, little is known about how captivity during adulthood affects post-release survival and behaviour. This study evaluated SAS as a conservation approach for endangered Atlantic salmon populations with high marine mortality by comparing the survival, acceleration, riverine movement, river exit, and ocean migration of SAS and wild adult salmon in the Cape Breton Highlands, Nova Scotia, Canada. Using acoustic telemetry, we tracked post-spawn wild salmon and hatchery-reared SAS salmon throughout the winter and into the marine environment in two rivers. SAS salmon exhibited significantly lower freshwater survival, greater acceleration levels and more frequent high-energy bursts, atypical river movements, premature river exit, and unexpected marine migration routes compared to wild salmon. Notably, SAS salmon held in captivity for two years had higher survival than those held for one year, but exhibited atypical river movement and little upstream movement which raises the concerns of whether any spawning activity occurred. In contrast, SAS salmon with shorter captivity duration had higher mortality, but their last movements and detections were near presumed spawning grounds, suggesting at least some reproductive activity. Additionally, SAS salmon exited the river significantly earlier than wild salmon. Unlike the wild salmon that followed the expected ocean migration route through the Gulf of St. Lawrence and north to Labrador, SAS salmon were instead detected in the Atlantic Ocean off the coast of Cape Breton, including at St. Ann's Bank Marine Protected Area and Sable Island. These findings highlight the complex effects of adult captivity and underscore the need for more nuanced management approaches, including the duration of captivity, feeding strategies, and improved release methods.

3.2 INTRODUCTION

During recent decades, Atlantic salmon (*Salmo salar*) populations have experienced historically low abundances due to many threats including overexploitation, habitat alteration/loss, climate change, and changing marine conditions (Lehnert et al., 2019; NASCO, 2019). Marine survival has been recognized as a life-history bottleneck for Atlantic salmon with record-low adult returns in populations from North America and Europe (Fraser, 2016; Pardo et al., 2021; Vollset et al., 2022). Adams et al. (2022) argued that the costs of anadromy for Atlantic salmon (i.e., energetic demands, time investment, navigational risks, and mortality) have increased in recent decades due to mounting anthropogenic pressures. Population estimates across the Atlantic salmon's global range have revealed a consistent decline in the number of adult salmon returning to their natal rivers to spawn, thus smolt to adult mortality has increased (ICES, 2022; Thorstad et al., 2021). As environmental conditions continue to change rapidly, these compounded costs may further threaten future salmon populations.

To help counter these population losses, the use of supplementation programs, such as hatcheries (i.e. artificial breeding and rearing), have been increasingly used as a conservation strategy for freshwater species (Fraser, 2016; Snyder et al., 1996; WWF, 2022). The process that generally defines traditional stocking involves capturing wild adult salmon, artificially breeding them, and releasing their captive-reared offspring back into the river at some juvenile stage (e.g., eggs, fry, parr, smolt) (Fraser, 2016). Hatcheries have played a key role in salmonid management for over 150 years, serving economical (e.g., supporting commercial fisheries and aquaculture industries), recreational (e.g., enhancing angling opportunities through stocked river systems), and conservational purposes (e.g., rebuilding endangered populations; Bordeleau et al., 2018; Maynard & Trial, 2014; McMillian et al., 2023). However, these programs require careful consideration because of the potential ecological and genetic risks that they pose. Uncertainties exist about the efficacy of hatcheries and the negative consequences that stocking can have on wild populations because it is now well-documented that the conditions animals experience during captivity may quickly lead to selection of domesticated traits that negatively affects their behaviour, physiology, and thus their fitness when released into the wild (Araki et al., 2008; Fleming & Petersson, 2001; Jonsson, 1997; Milot et al., 2013). The effects of domestication on hatchery-reared fish upon release into the wild include increased mortality (Jonsson et al., 2003), reduced reproductive success (Christie et al., 2012, 2014), altered freshwater behaviour (Jonsson et al., 1991; Nilsen et

al., 2023), and differing migration routes (Kallio-Nyberg et al., 2011; Thorstad et al., 2012). In theory, the goal of hatcheries is to reduce juvenile mortality and increase population productivity, but a consequence is releasing salmon that are behaviourally and genetically suited for captive conditions and are therefore less likely to survive and reproduce in the wild, undermining conservation goals (Araki et al., 2008; Carr et al., 2004; Milot et al., 2013).

A lesser employed supplementation strategy, smolt-to-adult supplementation (SAS), has been proposed as a more advantageous approach for salmon populations experiencing low marine returns, compared to traditional juvenile supplementation programs (DFO, 2018; Fraser, 2016). The SAS approach includes capturing wild smolts during their downstream migration, rearing them in captivity until they reach sexual maturity (i.e., one to two years in captivity), and then releasing them back into their natal river to spawn naturally (DFO, 2018; Stark et al., 2014). Unlike traditional hatchery programs, which release salmon into the wild at a juvenile stage before their ocean migration, the SAS method shifts the period of captivity to bypass the high-mortality marine phase (Fraser, 2016). Marine survival of smolts is one of the major bottlenecks for Atlantic salmon, with typically fewer than 5% returning as adults in recent decades (Dadswell et al., 2022; Nieland et al., 2015). By rearing fish in captivity from smolt to adult, SAS substantially increases marine survival by eliminating the energetically costly marine migration and any predation. In addition to improving marine survival, SAS aims to: 1) maintain genetic integrity by avoiding captive rearing during early life stages (because juveniles grow up within their natal rivers from egg to smolts and thus undergo natural selection and imprinting processes); 2) ensure a known number of adults return to spawn, unlike traditional hatcheries that rely on released juveniles to survive and return from the ocean; and 3) allow natural mate choice, because SAS adults are released into the wild in time for spawning, rather than using breeding programs typical of hatchery practices (Fraser, 2016; Young et al., 2017). Stark et al (2014) evaluated behaviours such as habitat selection, courting, and spawn timing in SAS-reared Chinook salmon (*Oncorhynchus tshawytscha*) and Atlantic salmon. The results suggested that habitat selection and spawning behaviour was similar between SAS-reared and wild salmon, but there were some differences with spawn timing. Egg and fry production were also assessed and indicated successful spawning of the SAS-reared salmon (Stark et al., 2014). However, there has been no comprehensive evaluation of the efficacy of SAS programs for Atlantic salmon, particularly in terms of whether proposed benefits are fully realized once fish are released into the wild.

Atlantic salmon populations across Canada have experienced steep declines with five of the 16 extant populations assessed as Endangered (COSEWIC, 2010). Parks Canada has monitored adult salmon returns to Clyburn Brook in Cape Breton Highlands National Park since 1985, with Levy & Gibson (2014) reporting a 95% decline in adult spawners over the first three decades of monitoring. Monitoring has continued to the present day and continues to observe a decline in returning adults. In response, Parks Canada began a SAS program which created an opportunity to further assess whether released SAS salmon are behaviourally similar to their wild counterparts and successful in population recovery efforts. This study aims to address this gap by evaluating differences in survival, acceleration levels, freshwater movement, river exit, and marine migration of adult Atlantic salmon from wild and SAS origin. Using acoustic telemetry and accelerometer transmitters, we tracked both groups from their time in the river through to the marine environment. Compared to local wild populations, we hypothesized that SAS salmon would: 1) experience greater overwintering mortality; 2) show increased acceleration values; 3) exhibit similar exploratory upstream river movements toward presumed spawning habitat; 4) exit the river within the same time window; and 5) follow the same expected northerly marine migration route. Predictions were based on previous literature of known physiological and behavioral differences between hatchery-reared and wild salmon and the results of the few studies on post-release SAS salmon (Carr et al., 2004; Dempson et al., 1999; Stark et al., 2014). Additionally, within the SAS salmon group, some individuals spent one-year in captivity (SAS1) vs. two-years in captivity (SAS2). Based on literature showing that an individual's fitness, survival, and reproductive success decline the longer they spend in captivity (Jonsson et al., 2003; Milot et al., 2013; O'Sullivan et al., 2020; Theriault et al., 2011), we hypothesize that SAS1 salmon will outperform SAS2 salmon in a wild setting (i.e., exhibit higher survival rates, lower acceleration values, typical river movements, and migration decisions more similar to wild salmon). These findings will offer key insights into how captivity from smolt-to-adult influences post-release survival, behaviour, and migration in SAS fish, and will help assess the overall viability of SAS as a long-term conservation strategy for Atlantic salmon.

3.3 METHODS

3.3.1 STUDY SITE

Atlantic salmon were tagged from two rivers in the Cape Breton Highlands, Nova Scotia: Clyburn Brook and Chéticamp River (Figure 6). Covering 950 km², the Cape Breton Highlands extend to 500 meters above sea level and is a part of the Appalachian Mountain range. This montane environment produces rivers with steep gradients and fast currents (O'Reilly et al., 2013). Although the Cape Breton Highlands have been a national park since 1936, the Atlantic salmon populations are not well-documented with significant gaps in our understanding of their movement, habitat use, and survival.

Clyburn Brook - SAS salmon

Clyburn Brook is located on the eastern shore of Cape Breton Island in the Eastern Cape Breton Designatable Unit (ECB DU; Figure 6). The headwaters begin in the Highlands and run 19.4 km before draining straight into the Atlantic Ocean with the majority of the river within the Cape Breton Highlands National Park boundary. The Clyburn Brook salmon population is a mix of multi-sea-winter salmon (MSW, spends more than one year in marine environment before returning to natal river) and one sea-winter salmon (1SW, spent one year in marine environment before returning to natal river) and is considered a late running salmon river with some salmon not entering until November of their spawning year (Grey, 1984).

Wild Salmon Reference Population

Due to the critically low number of wild adult Atlantic salmon returning to Clyburn Brook, it was not feasible to include wild Clyburn Brook salmon as a wild comparison in this study because acoustic tagging would have posed an unacceptable risk to the population (estimated in swim through surveys to be ~31 spawners in 2023 (Parks Canada, pers. comm)). As a result, while all SAS fish in this study originated from Clyburn Brook, wild fish used for reference to SAS adults were sourced from the nearby Chéticamp River (described below) because this system still supports a wild population large enough to allow limited tagging without negatively impacting conservation efforts.

Chéticamp River - Wild salmon

Chéticamp River is located on the western shore of Cape Breton Island in the Gaspé-Southern Gulf of St. Lawrence Designatable Unit (GSGSL DU; Figure 6). The river is 35 km in length before draining into the Gulf of St. Lawrence and is entirely within the boundary of the Cape Breton Highlands National Park, other than the headwater source in the Highlands, Chéticamp Lake. The lake was removed from the Park boundary in the 1970's to build the Wreck Cove Hydroelectric Project, which some of the lake's outflow is diverted towards. The Chéticamp River has been monitored by Parks Canada and the Chéticamp River Salmon Association for decades via counting fences, river surveys, instream restoration projects, river temperature loggers, and other metrics for the conservation and understanding of the rivers' Atlantic salmon population.

The Chéticamp River has a low percentage of 1SW adult salmon with an early run peaking in June and July (Grey, 1984) and is the only river in the Cape Breton Highlands National Park where recreational catch and release angling occurs of Atlantic salmon. In 2004, Fisheries and Oceans Canada (DFO) assessment determined that the total number of adult Atlantic salmon (large and small) returning to the Chéticamp River was 409 (95% confidence interval: 277 to 1270 fish), meeting the rivers conservation requirement by 110% (Landry et al., 2005). For these reasons, the Chéticamp River was selected as a local wild reference population to SAS Atlantic salmon in the Clyburn Brook, as it supports a healthy salmon population.

3.3.2 RECEIVER DEPLOYMENT

Salmon were tracked using VR2W-69kHz (12-month battery life; Innovasea, Bedford, Nova Scotia, Canada) acoustic receivers deployed in each river system. From October 2023 to April 2025, a total of 13 receivers were deployed in Clyburn Brook from the estuary mouth to 9 km upstream (Figure 7a). From November 2023 to May 2024, a total of seven receivers were deployed in the Chéticamp River from the estuary mouth to 9 km upstream. The last estuary receiver remained in the river until 2025 to ensure any detections from returning fish were recorded (Figure 7b). For each river, receiver placement ranged from far upstream spawning reaches down to the estuary and river mouth to cover the full movement range of the salmon. Pools were selected based on depth to reduce the likelihood of exposure during low water levels, while also avoiding areas of high flow where the receiver could be displaced or swept onto shore. Pool substrate was also

considered so that, whenever possible, receivers were positioned on larger, cobblestone substrate to prevent burial by fine sediment. Despite these precautions, intense flooding events and sedimentation resulted in the loss of two receivers, leaving a total of 11 operational units in Clyburn Brook.

Marine detection data from ocean arrays were obtained through the extended receiver network supported by the Ocean Tracking Network (OTN), which aggregates acoustic telemetry data from collaborative deployments across the Northwest Atlantic (OTN Data Policy, 2024). An array refers to a distinct spatial grouping of deployed acoustic receivers that passively detects acoustically tagged animals as they move through the area.

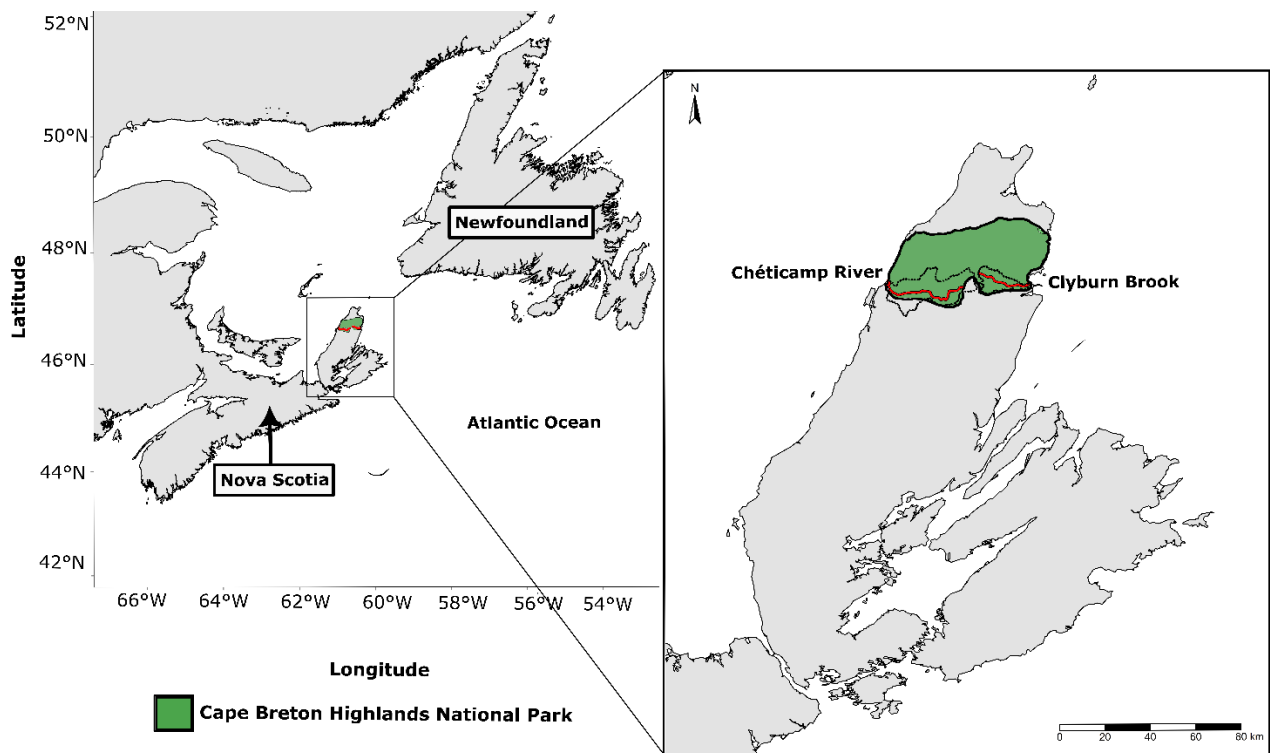


Figure 6. Map showing the broader Atlantic Canada region with a zoomed-in inset of Cape Breton Island, Nova Scotia, highlighting the two river systems included in this study: Clyburn Brook (SAS salmon) and Chéticamp River (wild salmon). Black dashed lines represent the two rivers watershed boundaries.

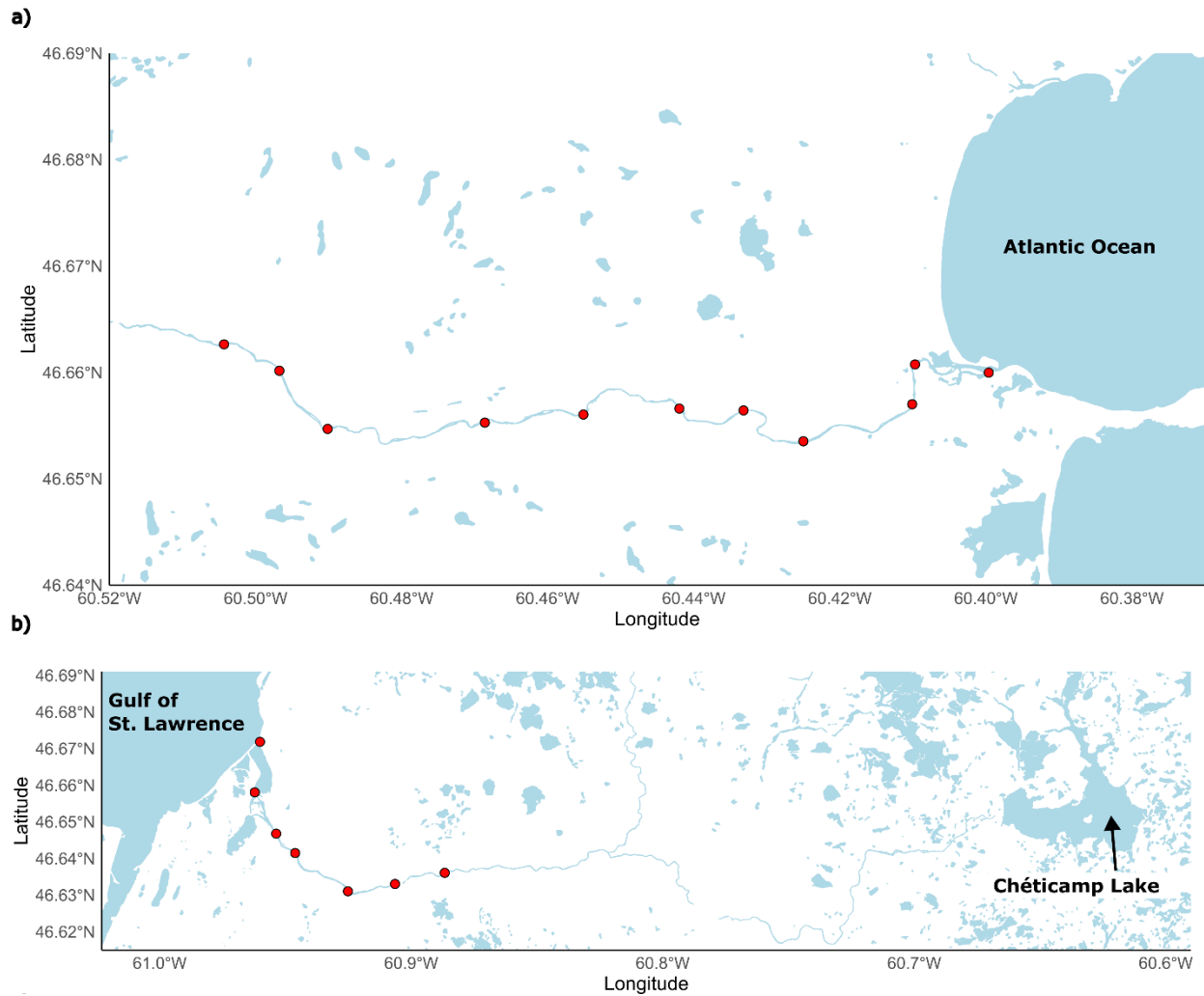


Figure 7. a) Map of the Clyburn Brook acoustic receiver deployment locations (red points) for 2023-2025. b) Map of the Chéticamp River acoustic receiver deployment locations for 2023-2024, other than the last estuary receiver which remained until 2025 to ensure any detections from returning fish were recorded. The headwater source, Chéticamp Lake, is labelled.

3.3.3 EXPERIMENTAL DESIGN

Smolt-to-Adult Supplementation (SAS) rearing

Throughout the month of May in 2021 and 2022, wild Atlantic salmon smolts were captured using fyke nets from the Clyburn Brook. Smolts were transferred 450 km (~5-hour drive) to Dalhousie University Aquatron facilities in a 500 L holding tank filled with Clyburn Brook river water. Water quality measurements (temperature, dissolved oxygen, pH, ammonium, and nitrates) were monitored throughout the transfer process. The smolts were evenly split between two 500 L

holding tanks with artificial lighting that mimicked the natural photic period. Salmon were fed a high-energy diet once daily to support rapid growth, with feeding times varying day to day (Nutra RC, Skretting, St. Andrews, New Brunswick Canada).

The salmon remained in freshwater holding tanks, growing to adulthood and reaching sexual maturity under consistent monitoring. Salmon that were deemed sexually mature based on body size and gonadal maturity were released back into Clyburn Brook that year. However, if a salmon was deemed to be sexually immature, it was retained at the Aquatron for a second year. Therefore a SAS salmon spent either one or two years in captivity (herein SAS1 and SAS2, respectively).

Tagging procedure

Tagging of SAS salmon occurred in two rounds at the Aquatron facilities, first in September 2023 and again in August 2024 (Table 2). In 2023, 30 SAS salmon (SAS1 n=15, SAS2 n=15) were tagged with 20 69 kHz V13A acoustic accelerometers (15mm X 44mm, 12g in air, R64k protocol, 60-120s transmit interval, 414 days of battery; Innovasea) and 10 69 KHz MM-MR-11-28 acoustic transmitters (12mm x 60mm, 10.5g in air, R64k protocol, 60-120s transmit interval, 429 days of battery; Lotek, Newmarket, Ontario, Canada) evenly split between year-groups. In 2024, 13 SAS2 salmon were tagged with nine Innovasea accelerometers and four Lotek transmitters. The Innovasea accelerometers measure acceleration in ms^{-2} which results in a vector quantity of acceleration along three axes: horizontal, vertical, and depth (x, y, and z). The tag calculates root mean square (RMS) from the contribution of acceleration from each axis. Thus, the transmitted output is the average acceleration from each axis over the sampling period.

SAS salmon were anaesthetized in a 300 L aerated holding tank with Tricane Methanesulfonate (TMS)(0.01gL^{-1}) until loss of equilibrium. Weight, length, and condition were recorded before being placed in the operating trough where gills were constantly irrigated. A small incision was then made on the mid-ventral line and the sterile transmitter placed intraperitoneally. The transmitters were gas sterilized with ethylene oxide and surgical tools disinfected with glutaraldehyde before being rinsed in saline. The incision was closed with 4-0 monofilament in 2-3 interrupted sutures. The fish were immediately taken to a recovery tank where their healing success was monitored for one month. Recovered SAS salmon were then transported using the same methods and released into Clyburn Brook (one month post-tagging in 2023 (October 19) and three

months post-tagging in 2024 (October 16)) at a deep pool located 2 km from the river mouth and 1 km downstream of known spawning grounds.

All fish handling, and tagging procedures conformed to the guidelines established by the Canadian Committee on Animal Care, approved by the Dalhousie University Animal Care Committee (protocol #1039341), and wild salmon angling was conducted under permits issued by Parks Canada and DFO (373082, 375879).

Wild salmon handling and tagging procedure

Wild kelts were angled and tagged in Chéticamp River in December 2023. Local volunteer anglers belonging to the Chéticamp River Salmon Association helped catch the salmon. The salmon were allowed to recover from the angling process stress for 10 minutes in a floating lobster crate that river water flowed freely through. A total of 17 kelts were tagged with 10 Innovasea accelerometers and seven Lotek transmitters. The same tagging methods used for the SAS salmon were applied, with the exception that the anesthetic holding tank was located on site. The fish was immediately placed back in the lobster crate with free-flowing river water to recover for at least 10 minutes before being released back into the river.

3.3.4 DATA ANALYSIS AND MODELING

Data were processed using Rstudio 4.4.2 (R Core Team, 2024) and acoustic telemetry summary packages of *actel* (Flávio & Baktoft, 2021) and *glatos* (Holbrook et al., 2024). For data filtering, detections were evaluated based on the time taken for individual fish to move between detections. Any detection was removed if the implied travel speed exceeded 3.5 km/h, because average kelt migration speeds range from 0.94 to 2.1 km/h (Halttunen et al., 2009; Remen et al., 2016; Thorstad et al., 2004). The speed threshold helped identify and exclude false detections caused by unrealistically fast movements.

Survival

Fish were assigned a fate of either successfully exiting the river or given an estimated time of death based on their last detection within the river. In cases where a salmon's final detection occurred within the array but was not followed by any further detections, it was assumed the individual had died. This assumption is supported by the high detection efficiency of the receiver arrays (calculated by the Rstudio package *actel*; Flávio & Baktoft, 2021) and the expectation that healthy

individuals continue to move and exhibit detectable activity throughout the river (Klinard & Matley, 2020). A lack of movement or absence from downstream receivers despite prolonged monitoring is therefore considered a reliable indicator of in-river mortality or tag failure (Klinard & Matley, 2020), though the latter is less likely given consistent detection histories before disappearance.

Survival modeling was only performed between SAS age stages (SAS1 and SAS2 cohorts) because all wild salmon from the Chéticamp River survived. To assess survival differences between SAS1 and SAS2 groups, a Cox proportional hazards model was used, implemented via the `coxph` function from the survival package (Therneau, 2024). Hazard (risk) of mortality was modelled over time while incorporating the explanatory variables including years spent in captivity and sex. Length was excluded due to collinearity with age (i.e. years spent in captivity). Given that the analysis was focused on comparing post-release mortality of SAS in the river rather than calendar year effects, time until death was calculated as the number of days since the release of the salmon back into the river after being tagged.

Acceleration

The accelerometer transmitter output was used to compare the acceleration levels of wild and SAS salmon within the river. Raw acceleration values, transmitted as integers ranging from 1 to 255, were calibrated to true acceleration values by multiplying them by 0.01922 as per manufacturer specifications.

To examine salmon acceleration levels during the overwintering period, a generalized additive model (GAM) was fitted using the `bam` function from the R package `mgcv` (Wood, 2024). The response variable, acceleration, was modeled using a Gamma distribution with a log-link function, because acceleration values are strictly positive and right-skewed. Because high-resolution detections from fish remaining near receivers can lead to strong temporal autocorrelation, data were downsampled by retaining only the first detection per fish per receiver within one-hour windows. Additionally, to ensure direct comparisons between wild and SAS salmon, the dataset was filtered to include only periods when acceleration data were collected for both groups (December 10 to January 15). Explanatory variables included salmon origin (SAS vs wild), hour of the day, and date (measured in Julian days). Individual fish ID was included as a random effect to account for repeated measures. An appropriate number of basis functions were

applied to smoothing terms to balance model flexibility with biological interpretability, and reduce overfitting (Pederson et al., 2019). The basis functions for each smoothing term were initially set high, but the final k-value was selected by gradually lowering k and picking based on the first noticeable drop in model fit quality (via AIC and visual inspection). A cyclic cubic spline (k=5) was applied to hour of day to model diel patterns in activity while accounting for 24-hour structure. A thin plate regression spline (k=5) was applied to date with a group-specific smooth to allow seasonal activity patterns to vary between SAS and wild salmon.

River exit and movement

The timing of river entry and exit was extracted from individual detection histories using the `detection_event` function from the `glatos` package (Holbrook et al., 2024). Individual detections were consolidated into distinct detection events with an event defined as either a change in receiver location or a lapse in detections of seven days or more before re-detection on the same receiver (Holbrook et al., 2024). River exit was determined as the final detection in the estuary, near the river mouth, before no re-detection in the river or any recorded ocean detections. To examine differences in river exit timing between SAS and wild salmon a linear regression with Gaussian distribution was fitted using the base R function `lm` (R Core Team, 2024). The response variable was river exit converted into days spent in the river by taking the difference between river entry/release and exit date. The explanatory variable was salmon origin of SAS vs. wild salmon. Individual fish were included as a random effect. Individuals that did not exit the river were omitted from the analysis.

Marine detection data from ocean arrays were obtained through OTN. To examine early ocean movement, detections were filtered to include only post-river exit records and 100% minimum convex polygons (MCPs) were applied around all ocean detections for hatchery and wild smolts to visualize spatial extent. These MCPs represent the total area encompassed by each group's marine detections.

3.4 RESULTS

A total of 60 Atlantic salmon (SAS n=43, wild n=17) were tagged and tracked from 2023 to 2025 from the two Cape Breton rivers: Clyburn Brook and Chéticamp River. There were a total of 2,120,164 individual detections that were summarized to 803 distinct detection events across 59

salmon; one tagged SAS salmon was never detected once released and was thus excluded from analysis. Of the original detections, 1780 (0.084%) occurred in the ocean environment. The 30 SAS salmon tagged in 2023 included 18 females, eight males, and four of unknown sex. The cohort was an even split of SAS1 and SAS2 salmon in captivity. The 13 SAS salmon tagged in 2024 were all SAS2 and included six females, five males, and two of unknown sex. The 17 wild Chéticamp salmon included 15 females and two males (Table 2).

Table 2. Summary of salmon tagged for Clyburn Brook and Chéticamp River including release year, sample size, origin (wild or SAS), SAS stage if applicable (SAS1=salmon spent one year in captivity, SAS2=salmon spent two years in captivity), mean fork length (mm) with standard deviation (\pm SD), and sex (female/male/unknown).

River	River Release Date	Sample Size	Wild or SAS Origin	SAS Stage	Mean Length (mm \pm SD)	Sex (F/M/Unknown)
Clyburn Brook	Oct 2023	30	SAS	15 SAS1	485 \pm 28	5 / 6 / 4
				15 SAS2	510 \pm 37	13 / 2 / 0
	Oct 2024	13	SAS	13 SAS2	507 \pm 45	6 / 5 / 2
Chéticamp River	Dec 2023	17	Wild	-	813 \pm 52	15 / 2 / 0

3.4.1 SURVIVAL

Of the 43 SAS salmon tagged in the Clyburn Brook, 53% (23 of 43) were last detected in the river and presumed dead. SAS1 salmon had a notably higher mortality rate of 73% (11/15) compared to SAS2, which had a 43% (12/28) mortality rate. Spatially, 64% of SAS1 mortalities occurred upstream near presumed spawning grounds, while 50% of SAS2 deaths occurred upstream (Figure 8a). In contrast, all 17 wild salmon from Chéticamp River survived and exited the river. The Cox proportional hazards model revealed that SAS1 salmon had significantly greater mortality than

SAS2 salmon (hazard ratio = 16.5, $p < 0.001$; Figure 8b). Males had a slightly higher mortality, although the difference was not significant. The unadjusted survival probability for SAS1 decreased to 27%, while SAS2 only decreased to 57% by the end of the study period. Mortality timing was different between groups with SAS2 salmon experiencing greater early losses (30 days post-release) compared to SAS1 salmon (mid-October to end of November; SAS1 $n=4$; SAS2 $n=11$) with most SAS1 deaths ($n=7$) occurring around 65-95 days post-release (December 2023 - January 2024). SAS2 salmon survived for a maximum of two months in the river, with the latest recorded death in mid-December.

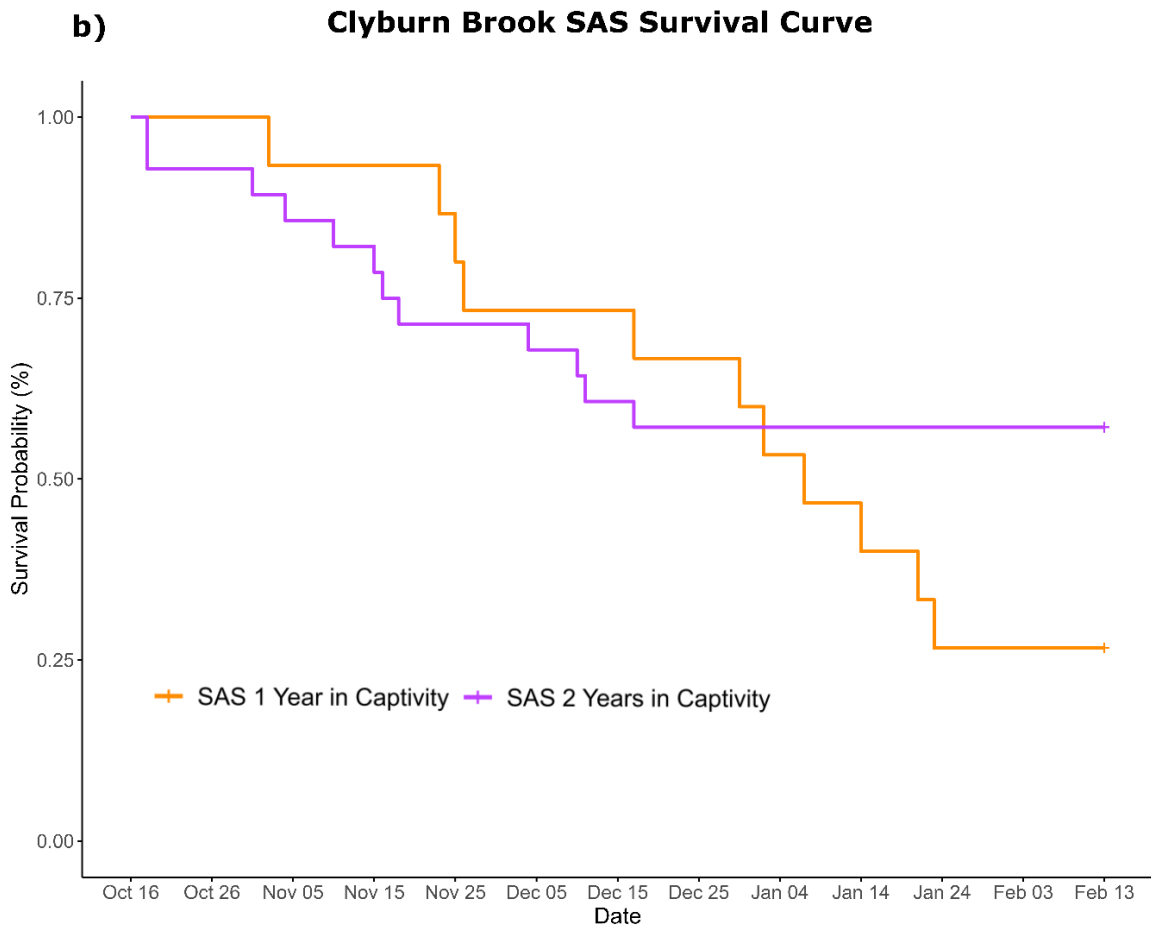
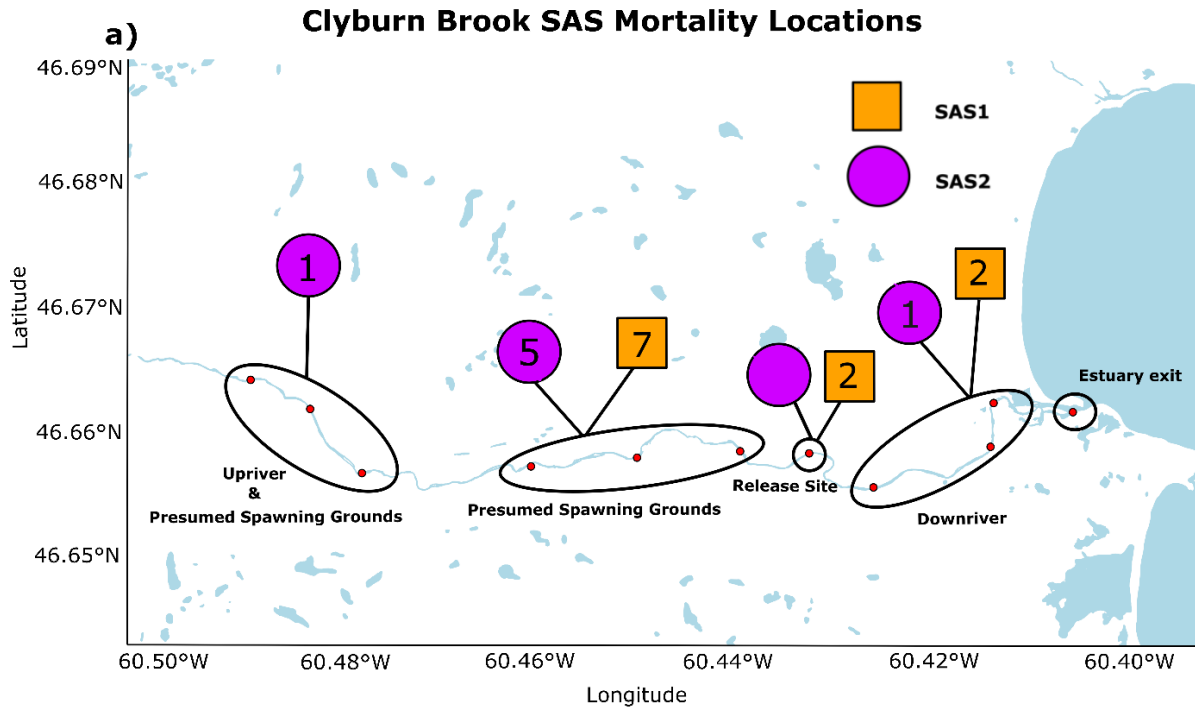


Figure 8. a) Map of Clyburn Brook showing last detection locations of SAS salmon assigned mortalities. Receiver sections represent the area where salmon had their final in-river detection and were subsequently classified as mortalities. SAS1 are shown as pentagons, while SAS2 are shown as stars. The numbers within each symbol denote the number of mortalities from that group detected in each section. b) Comparison of unadjusted survival probabilities between SAS1 and SAS2 after release in Clyburn Brook ($p=0.002$). SAS1 $n=15$; SAS2 $n=28$.

3.4.2 ACCELERATION

A total of 43 Atlantic salmon were tagged with accelerometers (SAS $n=29$; wild $n=14$), yielding 200,521 detections between October 19, 2023, and November 27, 2024. Acceleration events for both SAS and wild salmon overlapped primarily from early December to mid-January reflecting that wild fish were only tagged in early December and many SAS fish had either died or exited the river by late January. During this period of overlap, SAS salmon were found to have more high speed burst outliers (6.7% of acceleration detections) compared to wild salmon (1.5% of acceleration detections; Figure 9a). The GAM showed a highly significant effect of origin on acceleration ($\beta = -0.42$, $p < 0.001$), with SAS salmon consistently displaying higher acceleration than Chéticamp wild fish (SAS: 0.618 ± 0.362 SD m/s^2 ; wild: 0.338 ± 0.224 SD m/s^2) (Figure 9b).

Origin-specific smooth terms for date revealed distinct temporal patterns with SAS salmon exhibiting a significant increase in predicted acceleration from approximately 0.68 to 0.74 m/s^2 throughout December ($F=13.61$, $p < 0.001$). In contrast, wild salmon exhibited a gradual decline from about 0.57 to 0.39 m/s^2 during the same time period ($F=8.13$, $p < 0.001$; Figure 9b). A cyclic smoother for hour of day was also significant for both SAS and wild salmon ($F=65.37$, $p < 0.001$), capturing a diel rhythm of increased activity around noon and reduced acceleration at night. The random smoother for individual fish was also significant ($F=4.15$, $p < 0.001$), indicating individual-level variability. Acceleration was not significantly different between SAS1 and SAS2 salmon

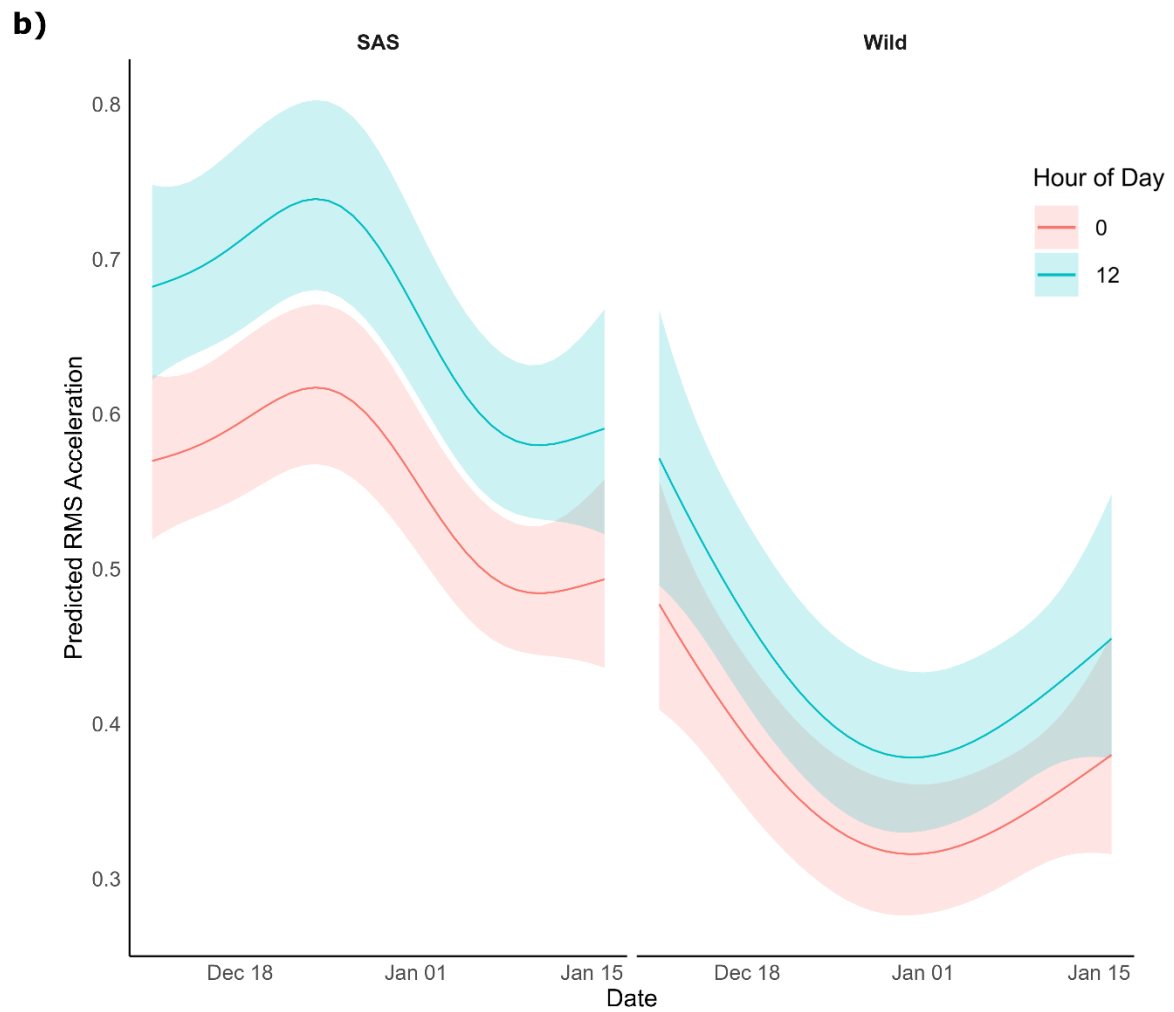
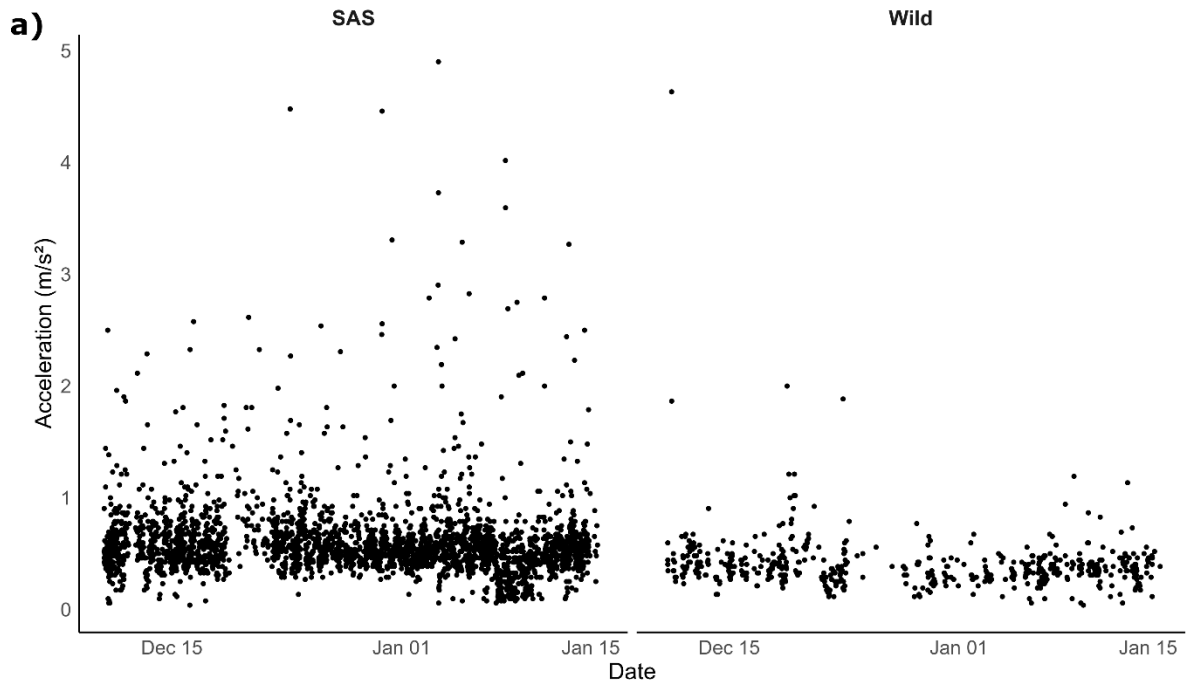


Figure 9. Comparison of observed and predicted acceleration (m/s^2) of SAS and wild salmon over time in Clyburn Brook and Chéticamp River respectively. a) Raw acceleration detections for individual salmon over the same time period, faceted by group. Each point represents a single acceleration reading from an individual fish tag. b) Generalized additive model (GAM) predictions of root mean square (RMS) acceleration faceted by group (SAS or wild) and coloured by hour of day). Shaded ribbons represent the standard error of the GAM predictions.

3.4.3 RIVER MOVEMENT

We observed more than half of SAS salmon (27 of 43, 62%) exhibit atypical river movement (i.e., no upstream movement or typical spawning patterns such as spawning site exploration or holding), while other SAS salmon showed typical movements (i.e., upstream movement, spawning site exploration, holding near spawning sites; Figure 10a,b). The majority of upstream movement from both SAS1 and SAS2 occurred from mid-October to early December. SAS1 salmon exhibited greater upstream movement with more individuals detected in the presumed spawning grounds following release compared to SAS2 salmon. A total of 87% of SAS1 individuals (13/15) were detected upstream from the release site at least once during the tracking period, whereas only 46% of SAS2 fish (13/28) were detected upstream. The majority of SAS2 salmon did not move more than 2 km upstream from the release site, and instead appeared to move downstream with some individuals either exiting quickly or having a last detection downstream. Detections for both age-groups began to decline in January 2024, coinciding with the timing of mortality assignments for SAS1 and river exits for SAS2. The furthest upstream movement recorded (9 km from the river mouth) was from three salmon (SAS1 $n=2$, unknown sex; SAS2 $n=1$, female) that were detected between November 4 and November 18, 2023 (15 to 30 days post-release). In contrast, wild salmon exhibited typical post-spawn behaviour with very little movement from where they were angled and none detected moving upstream. Post-release, most wild salmon were detected repeatedly at a single, tidally influenced receiver location before the majority of them exited the river, with 29% moving between the tidal and estuary receivers at least once.

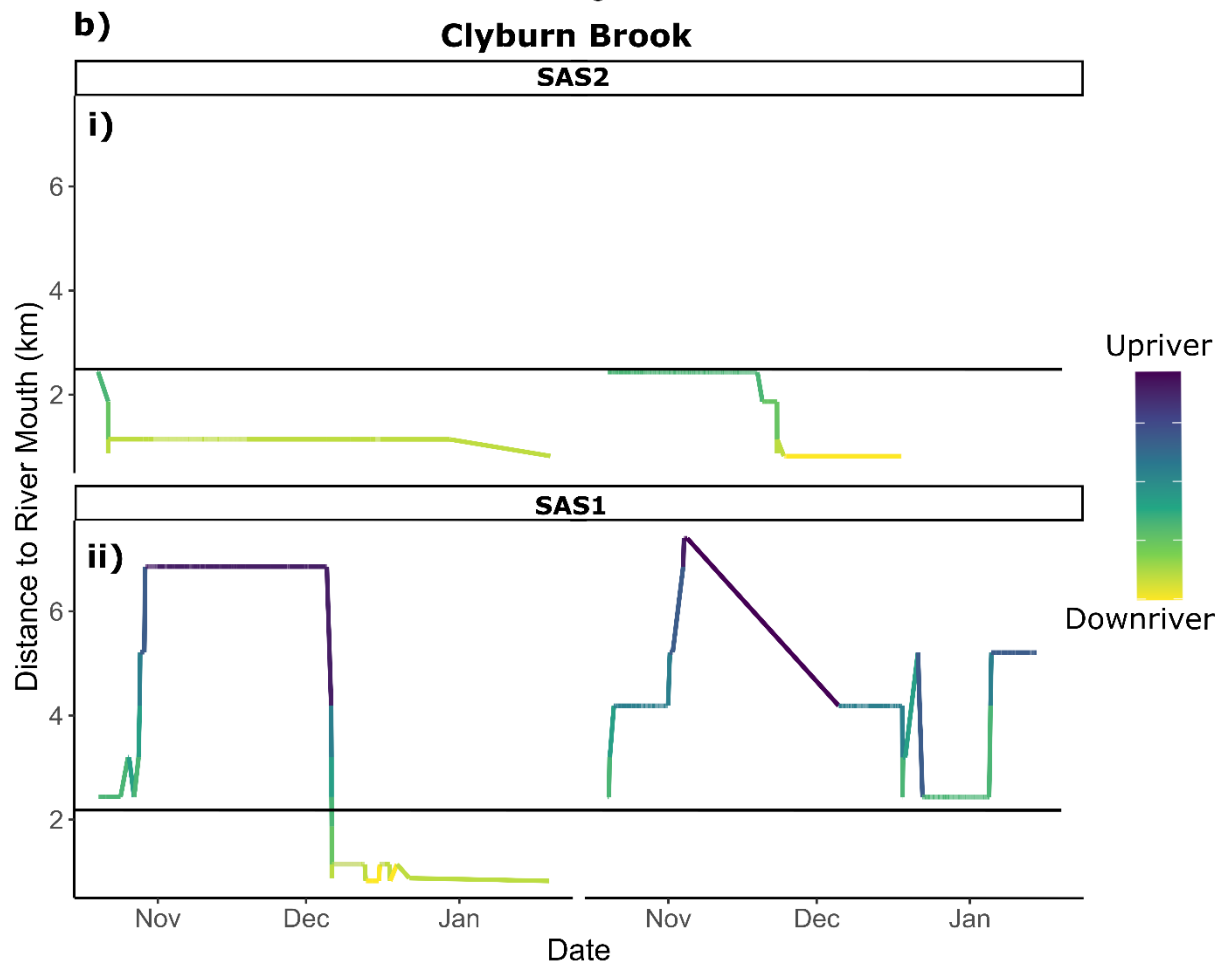
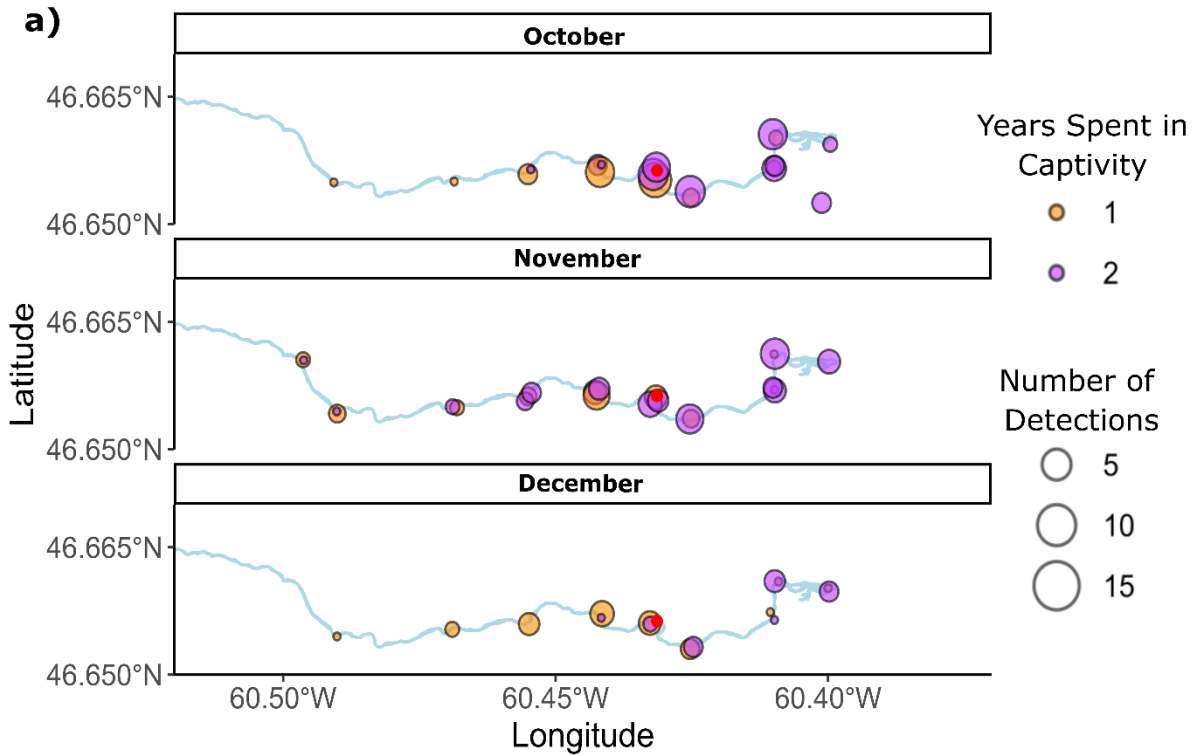


Figure 10. a) Map of Clyburn Brook showing detection locations of SAS salmon three months post-release coloured by group. The size of detection bubbles indicates the number of salmon detected at that location. The release site is denoted by the red point in each panel. Data from 2023 and 2024 were combined to highlight overall patterns, rather than interannual variation. b) Examples of directional river movement of individual SAS salmon in Clyburn Brook. The black horizontal line represents release site longitude. i) Represents atypical salmon paths of only downstream movement before exit of SAS2 salmon. ii) Represents ideal salmon paths of upstream exploration and holding near presumed spawning grounds of SAS1 salmon.

3.4.4 RIVER EXIT

Overall, 47% of SAS salmon (20/43) exited the river, compared to 100% of wild salmon. On average, SAS salmon exited the river 76 ± 39 days after release, whereas wild salmon exited the river 130 ± 47 days after release. The linear regression revealed a significant effect of origin on river exit timing with wild salmon spending 54 days longer in the river than SAS salmon on average ($p < 0.001$, $SE = 14.2$). SAS salmon released in 2023 showed a broad range in migration timing, exiting the river between October 21, 2023 (2 days post-release), and February 11, 2024 (114 days post-release; Figure 11). The three SAS salmon released in 2024 that successfully exited the river left early between October 26, 2024 (10 days post-release) and November 27, 2024 (32 days post-release). In contrast, the majority of wild salmon in the Chéticamp River exited the river three months later and in a more narrow time window compared to SAS salmon who exited earlier and more evenly distributed throughout the winter and spring. All 17 wild salmon released into the Chéticamp River successfully exited the river with the majority (14/17, 82%) exiting within an 18-day period between April 27 and May 15, 2024 (139–157 days post-release). However, three wild salmon exited earlier, between late January and February 2024 (Figure 11).

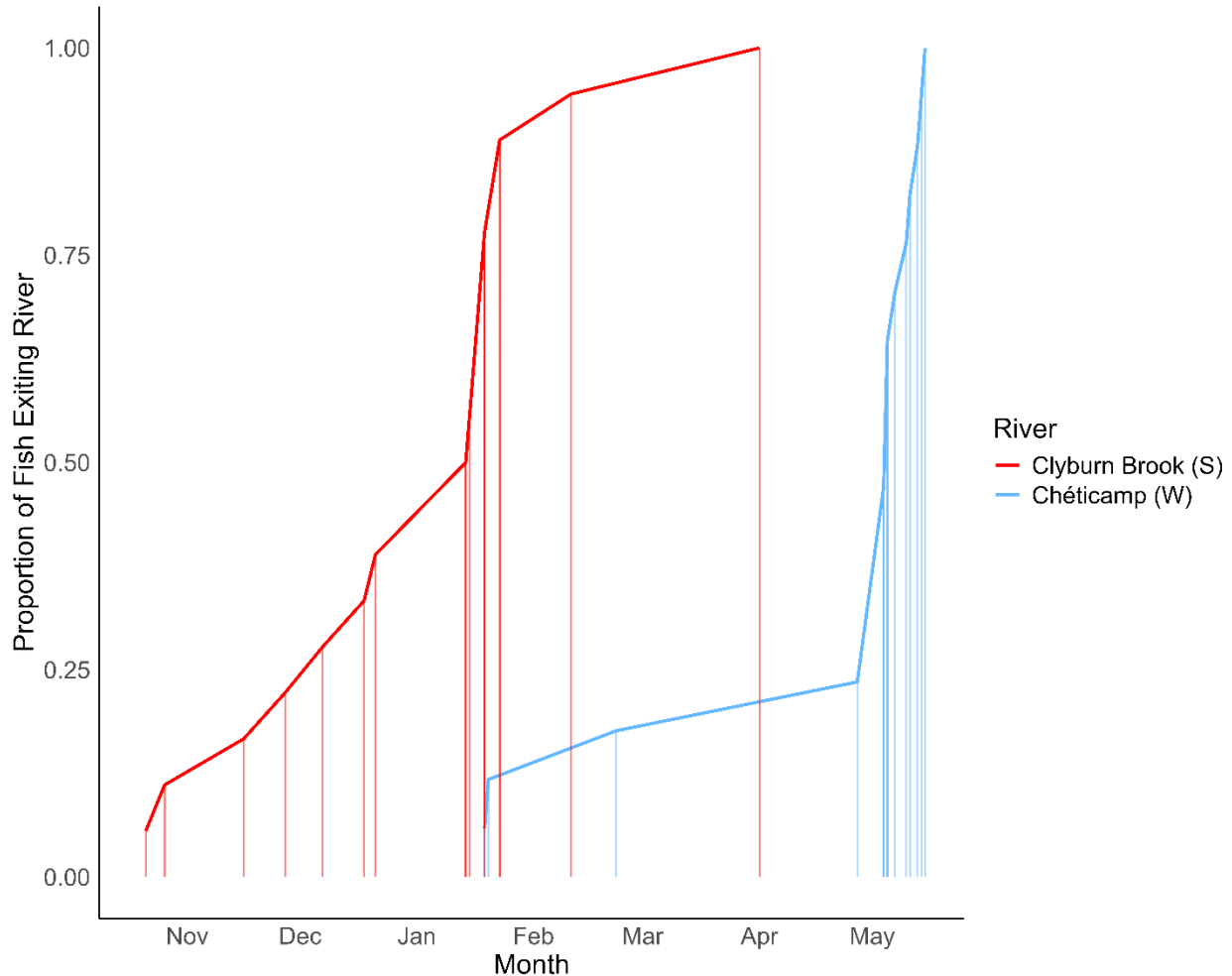


Figure 11. Cumulative proportion and timing of river exit for all SAS salmon (S) from Clyburn Brook (n=20; SAS1 n = 4, SAS2 n=16), wild salmon (W) from the Chéticamp River (n=17). Each step in the line represents an individual salmon exiting the river, resulting in an increase in the cumulative proportion of fish that have left. SAS salmon data from 2023 and 2024 were combined to highlight overall exit timing patterns, rather than interannual variation.

3.4.5 OCEAN DETECTIONS

Ocean detection data only includes the first cohort of SAS salmon (2023 release, SAS1 n=15, SAS2 n=15) and the wild Chéticamp River salmon (n=17) because the ocean arrays will not be downloaded again until end of summer 2025. After leaving their respective rivers, 12 SAS and 14 wild Atlantic salmon were detected on 10 marine acoustic receiver arrays between late October 2023 and mid-July 2024. More SAS2 (n=9) were detected in the ocean than SAS1 (n=3). SAS salmon were first detected earlier (October–November) than wild salmon (starting January). Most SAS detections were female (10 of 12), similar to the wild group (12 of 14).

SAS salmon showed limited ocean movement and did not follow the expected northerly migration route, instead mostly remained along the eastern shores of Cape Breton Island (Figure 12a). Notable detections included four SAS2 females at St. Anne's Bank Marine Protected Area (SABMPA; January–March), one SAS2 female off the southwestern shore of Newfoundland, and another near Halifax, Nova Scotia on the Halifax Line. Only three SAS salmon may have entered the Gulf of St. Lawrence, determined by a last detection at the Cabot Strait. One SAS female showed wide-ranging movement, including reaching Sable Island before reappearing at the Cabot Strait gate in June 2024 (Figure 12b). In contrast, wild salmon largely migrated north towards the Strait of Belle Isle (SOBI; Figure 12a). Wild salmon from the Chéticamp River were first detected at Cabot Strait in January, with detections increasing in May after the rest of the salmon exited the river. Three wild salmon were detected at SABMPA, and many moved into the Gulf of St. Lawrence, with detections around the Magdalen Islands and Anticosti Island. Detections at the SOBI receiver line were highly synchronized, with 79% (11 of 14 wild salmon detected at sea) detected there in a narrow time window, between June 8 and June 23. After passing the SOBI receiver line, seven wild salmon reached the coastal waters near southern Labrador, approximately 170 km from SOBI, between June 12 and June 28 2024. These detections located on the Labrador shelf represent the most northerly movements recorded in this study (Figure 12b).

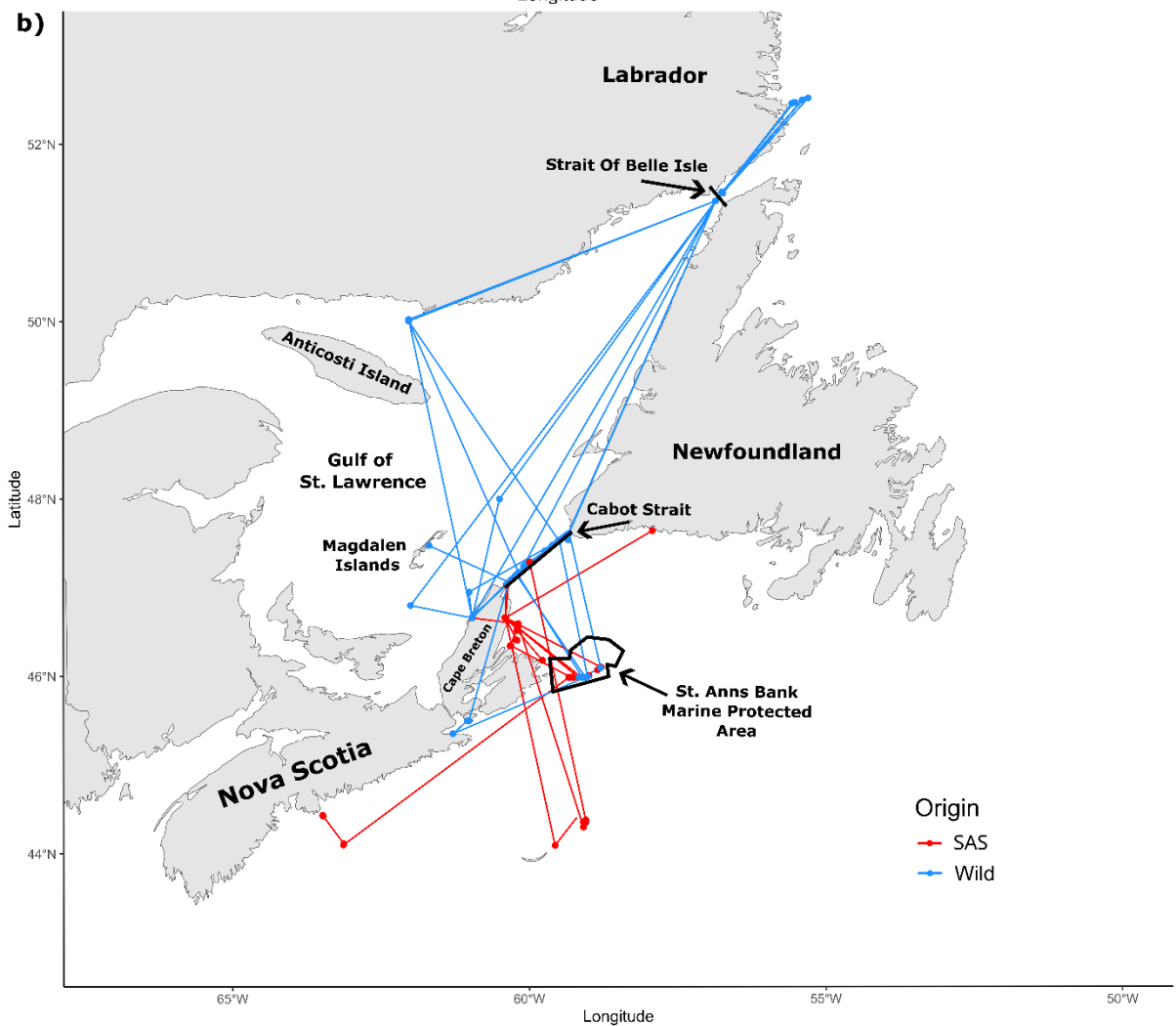
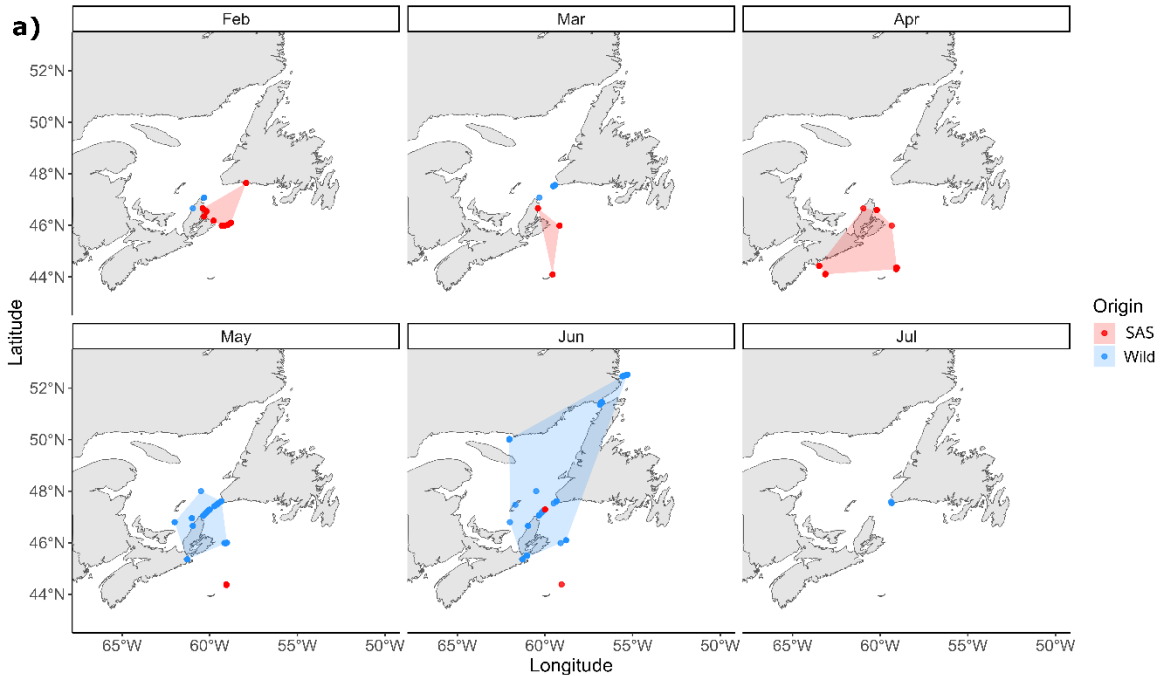


Figure 12. a) Map of individual detections in the ocean, faceted by most active months, of tagged Atlantic salmon from smolt-to-adult supplementation (SAS; n=12; red) and wild salmon (n=14; blue) origin. Origin ranges are represented by 100% minimum convex polygons. b) Ocean movements of tagged Supplementary (SAS; n=12; red) and wild (n=14; blue) Atlantic salmon. Lines represent individual movement paths between sequential detections, and points indicate detection locations.

3.5 DISCUSSION

This study evaluated the efficacy of a smolt-to-adult supplementation (SAS) conservation strategy by comparing survival, acceleration levels, freshwater movement, river exit timing, and ocean migrations of SAS Atlantic salmon to their wild counterparts in the Cape Breton Highlands, Nova Scotia. Acoustic tracking of adult SAS and wild Atlantic salmon revealed several important differences. Compared to wild salmon, SAS individuals: 1) experienced significantly reduced freshwater survival rates; 2) exhibited greater acceleration levels and more frequent high-speed bouts of activity; 3) displayed atypical river movement; 4) exited the river earlier and over a longer timeframe; and 5) diverged from expected ocean migration routes compared to wild fish. Importantly for the supplementation program, age at release was found to be an important factor influencing survival, river movement, and potential spawning ability of the SAS salmon. Together, these results suggest that there are behavioural consequences of captive-rearing Atlantic salmon from smolt-to-adulthood, with potential implications for both individual success and broader population recovery goals of the released fish.

Wild salmon from Chéticamp River had much higher freshwater survival than Clyburn Brook SAS salmon, with all wild individuals surviving the winter season, while 53% of the SAS salmon died post-release. The reduced freshwater survival of the SAS salmon aligns with prior studies showing that hatchery-reared salmon tend to have lower survival in natural environments due to captivity-induced effects (Carr et al., 2004, Christie et al., 2012; Jonsson et al., 1991; Jonsson et al., 2003). Carr et al. (2004) found a similar survival rate of 50% in adult Atlantic salmon that were raised from egg-to-smolt in facilities, and then smolt-to-adult in additional freshwater or saltwater pens. Although the salmon in that study were not wild-reared as juveniles like the SAS salmon in our study, their findings similarly suggested that adult Atlantic salmon with any history of captivity may have a reduced freshwater survival rate.

The increased mortality of SAS salmon compared to wild salmon likely reflects influences associated with their time in captivity. Although SAS salmon are initially wild-reared as juveniles and experience natural conditions, their extended period of one or two years in captivity during adulthood placed them in an artificial environment where they were sheltered from predators, provided with constant food, and held in simplified environments that removed natural selection pressures that would otherwise filter out individuals poorly suited to survival in the wild (Fleming, 1994). Captivity of fish can impair swimming ability and endurance due to limited physical activity (McDonald et al., 1998), and reduce predator awareness or responsiveness without exposure to natural threats (Salvanes & Braithwaite, 2006). Additionally, morphological traits like body colouration can change to match captivity conditions. Maynard et al. (2004) found that chinook salmon reared in tanks with seminatural habitat (such as gravel, structure, and cover) developed more cryptic colouration and had higher post-release survival compared to those raised in bare tanks, likely due to reduced visibility to predators. Similarly, during a post-release dive survey, SAS salmon in this study were noticeably paler, appearing light blue with distinct dark spots, in contrast to the darker, more camouflaged wild fish. This difference in coloration may have made SAS individuals more visible to avian and mammalian predators, contributing to their lower survival. Finally, stress is a well-documented consequence of captive rearing in fish (Bordeleau et al., 2018; Huntingford, 2004; Iversen et al., 1998; Näslund et al., 2013). For example, Bordeleau et al. (2018) found that adult Atlantic salmon held in captivity for just two months had significantly higher cortisol, and signs of altered immune function compared to wild-spawned counterparts. Given that SAS fish are held in captivity for at least a year, it is plausible that the cumulative stress burden is even greater. Cogliati et al. (2019) found that juvenile chinook salmon reared in a complex rearing environment had lower cortisol levels than those reared in empty tanks, indicating that tank structure complexity can affect stress levels, which may help explain lower survival in captivity-held fish. These compounded captivity-effects likely contribute to the higher post-release mortality observed in SAS salmon compared to wild salmon. To improve survival outcomes, management strategies should incorporate structural enrichment to retain natural, cryptic colouring and reduce stress levels in captivity-reared salmon.

Contrary to expectations, SAS2 salmon (reared ~29 months) had higher freshwater survival than SAS1 salmon (~17 months). These findings contradict previous studies that demonstrate the longer a fish spends in captivity the more its phenotype diverges from that of a wild fish and the

worse its performance in the wild is expected to be (Jonsson et al., 2003; Milot et al., 2013; O’Sullivan et al., 2020, Theriault et al., 2011). Although SAS2 salmon spent an additional year in captivity, their body size was not significantly larger than SAS1 salmon. Body size therefore is not likely a factor to explain why SAS2 salmon had greater survival than SAS1 salmon. A possible explanation for the higher survival of SAS2 fish may be linked to their observed conservative movement within the river. SAS2 salmon were more frequently detected downstream of the release site or exiting the river entirely compared to SAS1 salmon. This reduced exploration and greater downstream residency may have helped SAS2 salmon conserve energy, avoid risky or energetically costly habitats such as upstream movement, and thereby increase their chances of survival, however, it raises concerns about whether they attempted to spawn. Anadromous Atlantic salmon expend on average 59% of their total energy reserves during upstream migration and reproduction (Jonsson, 1997). This substantial energetic investment comes at a steep survival cost with typically less than 10% of adults surviving to breed a second time (Fleming & Reynolds, 2004). SAS2 salmon may have reduced their risk of exhaustion and death by not moving upstream, but in trade of limited spawning opportunity. In contrast, the majority of SAS1 salmon had greater upstream movement and those that died were often last detected in areas presumed to be spawning sites suggesting potential spawning activity. Thus, although more SAS1 fish died, likely from energy exhaustion related to upstream movement and reproduction, they may have contributed to population recruitment. Taken together, these observations raise a potential trade-off: the higher survival of SAS2 salmon may have come at the cost of lower reproductive output. In contrast, while SAS1 fish experienced higher in-river mortality, they may have at least attempted to spawn. Clarke et al. (2016) recommended minimizing time in captivity to increase post-release survival in Atlantic salmon juveniles. However, in the context of adult-rearing, extended captivity may improve survival, but potentially at the cost of reduced reproductive success. Managers aiming to boost population numbers using SAS must weigh the benefits of survival against the likelihood of successful spawning. If the ultimate goal of SAS is to increase natural recruitment, management of captivity duration may need to optimize both survival and reproductive output, possibly by refining rearing practices to retain natural spawning behaviours in longer-reared fish.

Irrespective of age, SAS salmon showed significantly greater acceleration values and more frequent high-speed bursts of activity compared to wild salmon. To our knowledge, no previous study has compared the in-situ acceleration levels of supplemented and wild adult Atlantic salmon.

However, the greater acceleration values of SAS salmon may reflect the erratic and inefficient movement behaviours often observed in captive Atlantic salmon (Iversen et al., 1998; Jonsson et al., 1991; Nilsen et al., 2023; Power & McCleave, 1980). In captivity-reared Florida bass (*Micropterus salmoides*), Garlock et al. (2014) found increased metabolic rates and significantly more activity than findings for wild bass, with a negative correlation between activity and survival. Elevated acceleration levels may reflect physiological effects of captivity (e.g., heightened stress or metabolic demands) as well as behavioural effects, such as frequent burst swimming and inefficient movement. Stress is a well-known carry-over effect from captivity in fish (Iversen et al., 1998; Rosengren et al., 2017; Zarate & Bradley, 2003). A study from a nearby river system in Cape Breton, Bordeleau et al. (2018) compared the movement and physiology of wild-origin adult salmon collected as broodstock for a traditional hatchery supplementation program (spending two months in captivity) with that of wild-spawned kelts. Physiologically, adults held in captivity for just two months showed significantly higher stress levels (measured by cortisol and glucose) and signs of altered immune function compared to wild-spawned kelts. These findings suggest that even short-term captivity can cause substantial physiological changes, and that longer captivity periods, like those experienced by SAS fish, may lead to even greater stress-related effects after release. The increased acceleration levels observed in SAS salmon in our study may therefore reflect a heightened stress response which could lead to energetically inefficient movement such as more frequent high-speed bursts.

Another possible explanation for the elevated acceleration observed in SAS salmon compared to wild salmon is their captive feeding regime. Wild Atlantic salmon typically cease feeding upon entering freshwater and rely on somatic energy reserves accumulated during their time at sea (Kadri et al., 1995; Rubenstein et al., 2023). Hedger et al. (2022) found that 58% of wild adult Atlantic salmon returning to spawn had empty stomachs, and those with stomach contents had only heavily digested fish. In contrast to wild salmon, SAS salmon enter the river immediately after a period of controlled, high-nutrition feeding designed to promote growth. This sustained feeding likely results in increased energy reserves, particularly in the form of lipids, as commonly observed in hatchery fish (McDonald et al., 1998; Larsson et al., 2012; Eriksson et al., 2008). These greater energy stores may contribute to the increased acceleration and erratic movements observed in SAS salmon after release. Additionally, the SAS feeding regime may sustain a heightened metabolic state in SAS salmon, increasing the risk of energy depletion once

released back in the river, particularly during periods of low food availability like winter (Berg & Bremset, 1998; Murphy et al., 2006; Pickering & Pottinger, 1988). The risk of energy depletion may be additionally compounded by the reduced foraging efficiency typical of hatchery fish (Brown & Day, 2002; Jonsson et al., 1991; Larsson et al., 2012; Olla et al., 1998), increasing the likelihood of energetic shortfalls and reduced survival on release. These findings have important implications for SAS program management. Erratic movement may increase energy expenditure, potentially limiting reproduction, post-spawning survival, and competitive success at spawning sites (Thorstad et al., 2008). Thus, the increased acceleration levels and potentially inefficient energy use observed in SAS salmon could negatively affect survival and spawning success. To address this, management should gradually wean SAS salmon off their feed in the months before release to better mimic the fasting state of wild salmon before freshwater entry. Larsson et al. (2012) found that captively-reared brown trout smolts starved before release, and therefore carrying fewer lipid reserves, had comparable emigration success to the sea as wild smolts. Limiting food intake before release may help reduce metabolic rates and align post-release behaviour and energy expenditure more closely with that of wild salmon. Future research should combine physiological data such as stress levels (e.g., cortisol) and energy reserves with behavioural tracking using acoustic tags equipped with accelerometers (see Birnie-Gauvin et al., 2019; Bordeleau et al., 2018; Cooke et al., 2005) to better understand how captivity-induced physiological changes translate into behavioural patterns and survival outcomes after release.

Distinct differences were observed in river movement between SAS and wild salmon. Wild salmon exhibited minimal movement, did not move upstream, and the majority overwintered in a tidally influenced pool which is consistent with previously documented movement behaviour of post-spawned adults (Aarestrup et al., 2000; Fleming, 1996). The majority of SAS1 salmon displayed expected freshwater migration of a pre-spawned adult by traveling upstream with subsequent detections at multiple receiver locations near presumed spawning grounds. This behaviour may represent the typical “search phase” of a spawning Atlantic salmon observed in some studies (Finstad et al., 2005; ØKlamd et al., 2001) where individuals are potentially selecting a spawning area or orienting themselves to return to their natal area within the river system (Thorstad et al., 2008), suggesting potential spawning activity. In contrast, a minority SAS2 salmon were detected upstream and exhibited typical searching behavior with the majority remaining near the release site or moving between downstream receivers. This pattern may reflect

challenges in locating spawning grounds and readjusting to the river environment that could be energetically costly and negatively affect individual survival (Aarestrup et al., 2000; Fleming, 1996; Thorstad et al., 2008; Weir et al., 2004). Atypical river movement of SAS2 salmon mirrors findings from other studies suggesting longer captivity disrupts river familiarity, movement, and homing (Carr et al., 2004; Jonsson, 1997; Nilsen et al., 2023). To help mitigate these behavioural differences, Thorstad et al. (2008) recommended releasing supplemented salmon at multiple locations along the spawning grounds rather than at a single downstream site, in order to reduce the energetic costs and navigational challenges associated with an extended upstream migration. However, other studies have shown that captive-reared salmon released far downstream or at the river mouth may travel further upstream than if they were released closer to the spawning grounds (Dempson et al., 1999; Jokikokko, 2002; Jonsson et al., 1991; McKinnell et al., 1994; Power & McCleave, 1980). In contrast, salmon released further upstream in areas deemed suitable for spawning have been observed returning to the release site (Power & McCleave, 1980; Rivinoja et al., 2001). In future studies and releases of SAS salmon, two groups could be released at different areas along the river such as at the mouth (which may prompt typical upstream migration spawning behaviour) or along multiple spawning areas to determine which method leads to the most salmon displaying typical spawning riverine movement and behaviour.

River exit timing differed markedly between SAS and wild salmon with SAS salmon prematurely leaving the river and across a broader timeframe compared to the expected exit timing and synchrony of the wild salmon. Most wild salmon left the river within two weeks of each other between late April and mid-May, aligning with natural migration timing observed in other Cape Breton rivers (Bardonnet & Bagliniere, 2000; Bordeleau et al., 2018; Grey, 1984), while the majority of SAS salmon exited the river before January, which is a common observation for captive-held salmon (Bordeleau et al., 2018; Jonsson et al., 1991; Midwood et al., 2015). For example, Bordeleau et al. (2018) found that hatchery-spawned kelts held in captivity for just two months exited the river 66 days earlier than wild-spawned kelts and had lower estuarine survival, with elevated cortisol levels suggesting that even short-term captivity-induced stress can alter migration behaviour. Additionally, Birnie-Gauvin et al. (2019) found that Atlantic salmon and brown trout with higher cortisol levels left the river earlier and had reduced success of reaching the ocean. Our findings align with this pattern, as the broad and premature river exit of SAS salmon contrasts with the synchronized migration of wild salmon, likely guided by environmental cues

such as temperature and flow. Thus, the observed premature river exit of SAS salmon may be partly explained from stress-induced effects of captivity during smolt-to-adulthood disrupting how they respond to environmental cues and coordinate migration timing. In addition to stress, other studies have shown that increased energetic demands resulting from captivity and controlled feeding regimes likely contribute to the premature river exit observed in supplemented salmon (Larsson et al., 2012; Midwood et al., 2015). Once released, SAS salmon likely had difficulty adapting from regular feeding in captivity to the variable and often scarce food availability in the river overwinter, causing them to leave earlier in search of suitable habitats (Halttunen et al., 2013). The stress of handling and captivity in addition to the change of feeding regimes once released back into the wild river environment are likely large drivers of SAS salmon prematurely exiting the river. As discussed earlier, future studies could link physiological measurements such as energy stores and metabolism with behavioural tracking methods to better understand what is driving SAS salmon to exhibit different overwintering patterns than their wild counterparts. Decreasing captivity stress, and weaning SAS salmon off their high-caloric feeding regime a month before release may result in more similar river exit timing as wild salmon.

A full year of ocean detection data revealed minimal spatial and temporal overlap between SAS and wild salmon, despite both groups being expected to follow the same migration path (Bordeleau et al., 2018; ESRF, 2023). Wild salmon followed expected migratory routes through the Gulf of St. Lawrence and SOBI toward known feeding areas in the Labrador Sea, consistent with previous studies (ESRF, 2023; Ritter, 1997). In contrast, SAS individuals remained nearshore along the Atlantic coast, particularly near the Cabot Strait and SABMPA. These observations of SAS salmon straying from expected ocean migration routes is consistent with observations of altered migratory behaviour in captive-reared salmon (Bordeleau et al. 2018; Hansen et al., 1984; Jonsson, 1997; Jonsson & Fleming, 1993). Bordeleau et al. (2018) tracked wild and hatchery-spawned kelts that spent two months in captivity from two nearby Cape Breton rivers (Middle and Baddeck Rivers) during their ocean migrations. Wild kelts entered the Gulf of St. Lawrence and many exited through the SOBI receiver line, comparable to wild kelts in our study. In contrast, hatchery-spawned kelts were not detected at SOBI and none returned to spawn again, whereas 10% of wild kelts returned to spawn two years later (Bordeleau et al., 2018). While SAS salmon in our study spent their juvenile stages in the wild (unlike traditional hatchery fish), the adult rearing period in captivity may still have disrupted internal cues required for long-distance

orientation and navigation, a risk identified in DFO, 2016. Because smolt-to-adult survival is much higher using a SAS program compared to wild salmon (Dempson et al., 1999; Fraser, 2016), there is likely a relaxation of selective pressures with regard to marine predation, immunity (marine pathogens and parasite resistance), and navigation (Fraser, 2016). Hansen et al. (1994) proposed that captive-reared salmon retain only a general sense of direction and lack specific homing ability without prior adult river experience, perhaps it is the same while leaving the river for SAS adults; SAS adults have reduced capacity when they leave the river to navigate their ocean migration having now lacked their first marine phase by being raised in SAS captivity. There was some overlap between SAS and wild salmon at Cabot Strait and SABMPA, suggesting that SAS salmon may retain a degree of directional orientation. Multiple salmon populations clearly traverse this region with SABMPA likely being an important foraging ground, especially since wild Chéticamp River salmon were observed migrating to SABMPA, adding hundreds of kilometers to their migration before travelling north through SOBI. Jonsson & Fleming (1993) found that hatchery smolts migrated to the same feeding area of wild salmon. However, the lack of returns among this study's SAS salmon released in 2023 raises concerns about their ability to return to natal rivers for a repeat spawn or first time spawning event if they exited without spawning post-release.

Due to the critically low adult returns and conservation status of salmon in Clyburn Brook, wild fish were unavailable for tagging in this river. As a result, we used wild kelts from a nearby river as a reference group to assess survival and behavioural differences. However, these wild salmon were tagged after spawning, meaning they had already survived upstream migration and spawning stress, potentially biasing survival estimates by excluding individuals that died earlier in the season. Differences in tagging timing may also explain some of the behavioural differences observed, such as acceleration levels and river movement. Wild salmon, tagged after the energetically costly spawning period, likely exhibited lower activity relative to SAS salmon tagged beforehand. Thus, our comparisons are confounded by differences in both river systems and tagging times, and future studies should tag wild and SAS salmon at the same life stage and in the same river to obtain more accurate and meaningful comparisons that can better inform conservation and management efforts.

3.6 CONCLUSION

This study offers new insights to the post-release behaviour of adult Atlantic salmon reared under smolt-to-adult supplementation (SAS) strategies. The results revealed clear survival and behavioural differences between SAS and wild salmon, with SAS salmon experiencing lower freshwater survival, higher acceleration levels, atypical river movement, earlier and more variable river exit timing, and divergent ocean migration routes. Notably, captivity duration was an important factor. SAS salmon that spent a year longer in captivity showed higher survival but exhibited more atypical river movements, which may have reduced their spawning success. In contrast, SAS salmon with shorter captivity duration had higher mortality, but near presumed spawning grounds, suggesting they engaged in at least some reproductive activity. Our findings demonstrate the importance of likely captivity-induced carryover effects on post-release survival and behaviour. Elevated acceleration levels in SAS salmon likely reflect heightened stress and metabolic demands due to captivity conditions, feeding regimes, and handling. These physiological effects could be associated with the observed erratic movement, premature river exit, and reduced fitness in the wild. Such behavioural divergence suggests that smolt-to-adult captivity potentially alters both internal physiological states and environmental responsiveness, contributing to the observed differences in survival and migration behaviour between SAS and wild fish, warranting further investigation into the underlying mechanisms. The use of wild salmon comparators from a different river system and as post-spawners should be considered when interpreting survival, acceleration levels, and river movement as both factors may have influenced the observed outcomes.

To improve the effectiveness of SAS as a conservation method, management strategies should focus on reducing stress and metabolic elevation prior to release by minimizing captivity duration to only one year, as long as the salmon are deemed sexually mature, adding natural structure to captivity tanks, and gradually decreasing feeding in the weeks leading up to release which may better replicate the fasting state of wild salmon. In addition, different release strategies, such as staggered along spawning grounds or at the river mouth, may help reinforce natural homing and improve reproductive opportunities. Lastly, combining physiological sampling such as stress indicators, body condition, and metabolic rate with behavioural tracking in future SAS evaluations is important not only for attaining a closer post-release comparison with wild salmon, but also for evaluating and improving the efficacy of these costly conservation programs. Overall, these results

indicate that SAS success depends on mitigating the behavioural and potential physiological consequences of captivity. Effective SAS management must balance maximizing survival and retaining behaviours essential for surviving and spawning in the wild.

CHAPTER 4: GENERAL DISCUSSION

4.1 EVALUATION AND IMPLICATIONS

This thesis evaluated the efficacy of captive-rearing as a conservation tool for Atlantic salmon by comparing the survival, movement, and migration of hatchery-reared fish to their wild counterparts at two critical life stages: traditional hatchery-reared smolts during freshwater outmigration and adults reared in captivity from smolt to maturity (SAS). Across both studies, captivity was consistently associated with reduced post-release survival relative to wild salmon. Hatchery-reared smolts in the LaHave River experienced higher predation risk and slower migration speeds in the upper river and lake habitats, although the timing of river exit and early ocean migration patterns were similar to those of wild smolts. By comparison, over half of SAS adult salmon displayed atypical movement behaviours, including premature river exit and divergent marine migration routes compared to wild adults. Together, these findings demonstrate that, despite the potential of supplementation programs to increase population numbers, the long-term success of such efforts is constrained by captivity-induced behavioural changes that reduce post-release performance and challenge the recovery of wild Atlantic salmon populations.

We found significantly greater mortality in supplemented salmon compared to wild salmon whether they were released as outmigrating smolts through a traditional captive-rearing program or as mature adults through a SAS program. Overall freshwater survival for hatchery smolts was 67.6%, meaning that one-third of released individuals were lost before ocean entry. These results are consistent with previous research demonstrating that hatchery smolts experience much higher mortality than wild smolts upon release (Hyvärinen & Rodewald., 2013; Jonsson et al. 2003; Jokikokko 2006; Larsson et al., 2012; Melnychuk et al., 2014; Saloniemi et al., 2004). Hatchery smolt mortality in the LaHave River was largely due to predation, with 75% of mortalities confirmed as predation events. The spatial distribution of these mortalities, which were concentrated in the upper reaches of the river and in Wentzell's Lake, aligned with previous reports identifying these areas as predation hotspots (Feener, 2017). High predation of hatchery smolts in this study is similar to previous study findings that hatchery smolts face greater predation risk than wild-reared fish (Braithwaite & Salvanes, 2005; Jonsson et al., 2003; Jokikokko, 2006; Larsson et al., 2012; Melnychuk et al., 2014). Captive-reared smolts often show poor antipredator behaviour, which increases their risk of mortality via predation post-release (Olla et al., 1998). Behavioural

anti-predator deficiencies can include more frequent surface feeding (Vincent, 1960), slower or weaker escape responses (Woodward & Strange, 1987), greater movement and a faster return to feeding after exposure to predation alarm cues (Fleming & Einum, 1997; Jackson & Brown, 2011), and a failure to avoid predators altogether (Jonsson et al., 1996). In natural environments, wild smolts are exposed to predators across several years, and individuals with more risky behaviour are more likely to be selected against by predation (Jonsson & Jonsson, 2014). In contrast, hatchery smolts are raised in safe, predictable environments without predators, so individuals with risky behaviour do not experience intense selective pressure demonstrated in the wild (Fleming & Petersson, 2001; Jackson & Brown, 2011). Additionally, hatchery fish may also fail to recognize predators after release having no prior exposure. Lack of wild experience and learned environmental cues, coupled with the stress of transitioning to the natural environment, likely elevate hatchery smolt predation risk. The vulnerable effects of captivity are further amplified by the increasing presence of invasive predators in Nova Scotia such as Chain pickerel and Smallmouth bass, which are both established throughout the LaHave watershed (Feener, 2017; DFO, 2024; Mensinger et al., 2025). Feener (2017) provided stomach analysis evidence of salmon smolts as the dominant prey in Chain pickerel diets from Wentzell's Lake, matching the locations of high mortality observed in our study. Our findings align with previous research that traditional hatchery practices may not effectively prepare juvenile salmon for the predation pressures they will face in the natural environment, thereby decreasing their chances of survival and reaching the sea.

Similar patterns of reduced survival following release were observed among released SAS adults highlighting the broader impacts of captive rearing across life stages. SAS salmon released into Clyburn Brook in the Cape Breton Highlands exhibited substantially lower survival relative to wild conspecifics with 51% of SAS salmon assumed dead before leaving freshwater compared to 100% survival for wild adults. The low mortality patterns observed in SAS adults are consistent with widespread evidence that captively held and reared fish typically have greater mortality once released in natural environments compared to wild fish because of captivity-induced deficits (Carr et al., 2004, Christie et al., 2012; Jonsson et al., 1991; Jonsson et al., 2003). The reduced freshwater survival of SAS salmon compared to wild salmon likely reflects the cumulative effects of captivity on the life skills of the SAS fish. Although SAS salmon fulfilled their juvenile years in the wild river setting, the 1-2 years they spent in artificial environments during adulthood sheltered them

from predators, provided them with an abundance of food, and held them in simplified environments that removed natural selection pressures that would otherwise have filtered out individuals poorly suited to survival in the wild (Jonsson & Fleming, 1993). Captivity can impair swimming performance (McDonald et al., 1997), reduce predator responsiveness, and alter morphology of salmonids (Braithwaite & Salvanes, 2005; Maynard et al., 2004). Beyond these behavioural and morphological effects, extended periods in captivity may impose physiological impairments like chronic stress (Jonsson & Jonsson, 2006; Näslund et al., 2013), with studies reporting elevated cortisol and immune dysfunction even after short periods of captivity (Bordeleau et al., 2018). Given SAS fish were held for over a year, these effects are likely amplified. Elevated stress from the captive environment, handling, and transport may have compounded these captive factors, increasing SAS vulnerability in the wild and reducing fitness.

Notably, variation in captivity duration added further complexity to survival outcomes among SAS salmon. Contrary to expectations based on previous work demonstrating longer captivity may lead to greater maladaptive divergence and worse survival outcomes (Christie et al., 2009; Jonsson et al., 2003; Milot et al., 2018; O'Sullivan et al., 2020, Theriault et al., 2011), SAS2 salmon (captively held for 29 months) had higher freshwater survival post-release than SAS1 salmon (captively held for 17 months). However, SAS2 individuals were observed to either exit the river shortly after release or remain in downstream areas below the release point. The limited upstream movement and exploration of SAS2 salmon likely helped conserve energy and thereby increase survival by avoiding energy costly behaviours such as swimming upstream and spawning activities. Anadromous Atlantic salmon invest substantial energy (on average 59% of their energy reserves) for upstream migration and spawning which results in fewer than 10% of adults surviving to repeat spawn (Fleming & Reynolds, 2004; Jonsson, 1997). Thus, although SAS2 had greater survival due to conservative movement patterns, this behaviour reduces the likelihood that they successfully spawned, as reduced upstream movement and less time spent in the river would constrain opportunities to locate and use suitable spawning habitat. A possible explanation for this limited movement is impaired river familiarity or a loss of homing ability, likely resulting from extended time spent in captivity (Carr et al., 2004; Jonsson, 1997; Nilsen et al., 2023). In contrast SAS1 salmon exhibited greater upstream movement and those that died were often last detected in areas presumed to be spawning sites. While this observed upstream movement and holding from SAS1 salmon suggests potential spawning activity, it also likely contributed to their elevated

mortality due to spawning being energetically costly (Jonsson et al., 1997). These observations seem to present a trade-off between survival and reproductive behaviour in SAS adults. While prolonged captivity may result in higher freshwater survival, it may simultaneously reduce the likelihood of spawning participation, which is a challenge for program managers aiming to maximize both survival and reproductive contribution. Considering such behavioural trade-offs in supplementation programs is critical to achieving recovery goals.

Across both supplementation approaches, captivity also altered salmon behaviour and movement after release. Although these effects manifested differently between hatchery-reared smolts and SAS adults, both groups displayed behaviours that likely compromised their ability to navigate in the wild environment. Overall river exit timing was similar between wild and hatchery smolts in the LaHave River with wild smolts migrating significantly faster and therefore more efficiently through specific river habitats, specifically in the upper river, Wentzell's Lake, and lower river. Section-specific differences between wild and hatchery smolts are likely explained by reduced swimming ability and disorientation to their novel wild environment caused by limited exposure to variable flow regimes, physical exercise, and natal river cues during rearing (Gale et al., 2004; Olla et al., 1998; Pedersen et al., 2008). The slower movements of hatchery smolts likely increased their vulnerability to predation, particularly in Wentzell's Lake, where predators are more abundant and shelter is limited. Prolonged residence in such areas, combined with likely poorer antipredator responses (Jonsson et al., 1996; Jackson & Brown, 2011), may have driven the high predation rates observed during migration.

Behavioural and potential physiological consequences of captivity on movement were also evident in SAS adults in the Clyburn Brook. SAS salmon exhibited significantly greater acceleration values and more frequent high-speed bursts compared to wild adults, likely reflecting the inefficient and erratic movement commonly documented in captive-reared fish (Jonsson et al., 1991; Nilsen et al., 2023; Power & McCleave, 1980). Similar patterns have been observed in other species, such as captively-reared Florida bass (*Micropterus salmoides*), where elevated acceleration levels were associated with higher metabolic rates and reduced survival post-release (Garlock et al., 2014). These high acceleration values observed in SAS salmon may partly reflect stress-related physiological changes, as captivity has been shown to elevate cortisol in salmonids (Bordeleau et al., 2018; Jonsson & Jonsson, 2006; Näslund et al., 2013). Another contributing factor may be the feeding regime of SAS salmon while held in captivity. Unlike wild salmon,

which typically cease feeding upon entering freshwater and rely on stored somatic energy reserves (Kadri et al., 1995; Rubenstein et al., 2022), SAS salmon enter the river shortly after a prolonged period of controlled, high-nutrition feeding. This sustained feeding likely increases lipid stores (Erikson et al., 2008; Larsson et al., 2011; McDonald et al., 1997), which may explain the heightened energy expenditure observed through increased acceleration and erratic movements. However, the SAS salmon's artificially elevated metabolic state may not be sustainable after release, especially when food availability is low during overwintering periods (Berg & Bremset, 1998; Murphy et al., 2006; Pickering & Pottinger, 1988). Increased energetic demands, combined with low food availability and potentially lower foraging efficiency typical of captive-reared salmon due to little experience of natural prey in holding tanks (Brown et al., 2003; Jonsson et al., 1991; Larsson et al., 2011), may increase the risk of energy depletion and mortality. Additionally, the broad and premature river exit of SAS salmon further supports the role of captivity-induced stress and negative energetic consequences in disrupting migration timing. While wild salmon left the river within a narrow, seasonally appropriate window, SAS salmon exited prematurely and across a much broader timeframe. Bordeleau et al. (2018) found that hatchery-spawned kelts held for just two months exited 66 days earlier than wild fish, supporting the idea that stress, disrupted environmental cues, and energetic imbalances contribute to these atypical patterns. Premature exit may also reflect difficulty adjusting to low overwinter food availability (Halttunen et al., 2013) and reduced responsiveness to environmental cues (Birnie-Gauvin et al., 2019).

While the patterns of mortality and movement varied between life stages and supplementation approaches, the overarching outcome remains similar: captivity produces salmon that are behaviourally unprepared for survival in wild environments. Our findings underscore the critical need for management strategies that move beyond a focus on releasing greater numbers of fish via artificial rearing. For hatchery smolts, several management interventions have been suggested by previous research such as predator cue conditioning. Vilhunen (2006) showed that hatchery-reared Arctic charr conditioned to recognize predator odours survived longer when exposed to real predators than untrained fish. Similar techniques, using predator odours or visual cues (e.g., chain pickerel in the LaHave River), could help prepare hatchery salmon when faced with a predator after release. Rearing environment enrichment is another potential improvement. Hyvärinen & Rodewald (2013) found that smolts raised in enriched tanks with structure and variable flow were twice as likely to survive outmigration compared to those from bare tanks.

Predation risk is further increased when smolts pass through lakes, which often lack shelter, have slower flow which can impact migration, and contain more predators (Hansen et al., 1984; Kennedy et al., 2018; Schwinn et al., 2019). For example, Hanssen et al. (2021) reported that 60% of tagged smolts died in lakes, with at least half of those deaths attributed to predation. Thus, hatcheries could release smolts downstream of high-risk areas like lakes to reduce these losses. For SAS programs, greater attention should be given to optimizing the duration of captivity to balance survival benefits with potential losses in reproductive success. One possible strategy is to rear SAS salmon for only one year in captivity to increase spawning potential, while releasing them closer to spawning grounds to reduce energetic costs and potentially improve post-spawn survival. Additionally, hatchery enrichment techniques, such as adding structure to rearing tanks to retain natural, cryptic colouring and reduce stress levels (Maynard et al., 2004; Näslund et al., 2013) may help mitigate some of the maladaptive traits that emerge in captivity. Cogliati et al. (2019) found that juvenile chinook salmon reared in a complex rearing environment had lower cortisol levels than those reared in empty tanks, indicating that tank structure complexity can affect stress levels, which may help explain lower survival in captively-held fish. Finally, releasing SAS salmon at multiple river locations could reduce navigational challenges and energetic costs associated with finding spawning grounds. Thorstad et al. (2008) specifically recommended staggered release points for this reason, while Rivinoja et al. (2001) found that salmon released closer to suitable spawning areas often returned to the release site, emphasizing the importance of release-site selection. Without focused efforts to improve these outcomes, supplementation programs risk failing to meet their conservation objectives despite significant investments of time, effort, and resources.

Marine migration patterns differed between supplementation methods. Hatchery-reared smolts had similar spatial and temporal overlap during early marine migration following the same migration route as wild smolts. Both smolt origins were detected migrating along Nova Scotia's southern coast, including the Halifax Line, before moving offshore near Sable Island, aligning with known migration routes toward eastern Newfoundland and the Labrador Sea (ESRF, 2021; Reddin & Lear, 1990). Similar migration overlap between wild and hatchery-reared smolts has been reported previously (Jonsson et al., 1993), indicating that traditional hatchery rearing may not impair large-scale marine orientation in the same way adult SAS captivity does. In contrast, SAS adults exhibited unexpected marine movements that raise concerns for their long-term survival,

repeat spawning chances, and migration ability. We found minimal ocean detection overlap between SAS and wild adults despite both groups being expected to follow similar migratory paths (Bordeleau et al., 2018; ESRF, 2021). Wild salmon migrated through the Gulf of St. Lawrence and the Strait of Belle Isle (SOBI) toward known feeding grounds in the Labrador Sea (ESRF, 2021; Ritter, 1989). In contrast, SAS individuals did not migrate far after exiting freshwater, remaining along Cape Breton's Atlantic coast, particularly near Cabot Strait and the St. Anns Bank Marine Protected Area (SABMPA). The altered migration routes of SAS salmon are consistent with previous studies on captive-reared salmon (Bordeleau et al., 2018; Hansen et al., 1987; Jonsson et al., 1993). For example, Bordeleau et al. (2018) tracked hatchery-spawned kelts from Cape Breton rivers that failed to enter the Gulf of St. Lawrence, unlike wild kelts, and none returned to spawn, while 10% of wild kelts successfully returned two years later. The extended period of captivity and artificially high survival rates during SAS rearing may relax natural selective pressures for traits such as marine navigation and limit exposure to learned environmental cues essential for successful long-distance marine migration (DFO, 2016; Hansen et al., 1993). While detections of SAS salmon at Cabot Strait and SABMPA may suggest a partial retention of directional ability as wild salmon were also detected in these areas, their absence from key foraging grounds and migration points (i.e., the Gulf of St. Lawrence, SOBI), and lack of returns in 2024 raise clear concerns about their capacity for successful ocean navigation and homing.

Improving marine migration outcomes for SAS salmon will require targeted changes to rearing practices and further research. One possibility is transitioning SAS rearing to saltwater or brackish environments. Exposure to marine conditions before release may promote physiological adaptations and environmental imprinting necessary for successful marine navigation (DFO, 2016; Jonsson et al., 1993). While this study did not track successful returnees, emerging evidence suggests potential benefits. For example, Fundy National Park in has been undertaking a SAS program for an endangered inner Bay of Fundy Atlantic salmon population, where smolts are raised to adults in sea-cages. The park has reported some supplemented salmon successfully returning from marine migration. Although we do not know whether these individuals followed the same expected marine migration routes as wild salmon since they were not tracked, their successful returns highlight that modifications to rearing or release strategies could improve marine migration outcomes (Maysonet & Murphy, n.d.). For hatchery smolts, Thorstad et al. (2012) found that early marine survival was higher in smolts released at the river mouth compared

to those released further upstream. This supports the suggestions that management could improve survival by releasing hatchery smolts lower in the river. Doing so may help avoid freshwater mortality hotspots, such as Wentzell's Lake, and potentially further improve early marine survival.

Supplementation has the potential to support salmon recovery, but its effectiveness depends on how well practices are tailored to promote survival and integration with wild populations. Future research should investigate whether exposing SAS salmon to natural environmental cues during rearing, such as tidal cycles, salinity gradients, or estuarine chemical signatures, can promote more typical marine orientation and help SAS salmon better integrate with wild populations en route to established feeding grounds (Carr et al., 2004; Hansen et al., 1993). Using longer-term acoustic transmitters will be essential to evaluate whether these interventions improve marine migration success and return rates. Coded transmitters with customized transmission schedules, such as those piloted by Kennedy et al. (2023), offer a promising solution for long-term tracking, enabling detection of both the smolt's initial seaward migration and their potential return as adults over a year later. Without targeted improvements, SAS salmon may continue to face challenges during the marine phase, reducing their effectiveness in contributing to population recovery despite the significant logistical investment involved in these programs. For hatchery-reared smolts, although hatchery and wild smolts exhibited overlapping distributions during the first month of their marine migration, a limitation of this study is the lack of tracking data beyond this period, leaving the subsequent stages of their oceanic movements and survival unknown. Long-term marine survival and return rates also remain unknown, due in part to limited tag battery life. Future studies should consider using tags with longer battery life to track smolt movements beyond the Nova Scotia coast because it would help determine whether hatchery smolts successfully reach key areas along their marine migration such as Newfoundland's Grand Bank or the Labrador Sea. Smolts could also be double-tagged with passive integrated transponder (PIT) tags or physical tags (e.g., Floy tags) to monitor the return rates for hatchery and wild smolts. If returning smolts could be recaptured and measured, researchers could also gain valuable insights into growth rates and identify successful marine feeding grounds (Jensen et al., 2012; Thomas et al., 2019).

4.2 CONCLUSION

Overall, this thesis highlights the complex challenges of using captive-rearing to support Atlantic salmon recovery in Nova Scotia. While supplementation programs aim to bolster population numbers, these efforts will remain limited in effectiveness unless post-release survival, behaviour, and recruitment are strategically improved. Across both supplementations studied here, traditional hatchery-reared smolts and smolt-to-adult supplementation (SAS), captivity imposed maladaptive behavioural and likely physiological effects that reduced fitness in the natural environment relative to wild salmon. Critically, the factors driving post-release mortality differed between life stages, demonstrating that a singular management approach is unlikely to succeed. Instead, supplementation programs must be tailored to the specific challenges associated with the river and salmon life-stage. For hatchery-reared smolts, the primary threat to survival was predation, particularly in lentic areas like Wentzell's Lake. Future management should focus on enriching rearing environments to promote stronger swimming ability and predator responsiveness, incorporating predator conditioning prior to release to reduce predation risk, and releasing smolts downstream of known predation hotspots. Additionally, extending post-release tracking using longer-life acoustic tags, PIT tags, or Floy tags would provide critical data on marine survival, return rates, and key feeding grounds, helping to refine management practices further. For SAS adults, improving post-release success will require targeted changes to rearing and release practices. While longer periods in captivity appeared to enhance short-term freshwater survival, these conditions may have simultaneously reduced reproductive contribution, thereby undermining the primary objective of the program to increase population numbers through successful spawning post-release. Potential solutions include reducing captivity duration as long as individuals are sexually mature to ensure spawning is possible, gradually reducing feeding prior to release to better align metabolic demands with wild salmon, spatially staggering release sites to reduce energetic costs and navigational issues of searching for spawning grounds, and experimenting with marine-based rearing environments. Future research should combine behavioural monitoring, physiological assessments (e.g., stress indicators, energetic reserves), and long-term return data to evaluate whether program modifications would improve survival or reproductive success in the wild. Importantly, supplementation success should not be measured solely by survival rates but also by monitoring the successful contribution of these individuals to wild spawning populations. Without mitigating the behavioural and potential physiological

consequences of captivity to improve post-release performance, supplementation programs become an expensive and potentially ineffective long-term conservation tool. Supplementation may have a role to play in Atlantic salmon conservation, but only if grounded in careful evaluation and evidence-based management actions.

REFERENCES

- Aarestrup, K., Jepsen, N., Rasmussen, G., Økland, F., Thorstad, E. B., & Holdensgaard, G. (2000). Prespawning migratory behaviour and spawning success of sea-ranched Atlantic salmon, *Salmo salar* L., in the River Gudena, Denmark. *Fisheries Management and Ecology*, 7(5), 387–400. <https://doi.org/10.1046/j.1365-2400.2000.00210.x>
- Adams, C. E., Chavarie, L., Rodger, J. R., Honkanen, H. M., Thambithurai, D., & Newton, M. P. (2022). An opinion piece: The evolutionary and ecological consequences of changing selection pressures on marine migration in Atlantic salmon. *Journal of Fish Biology*, 100(4), 860–867. <https://doi.org/10.1111/jfb.15024>
- Almodóvar, A., Leal, S., Nicola, G. G., Hórreo, J. L., García-Vázquez, E., & Elvira, B. (2020). Long-term stocking practices threaten the original genetic diversity of the southernmost European populations of Atlantic salmon *Salmo salar*. *Endangered Species Research*, 41, 303–317. <https://doi.org/10.3354/esr01029>
- Almond, R. E. A., Grooten, M., Juffe Bignoli, D., & Petersen, T. (Eds.). (2022). Living Planet Report 2022 – Building a nature-positive society. WWF.
- Araki, H., Berejikian, B. A., Ford, M. J., & Blouin, M. S. (2008). Fitness of hatchery-reared salmonids in the wild. *Evolutionary Applications*, 1(2), 342–355. <https://doi.org/10.1111/j.1752-4571.2008.00026.x>
- Baglinière, J. L., Maise, G., & Nihouarn, A. (1990). Migratory and reproductive behaviour of female adult Atlantic salmon, *Salmo salar* L., in a spawning stream. *Journal of Fish Biology*, 36(4), 511–520. <https://doi.org/10.1111/j.1095-8649.1990.tb03553.x>
- Baker, L. L., Mills Flemming, J. E., Jonsen, I. D., & others. (2015). A novel approach to quantifying the spatiotemporal behavior of instrumented grey seals used to sample the environment. *Movement Ecology*, 3, Article 20. <https://doi.org/10.1186/s40462-015-0047-4>
- Bardonnnet, A., & Baglinière, J.-L. (2000). Freshwater habitat of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 57(2), 497–506. <https://doi.org/10.1139/f99-226>
- Bean, C. (2020, April). *Atlantic Salmon and Non-Native Species: Is There an Issue?* [Conference Proceedings]. NASCO Symposium for the International Year of the Salmon: Managing the Atlantic Salmon in a Rapidly Changing Environment – Management Challenges and Possible Responses. <https://eprints.gla.ac.uk/216551/>
- Berg, O. K., & Bremset, G. (1998). Seasonal changes in the body composition of young riverine Atlantic salmon and brown trout. *Journal of Fish Biology*, 52(6), 1272–1288. <https://doi.org/10.1111/j.1095-8649.1998.tb00971.x>
- Birnie-Gauvin, K., Flávio, H., Kristensen, M. L., Aarestrup, K., & Cooke, S. J. (2019). Cortisol predicts migration timing and success in both Atlantic salmon and sea trout kelts. *Scientific Reports*, 9, Article 2422. <https://doi.org/10.1038/s41598-019-39153-x>

- Bordeleau, X., Hatcher, B. G., Denny, S., Fast, M. D., Whoriskey, F. G., Patterson, D. A., & Crossin, G. T. (2018). Consequences of captive breeding: Fitness implications for wild-origin, hatchery-spawned Atlantic salmon kelts upon their return to the wild. *Biological Conservation*, 225, 144–153. <https://doi.org/10.1016/j.biocon.2018.06.033>
- Bourgeois, C. E., & O'Connell, M. F. (1988). Observations on the seaward migration of Atlantic salmon (*Salmo salar* L.) smolts through a large lake as determined by radiotelemetry and Carlin tagging studies. *Canadian Journal of Zoology*, 66(3), 685–691. <https://doi.org/10.1139/z88-101>
- Bowlby, H.D., Gibson, A.J.F., and Levy, A. (2013). Recovery Potential Assessment for Southern Upland Atlantic Salmon: Status, Past and Present Abundance, Life History and Trends. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/005. v + 72 p.
- Breed, G. A., Jonsen, I. D., Myers, R. A., Bowen, W. D., & Leonard, M. L. (2009). Sex-specific, seasonal foraging tactics of adult grey seals (*Halichoerus grypus*) revealed by state–space analysis. *Ecology*, 90(11), 3209–3221. <https://doi.org/10.1890/07-1483.1>
- Brown, C., & Day, R. L. (2002). The future of stock enhancements: Lessons for hatchery practice from conservation biology. *Fish and Fisheries*, 3(2), 79–94. <https://doi.org/10.1046/j.1467-2979.2002.00077.x>
- Buddendorf, W. B., Jackson, F. L., Malcolm, I. A., Millidine, K. J., Geris, J., Wilkinson, M. E., & Soulsby, C. (2019). Integration of juvenile habitat quality and river connectivity models to understand and prioritise the management of barriers for Atlantic salmon populations across spatial scales. *Science of The Total Environment*, 655, 557–566. <https://doi.org/10.1016/j.scitotenv.2018.11.263>
- Butler, J.R.A., Radford, A., Riddington, G., Laughton, R. (2009). Evaluating an ecosystem service provided by Atlantic salmon, sea trout and other fish species in the River Spey, Scotland: The economic impact of recreational rod fisheries. *Fisheries Research*, 96(2-3), 259-266. <https://doi.org/10.1016/j.fishres.2008.12.006>
- Carr, J. W., Whoriskey, F., & O'reilly, P. (2004). Efficacy of releasing captive reared broodstock into an imperilled wild Atlantic salmon population as a recovery strategy. *Journal of Fish Biology*, 65(s1), 38–54. <https://doi.org/10.1111/j.0022-1112.2004.00546.x>
- Chaput, G. (2012). Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. *ICES Journal of Marine Science*, 69(9), 1538–1548. <https://doi.org/10.1093/icesjms/fss013>
- Chaput, G., & Benoît, H. P. (2012). Evidence for bottom–up trophic effects on return rates to a second spawning for Atlantic salmon (*Salmo salar*) from the Miramichi River, Canada. *ICES Journal of Marine Science*, 69(9), 1656–1667. <https://doi.org/10.1093/icesjms/fss055>
- Chaput, G., Carr, J., Daniels, J., Tinker, S., Jonsen, I., & Whoriskey, F. (2019). Atlantic salmon (*Salmo salar*) smolt and early post-smolt migration and survival inferred from multi-year and multi-stock acoustic telemetry studies in the Gulf of St. Lawrence, northwest Atlantic. *ICES Journal of Marine Science*, 76(4), 1107–1121. <https://doi.org/10.1093/icesjms/fsy156>

- Chilcote, M. W., Goodson, K. W., & Falcy, M. R. (2011). Reduced recruitment performance in natural populations of anadromous salmonids associated with hatchery-reared fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 68(3), 511–522. <https://doi.org/10.1139/F10-168>
- Christie, M. R., Ford, M. J., & Blouin, M. S. (2014). On the reproductive success of early-generation hatchery fish in the wild. *Evolutionary Applications*, 7(8), 883–896. <https://doi.org/10.1111/eva.12183>
- Christie, M. R., Marine, M. L., French, R. A., Waples, R. S., & Blouin, M. S. (2012). Effective size of a wild salmonid population is greatly reduced by hatchery supplementation. *Heredity*, 109(4), 254–260. <https://doi.org/10.1038/hdy.2012.39>
- Clarke, C. N., Fraser, D. J., & Purchase, C. F. (2016). Lifelong and carry-over effects of early captive exposure in a recovery program for Atlantic salmon (*Salmo salar*). *Animal Conservation*, 19(4), 350–359. <https://doi.org/10.1111/acv.12251>
- Cogliati, K. M., Herron, C. L., Noakes, D. L. G., & Schreck, C. B. (2019). Reduced stress response in juvenile Chinook Salmon reared with structure. *Aquaculture*, 504, 96–101. <https://doi.org/10.1016/j.aquaculture.2019.01.056>
- COSEWIC. (2010). COSEWIC assessment and status report on the Atlantic Salmon *Salmo salar* (Nunavik population, Labrador population, Northeast Newfoundland population, South Newfoundland population, Southwest Newfoundland population, Northwest Newfoundland population, Quebec Eastern North Shore population, Quebec Western North Shore population, Anticosti Island population, Inner St. Lawrence population, Lake Ontario population, Gaspé-Southern Gulf of St. Lawrence population, Eastern Cape Breton population, Nova Scotia Southern Upland population, Inner Bay of Fundy population, Outer Bay of Fundy population) in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xlvii + 136 pp.
- Cooke, S. J., Crossin, G. T., Patterson, D. A., English, K. K., Hinch, S. G., Young, J. L., Alexander, R. F., Healey, M. C., Van Der Kraak, G., & Farrell, A. P. (2005). Coupling non-invasive physiological assessments with telemetry to understand inter-individual variation in behaviour and survivorship of sockeye salmon: Development and validation of a technique. *Journal of Fish Biology*, 67(5), 1342–1358. <https://doi.org/10.1111/j.1095-8649.2005.00830.x>
- Cooke, S. J., Bergman, J. N., Twardek, W. M., Piczak, M. L., Casselberry, G. A., Lutek, K., Dahlmo, L. S., Birnie-Gauvin, K., Griffin, L. P., Brownscombe, J. W., Raby, G. D., Standen, E. M., Horodysky, A. Z., Johnsen, S., Danylchuk, A. J., Furey, N. B., Gallagher, A. J., Lédée, E. J. I., Midwood, J. D., ... Lennox, R. J. (2022). The movement ecology of fishes. *Journal of Fish Biology*, 101(4), 756–779. <https://doi.org/10.1111/jfb.15153>
- Cormack, R. M. (1964). Estimates of Survival from the Sighting of Marked Animals. *Biometrika*, 51(3/4), 429–438. <https://doi.org/10.2307/2334149>
- Cunjak, R. A., & Therrien, J. (1998). Inter-stage survival of wild juvenile Atlantic salmon (*Salmo salar* L.). *Fisheries Management and Ecology*, 5(3), 209–223. <https://doi.org/10.1046/j.1365-2400.1998.00094.x>

- Dadswell, M., Spares, A., Reader, J., McLean, M., McDermott, T., Samways, K., & Lilly, J. (2022). The Decline and Impending Collapse of the Atlantic Salmon (*Salmo salar*) Population in the North Atlantic Ocean: A Review of Possible Causes. *Reviews in Fisheries Science & Aquaculture*, 30(2), 215–258. <https://doi.org/10.1080/23308249.2021.1937044>
- Dempson, J. (1999). Evaluation of an alternative strategy to enhance salmon populations: Cage rearing wild smolts from Conne River, Newfoundland. *ICES Journal of Marine Science*, 56(4), 422–432. <https://doi.org/10.1006/jmsc.1999.0453>
- den Heyer, C.E., and Bowen, W.D. 2017. Estimating Changes in Vital Rates of Sable Island Grey Seals Using Mark-recapture Analysis. DFO Can. Sci. Advis. Sec. Res. Doc. 2017/054. v + 27 p.
- DFO. (2018). Review of risks and benefits of Collaboration for Atlantic Salmon Tomorrow’s (CAST) smolt-to-adult supplementation (SAS) experiment proposal (Phase 1: 2018–2022) (Science Advisory Report 2018/014). Fisheries and Oceans Canada.
- DFO and MRNF (Canada Department of Fisheries and Oceans and Quebec Ministère des Ressources naturelles et de la Faune). 2009. Conservation status report, Atlantic salmon in Atlantic Canada and Quebec: Part II anthropogenic considerations. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2870.
- Einum, S., & Fleming, I. (2001). Implications of stocking: Ecological interactions between wild and released Salmonids. *Nordic Journal of Freshwater Research*, 75, 56–70.
- English, G., Wilson, B. M., Lawrence, M. J., Black, M., Hawkes, J. P., Hardie, D. C., Daniels, J. M., Carr, J. W., Rycroft, C., Crossin, G. T., Whoriskey, F. G., den Heyer, C. E., Bordeleau, X., McKindsey, C. W., & Trudel, M. (2024). Determining early marine survival and predation by endothermic predators on acoustically tagged Atlantic salmon (*Salmo salar*) post-smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, 81(4), 387–402. <https://doi.org/10.1139/cjfas-2023-0206>
- Environmental Studies Research Fund DFO. (2023). Atlantic salmon in the Eastern Canadian offshore regions (ESRF Regions 8 to 15): timing, duration and the effects of environmental variability and climate change (ESRF Project 2019-01S). [Video]. Facebook. <https://www.facebook.com/share/v/1HrnVQ1r5T/>
- Eriksson, L.-O., Rivinoja, P., Östergren, J., Serrano, I., and Larsson, S. (2008). Smolt quality and survival of compensatory stocked Atlantic salmon and brown trout in the Baltic Sea. Report 62, Department of Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden. pp. 1–23. Available from <http://www.slu.se/viltfiskmiljo>.
- Evans, A. F., Payton, Q., Turecek, A., Cramer, B., Collis, K., Roby, D. D., Loschl, P. J., Sullivan, L., Skalski, J., Weiland, M., & Dotson, C. (2016). Avian predation on juvenile salmonids: Spatial and temporal analysis based on acoustic and passive integrated transponder tags. *Transactions of the American Fisheries Society*, 145(4), 860–877. <https://doi.org/10.1080/00028487.2016.1150881>

- Falkegård, M., Lennox, R. J., Thorstad, E. B., Einum, S., Fiske, P., Garmo, Ø. A., Garseth, Å. H., Skoglund, H., Solberg, M. F., Utne, K. R., Vollset, K. W., Vøllestad, L. A., Wennevik, V., & Forseth, T. (2023). Predation of Atlantic salmon across ontogenetic stages and impacts on populations. *Canadian Journal of Fisheries and Aquatic Sciences*, 80(10), 1696–1713. <https://doi.org/10.1139/cjfas-2023-0029>
- Feener, S. (2017). LaHave River Invasive Species Project. Bluenose Coastal Action Foundation. <https://www.coastalaction.org/atlantic-salmon.html>
- Finstad, A. G., Økland, F., Thorstad, E. B., & Heggberget, T. G. (2005). Comparing upriver spawning migration of Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*. *Journal of Fish Biology*, 67(4), 919–930. <https://doi.org/10.1111/j.0022-1112.2005.00792.x>
- Flávio, H., & Baktoft, H. (2021). actel: Standardised analysis of acoustic telemetry data from fish migrations in R (Version 1.3.0) [R package]. [GitHub - hugomflavio/actel: Standardised analysis of acoustic telemetry data from fish moving through receiver arrays](https://github.com/hugomflavio/actel)
- Fleming, I. A. (1994). Captive Breeding and the Conservation of Wild Salmon Populations. *Conservation Biology*, 8(3), 886–888.
- Fleming, I. A. (1996). Reproductive strategies of Atlantic salmon: Ecology and evolution. *Reviews in Fish Biology and Fisheries*, 6(4), 379–416. <https://doi.org/10.1007/BF00164323>
- Fleming, I.A., & Einum, S. (1997). Experimental tests of genetic divergence of farmed from wild Atlantic salmon due to domestication. *ICES J. Mar. Sci.* 54: 1051–1063.
- Fleming, I. A., & Gross, M. R. (1993). Breeding Success of Hatchery and Wild Coho Salmon (*Oncorhynchus Kisutch*) in Competition. *Ecological Applications*, 3(2), 230–245. <https://doi.org/10.2307/1941826>
- Fleming, I., & Petersson, E. (2001). The ability of released, hatchery salmonids to breed and contribute to the natural productivity of wild populations. *Nordic Journal of Freshwater Research*, 75, 71–98.
- Fleming, I. A., & Reynolds, J. D. (2004). Salmonid breeding systems. Unpublished In A. P. Hendry, & S. C. Stearns (Eds.), *Evolution Illuminated, Salmon and Their Relatives* (pp. 264-294). Oxford University Press.
- Foldvik, A., Ulvan, E. M., & Næsje, T. (2024). Optimal timing of return migration in Atlantic salmon. *Fish and Fisheries*, 25, 429–440. <https://doi.org/10.1111/faf.12816>
- Ford JS, Myers RA (2008) A Global Assessment of Salmon Aquaculture Impacts on Wild Salmonids. *PLoS Biol* 6(2): e33. <https://doi.org/10.1371/journal.pbio.0060033>
- Ford, M., Pearsons, T. N., & Murdoch, A. (2015). The spawning success of early maturing resident hatchery Chinook salmon in a natural river system. *Transactions of the American Fisheries Society*, 144(3), 539–548. <https://doi.org/10.1080/00028487.2015.1009561>
- Forseth, T., Barlaup, B. T., Finstad, B., Fiske, P., Gjøsæter, H., Falkegård, M., Hindar, A., Mo, T. A., Rikardsen, A. H., Thorstad, E. B., Vøllestad, L. A., & Wennevik, V. (2017). The major threats to Atlantic salmon in Norway. *ICES Journal of Marine Science*, 74(6), 1496–1513. <https://doi.org/10.1093/icesjms/fsx020>

- Fraser, D.J. 2016. Risks and benefits of mitigating low marine survival in wild salmon using smolt-to-adult captive-reared supplementation. DFO Can. Sci. Advis. Sec. Res. Doc. 2016/030. v + 31 p.
- Fraser, D. J. (2008). How well can captive breeding programs conserve biodiversity? A review of salmonids. *Evolutionary Applications*, 1(4), 535–586. <https://doi.org/10.1111/j.1752-4571.2008.00036.x>
- Friedland, K. (2000). Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. *ICES Journal of Marine Science*, 57(2), 419–429. <https://doi.org/10.1006/jmsc.1999.0639>
- Gale, W. L., Hill, M. S., & Zydlewski, G. B. (2004). Physiological and behavioural differences of hatchery and wild-reared steelhead *Oncorhynchus mykiss* smolts of the same genetic origin. *Journal of Fish Biology*, 65(s1), 328–329. <https://doi.org/10.1111/j.1095-8649.2004.559ah.x>
- Garlock, T. M., Monk, C. T., Lorenzen, K., Matthews, M. D., & St Mary, C. M. (2014). Effects of hatchery rearing on Florida largemouth bass *Micropterus floridanus* resource allocation and performance under semi-natural conditions. *Journal of Fish Biology*, 85(6), 1830–1842. <https://doi.org/10.1111/jfb.12514>
- Gee, A. S., Milner, N. J., & Hemsworth, R. J. (1978). The Effect of Density on Mortality in Juvenile Atlantic Salmon (*Salmo salar*). *Journal of Animal Ecology*, 47(2), 497–505. <https://doi.org/10.2307/3796>
- Gibson, R. J. (2017). Salient needs for conservation of Atlantic salmon. *Fisheries*, 42(3), 163–174. <https://doi.org/10.1080/03632415.2016.1276331>
- Gibson, A. J. F., Bowlby, H. D., Hardie, D. C., & O'Reilly, P. T. (2011). Populations on the Brink: Low Abundance of Southern Upland Atlantic Salmon in Nova Scotia, Canada. *North American Journal of Fisheries Management*, 31(4), 733–741. <https://doi.org/10.1080/02755947.2011.613305>
- Gillis, C.-A., Ouellet, Valerie, Breau, Cindy, Frechette, Danielle, & Bergeron, N. (2023). Assessing climate change impacts on North American freshwater habitat of wild Atlantic salmon—Urgent needs for collaborative research. *Canadian Water Resources Journal / Revue Canadienne Des Ressources Hydriques*, 48(2), 222–246. <https://doi.org/10.1080/07011784.2022.2163190>
- Grant, J. W. A., & Kramer, D. L. (1990). Territory Size as a Predictor of the Upper Limit to Population Density of Juvenile Salmonids in Streams. *Canadian Journal of Fisheries and Aquatic Sciences*, 47(9), 1724–1737. <https://doi.org/10.1139/f90-197>
- Gray, R. W., Cameron, J. D., and Jefferson, E. M. J. 1989. The LaHave River: physiography and potential for Atlantic salmon production. Canadian Technical Report of Fisheries and Aquatic Sciences, No. 1710. 58 pp.
- Grey, J. T. (1984). Salmon rivers of Cape Breton Island: A guide to the lesser salmon rivers of Cape Breton Island. Yardley, PA: [Self-published].

- Gro Vea Salvanes, A., & Braithwaite, V. (2006). The need to understand the behaviour of fish reared for mariculture or restocking. *ICES Journal of Marine Science*, 63(2), 345–354. <https://doi.org/10.1016/j.icesjms.2005.11.010>
- Halfyard, E. A., Gibson, A. J. F., Ruzzante, D. E., Stokesbury, M. J. W., & Whoriskey, F. G. (2012). Estuarine survival and migratory behaviour of Atlantic salmon *Salmo salar* smolts. *Journal of Fish Biology*, 81(5), 1626–1645. <https://doi.org/10.1111/j.1095-8649.2012.03419.x>
- Halttunen, E., Rikardsen, A. H., Davidsen, J. G., Thorstad, E. B., & Dempson, J. B. (2009). Survival, Migration Speed and Swimming Depth of Atlantic Salmon Kelts During Sea Entry and Fjord Migration. In J. L. Nielsen, H. Arrizabalaga, N. Frago, A. Hobday, M. Lutcavage, & J. Sibert (Eds.), *Tagging and Tracking of Marine Animals with Electronic Devices* (pp. 35–49). Springer Netherlands. https://doi.org/10.1007/978-1-4020-9640-2_3
- Halttunen, E., Jensen, J. L. A., Næsje, T. F., Davidsen, J. G., Thorstad, E. B., Chittenden, C. M., Hamel, S., Primicerio, R., & Rikardsen, A. H. (2013). State-dependent migratory timing of postspawned Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 70(7), 1063–1071. <https://doi.org/10.1139/cjfas-2012-0525>
- Hansen, L. P., Jonsson, B., & Døving, K. B. (1984). Migration of wild and hatchery reared smolts of Atlantic salmon, *Salmo salar* L., through lakes. *Journal of Fish Biology*, 25(5), 617–623. <https://doi.org/10.1111/j.1095-8649.1984.tb04908.x>
- Hansen, L.P., Døsving, K.B. and Jonsson, B. (1987), Migration of farmed adult Atlantic salmon with and without olfactory sense, released on the Norwegian coast. *Journal of Fish Biology*, 30: 713-721. <https://doi.org/10.1111/j.1095-8649.1987.tb05800.x>
- Hansen, L. P., Jonsson, N., & Jonsson, B. (1993). Oceanic migration in homing Atlantic salmon. *Animal Behaviour*, 45(5), 927–941. <https://doi.org/10.1006/anbe.1993.1112>
- Hanssen, E. M., Vollset, K. W., Salvanes, A. G. V., Barlaup, B., Whoriskey, K., Isaksen, T. E., Normann, E. S., Hulbak, M., & Lennox, R. J. (2022). Acoustic telemetry predation sensors reveal the tribulations of Atlantic salmon (*Salmo salar*) smolts migrating through lakes. *Ecology of Freshwater Fish*, 31(2), 424–437. <https://doi.org/10.1111/eff.12641>
- Hays, G. C., Bailey, H., Bograd, S. J., Bowen, W. D., Campagna, C., Carmichael, R. H., Casale, P., Chiaradia, A., Costa, D. P., Cuevas, E., Bruyn, P. J. N. de, Dias, M. P., Duarte, C. M., Dunn, D. C., Dutton, P. H., Esteban, N., Friedlaender, A., Goetz, K. T., Godley, B. J., ... Sequeira, A. M. M. (2019). Translating Marine Animal Tracking Data into Conservation Policy and Management. *Trends in Ecology & Evolution*, 34(5), 459–473. <https://doi.org/10.1016/j.tree.2019.01.009>
- Hedger, R. D., Kjellman, M., Thorstad, E. B., Strøm, J. F., & Rikardsen, A. H. (2022). Diving and feeding of adult Atlantic salmon when migrating through the coastal zone in Norway. *Environmental Biology of Fishes*, 105(5), 589–604. <https://doi.org/10.1007/s10641-022-01269-x>
- Heggberget, T. G., Økland, F., & Ugedal, O. (1993). Distribution and migratory behaviour of adult wild and farmed Atlantic salmon (*Salmo salar*) during return migration. *Aquaculture*, 118(1), 73–83. [https://doi.org/10.1016/0044-8486\(93\)90282-4](https://doi.org/10.1016/0044-8486(93)90282-4)

- Holbrook, C. M., Binder, T. R., Tuel, J. E., & Vandergoot, C. S. (2024). *glatos*: A package for the Great Lakes Acoustic Telemetry Observation System (Version 0.8.0) [R package]. [GitHub - ocean-tracking-network/glatos](https://github.com/ocean-tracking-network/glatos)
- Hubley, P. B., Amiro, P. G., Gibson, A. J. F., Lacroix, G. L., & Redden, A. M. (2008). Survival and behaviour of migrating Atlantic salmon (*Salmo salar* L.) kelts in river, estuarine, and coastal habitat. *ICES Journal of Marine Science*, 65(9), 1626–1634. <https://doi.org/10.1093/icesjms/fsn129>
- Hubley, P. B., & Gibson, A. J. F. (2011). A model for estimating mortality of Atlantic salmon, *Salmo salar*, between spawning events. *Canadian Journal of Fisheries and Aquatic Sciences*, 68(9), 1635–1650. <https://doi.org/10.1139/f2011-074>
- Huntingford, F. A. (2004). Implications of domestication and rearing conditions for the behaviour of cultivated fishes. *Journal of Fish Biology*, 65(s1), 122–142. <https://doi.org/10.1111/j.0022-1112.2004.00562.x>
- Hyvärinen, P., & Rodewald, P. (2013). Enriched rearing improves survival of hatchery-reared Atlantic salmon smolts during migration in the River Tornionjoki. *Canadian Journal of Fisheries and Aquatic Sciences*, 70(9), 1386–1395. <https://doi.org/10.1139/cjfas-2013-0147>
- ICES. (2022). *North Atlantic salmon stocks* (p. 1917597 Bytes). ICES Advice: Recurrent Advice. <https://doi.org/10.17895/ICES.ADVICE.18668234>
- International North Atlantic Salmon Conservation Organization. (2019). State of North Atlantic salmon (SoS report). NASCO.
- Iversen, M., Finstad, B., & Nilssen, K. J. (1998). Recovery from loading and transport stress in Atlantic salmon (*Salmo salar* L.) smolts. *Aquaculture*, 168(1), 387–394. [https://doi.org/10.1016/S0044-8486\(98\)00364-0](https://doi.org/10.1016/S0044-8486(98)00364-0)
- Jackson, C. D., & Brown, G. E. (2011). Differences in antipredator behaviour between wild and hatchery-reared juvenile Atlantic salmon (*Salmo salar*) under seminatural conditions. *Canadian Journal of Fisheries and Aquatic Sciences*, 68(12), 2157–2166. <https://doi.org/10.1139/f2011-129>
- Jaervi, T., & Uglem, I. (1993). Predator training improves the anti-predator behaviour of hatchery reared Atlantic salmon (*Salmo salar*) smolt. *Nordic journal of freshwater research. Drottningholm*, (68), 63-71.
- Jensen, A. J., Ó Maoiléidigh, N., Thomas, K., Einarsson, S. M., Haugland, M., Erkinaro, J., Fiske, P., Friedland, K. D., Gudmundsdottir, A. K., Haantie, J., Holm, M., Holst, J. C., Jacobsen, J. A., Jensås, J. G., Kuusela, J., Melle, W., Mork, K. A., Wennevik, V., & Østborg, G. M. (2012). Age and fine-scale marine growth of Atlantic salmon post-smolts in the Northeast Atlantic. *ICES Journal of Marine Science*, 69(9), 1668–1677. <https://doi.org/10.1093/icesjms/fss086>
- Jepsen, N., Pedersen, S., & Thorstad, E. (2000). Behavioural interactions between prey (trout smolts) and predators (pike and pikeperch) in an impounded river. *Regulated Rivers: Research & Management*, 16(2), 189–198. [https://doi.org/10.1002/\(SICI\)1099-1646\(200003/04\)16:2<189::AID-RRR570>3.0.CO;2-N](https://doi.org/10.1002/(SICI)1099-1646(200003/04)16:2<189::AID-RRR570>3.0.CO;2-N)

- Johnsson, J. I., Petersson, E., Jönsson, E., Björnsson, B. T., & Järvi, T. (1996). Domestication and growth hormone alter antipredator behaviour and growth patterns in juvenile brown trout, *Salmo trutta*. *Canadian Journal of Fisheries and Aquatic Sciences*, 53(7), 1546–1554. <https://doi.org/10.1139/f96-090>
- Jokikokko, E. (2002). Migration of wild and reared Atlantic salmon (*Salmo salar* L.) in the river Simojoki, northern Finland. *Fisheries Research*, 58(1), 15–23. [https://doi.org/10.1016/S0165-7836\(01\)00364-2](https://doi.org/10.1016/S0165-7836(01)00364-2)
- Jokikokko, E. (2006). Atlantic salmon (*Salmo salar* L.) stocking in the Simojoki River as a management practice. University of Oulu. Jolly, G. M. (1965). Explicit Estimates from Capture-Recapture Data with Both Death and Immigration-Stochastic Model. *Biometrika*, 52(1/2), 225–247. <https://doi.org/10.2307/2333826>
- Jonsson, B. (1997). A review of ecological and behavioural interactions between cultured and wild Atlantic salmon. *ICES Journal of Marine Science*, 54(6), 1031–1039. [https://doi.org/10.1016/S1054-3139\(97\)80007-0](https://doi.org/10.1016/S1054-3139(97)80007-0)
- Jonsson, B. & Fleming, I. A. (1993). Enhancement of wild salmon populations. In *Human Impact on Self-Recruiting Populations* (G. Sundnes, ed), pp. 209–238. Trondheim: Tapir Press.
- Jonsson, B., & Jonsson, N. (2006). Cultured Atlantic salmon in nature: A review of their ecology and interaction with wild fish. *ICES Journal of Marine Science*, 63(7), 1162–1181. <https://doi.org/10.1016/j.icesjms.2006.03.004>
- Jonsson, B., Jonsson, N., & Hansen, L. P. (1991). Differences in life history and migratory behaviour between wild and hatchery-reared Atlantic salmon in nature. *Aquaculture*, 98(1), 69–78. [https://doi.org/10.1016/0044-8486\(91\)90372-E](https://doi.org/10.1016/0044-8486(91)90372-E)
- Jonsson, N., Jonsson, B., & Hansen, L. P. (2003). The marine survival and growth of wild and hatchery-reared Atlantic salmon. *Journal of Applied Ecology*, 40(5), 900–911. <https://doi.org/10.1046/j.1365-2664.2003.00851.x>
- Jonsson, B. and Jonsson, N. (2014), Early environment influences later performance in fishes. *J Fish Biol*, 85: 151-188. <https://doi.org/10.1111/jfb.12432>
- Kadri, S., Metcalfe, N. B., Huntingford, F. A., & Thorpe, J. E. (1995). What Controls the Onset of Anorexia in Maturing Adult Female Atlantic Salmon? *Functional Ecology*, 9(5), 790–797. <https://doi.org/10.2307/2390254>
- Kallio-Nyberg, I., Saloniemi, I., Jutila, E., & Jokikokko, E. (2011). Effect of hatchery rearing and environmental factors on the survival, growth and migration of Atlantic salmon in the Baltic Sea. *Fisheries Research*, 109(2), 285–294. <https://doi.org/10.1016/j.fishres.2011.02.015>
- Kekäläinen, J., Niva, T., & Huuskonen, H. (2008). Pike predation on hatchery-reared Atlantic salmon smolts in a northern Baltic river. *Ecology of Freshwater Fish*, 17(1), 100–109. <https://doi.org/10.1111/j.1600-0633.2007.00263.x>
- Kennedy, B. P., Nislow, K. H., & Folt, C. L. (2008). Habitat-Mediated Foraging Limitations Drive Survival Bottlenecks for Juvenile Salmon. *Ecology*, 89(9), 2529–2541. <https://doi.org/10.1890/06-1353.1>

- Kennedy, R. J., Rosell, R., Millane, M., Doherty, D., & Allen, M. (2018). Migration and survival of Atlantic salmon smolts in a large natural lake. *Journal of Fish Biology*, 93(1), 134–137. <https://doi.org/10.1111/jfb.13676>
- Kennedy, R., Rosell, R., Hunter, E., & del Villar-Guerra, D. (2023). Programmed acoustic tags reveal novel information on late-phase marine life in Atlantic salmon, *Salmo salar*. *Journal of Fish Biology*, 102(3), 707–711. <https://doi.org/10.1111/jfb.15292>
- Klinard, N. V., & Matley, J. K. (2020). Living until proven dead: Addressing mortality in acoustic telemetry research. *Reviews in Fish Biology and Fisheries*, 30(3), 485–499. <https://doi.org/10.1007/s11160-020-09613-z>
- Kocik, J. F., Hawkes, J. P., Sheehan, T. F., Music, A.P., Beland, K.F. (2009). Assessing Estuarine and Coastal Migration and Survival of Wild Atlantic Salmon Smolts from the Narraguagus River, Maine Using Ultrasonic Telemetry. *American Fisheries Society Symposium* 69 293-310.
- Laake, J. L. (2013). RMark: An R interface for analysis of capture–recapture data with MARK (Version 3.0.0) [R package]. GitHub - jlaake/RMark: R package for interface to MARK for mark-recapture data analysis
- Lacroix, G. L., & Knox, D. (2005). Distribution of Atlantic salmon (*Salmo salar*) postsmolts of different origins in the Bay of Fundy and Gulf of Maine and evaluation of factors affecting migration, growth, and survival. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(6), 1363–1376. <https://doi.org/10.1139/f05-055>
- Landry, D., Chaput, G., & Bridgland, J. (2005). Stock status of Atlantic salmon (*Salmo salar*) in the Cheticamp River, Cape Breton Highlands National Park, Nova Scotia, for 2004 (Research Document 2005/022). Fisheries and Oceans Canada, Canadian Science Advisory Secretariat.
- Larsson, S., Serrano, I., & Eriksson, L.-O. (2012). Effects of muscle lipid concentration on wild and hatchery brown trout (*Salmo trutta*) smolt migration. *Canadian Journal of Fisheries and Aquatic Sciences*, 69(1), 1–12. <https://doi.org/10.1139/f2011-128>
- Laundré, J.W., Hernández, L., Medina, P.L., Campanella, A., López-Portillo, J., González-Romero, A., Grajales-Tam, K.M., Burke, A.M., Gronemeyer, P. and Browning, D.M. (2014), The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance?. *Ecology*, 95: 1141-1152. <https://doi.org/10.1890/13-1083.1>
- Leber, K. M., Cantrell, R. N., & Leung, P. S. (2005). Optimizing Cost-Effectiveness of Size at Release in Stock Enhancement Programs. *North American Journal of Fisheries Management*, 25(4), 1596–1608. <https://doi.org/10.1577/M04-093.1>
- Lehnert, S. J., Kess, T., Bentzen, P., Kent, M. P., Lien, S., Gilbey, J., Clément, M., Jeffery, N. W., Waples, R. S., & Bradbury, I. R. (2019). Genomic signatures and correlates of widespread population declines in salmon. *Nature Communications*, 10(1), 2996. <https://doi.org/10.1038/s41467-019-10972-w>
- Lenky, C. C. (2011). Changes in Seal Habitat Use of Nearshore Waters around Newfoundland and Southern Labrador: Implications for Potential Predation on Salmon. *The Open Conservation Biology Journal*, 5(1), 13–24. <https://doi.org/10.2174/1874839201105010013>

- Lennox, R. J., Afonso, P., Birnie-Gauvin, K., Dahlmo, L. S., Nilsen, C. I., Arlinghaus, R., Cooke, S. J., Souza, A. T., Jarić, I., Prchalová, M., Říha, M., Westrelin, S., Twardek, W., Aspillaga, E., Kraft, S., Šmejkal, M., Baktoft, H., Brodin, T., Hellström, G., ... Reubens, J. (2024). Electronic tagging and tracking aquatic animals to understand a world increasingly shaped by a changing climate and extreme weather events. *Canadian Journal of Fisheries and Aquatic Sciences*, 81(3), 326–339. <https://doi.org/10.1139/cjfas-2023-0145>
- Lennox, R. J., Alexandre, C. M., Almeida, P. R., Bailey, K. M., Barlaup, B. T., Bøe, K., Breukelaar, A., Erkinaro, J., Forseth, T., Gabrielsen, S.-E., Halfyard, E., Hanssen, E. M., Karlsson, S., Koch, S., Koed, A., Langåker, R. M., Lo, H., Lucas, M. C., Mahlum, S., ... Vollset, K. W. (2021). The quest for successful Atlantic salmon restoration: Perspectives, priorities, and maxims. *ICES Journal of Marine Science*, 78(10), 3479–3497. <https://doi.org/10.1093/icesjms/fsab201>
- Lennox, R. J., Eldøy, S. H., Dahlmo, L. S., Matley, J. K., & Vollset, K. W. (2023). Acoustic accelerometer transmitters and their growing relevance to aquatic science. *Movement Ecology*, 11(1), 45. <https://doi.org/10.1186/s40462-023-00403-3>
- Lennox, R. J., Eliason, E. J., Havn, T. B., Johansen, M. R., Cooke, S. J., & Vollset, K. W. (2018). Bioenergetic consequences of warming rivers to adult Atlantic salmon (*Salmo salar*) during their spawning migration. *Freshwater Biology*, 63(11), 1381–1393. <https://doi.org/10.1111/fwb.13166>
- Levy, A.L., and Gibson, A.J.F. (2014). Recovery Potential Assessment for Eastern Cape Breton Atlantic Salmon (*Salmo salar*): Status, past and present abundance, life history, and trends. DFO Can. Sci. Advis. Sec. Res. Doc. 2014/099. v + 72 p.
- Limburg, K. E., & Waldman, J. R. (2009). Dramatic declines in North Atlantic diadromous fishes. *BioScience*, 59(11), 955–965. <https://doi.org/10.1525/bio.2009.59.11.7>
- Matley, J. K., Klinard, N. V., Larocque, S. M., McLean, M. F., Brownscombe, J. W., Raby, G. D., Nguyen, V. M., & Barbosa Martins, A. P. (2023). Making the most of aquatic animal tracking: A review of complementary methods to bolster acoustic telemetry. *Reviews in Fish Biology and Fisheries*, 33(1), 35–54. <https://doi.org/10.1007/s11160-022-09738-3>
- May, S. A., Shedd, K. R., Gruenthal, K. M., Hard, J. J., Templin, W. D., Waters, C. D., Adkison, M. D., Ward, E. J., Habicht, C., Wilson, L. I., Wertheimer, A. C., & Westley, P. A. H. (2024). Salmon hatchery strays can demographically boost wild populations at the cost of diversity: Quantitative genetic modelling of Alaska pink salmon. *Royal Society Open Science*, 11(7), 240455. <https://doi.org/10.1098/rsos.240455>
- Maynard, D., Riley, S., Flagg, T., Iwamoto, R., Mahnken, C., Berejikian, B., Tatara, C., Endicott, R., Atkins, J., Scheurer, J., LaRae, A., Colt, J., Dixon, J., McDowell, G., & Vander Haegen, G. (2004). Development of a natural rearing system to improve supplemental fish quality (Final Report, Project No. 199105500; BPA Report DOE/BP-00004768-2, 174 pp.). Bonneville Power Administration.
- Maynard, D. J., & Trial, J. G. (2014). The use of hatchery technology for the conservation of Pacific and Atlantic salmon. *Reviews in Fish Biology and Fisheries*, 24(3), 803–817. <https://doi.org/10.1007/s11160-013-9341-7>

- Maysonet, S., & Murphy, S. D. (n.d.). Recovery of Atlantic salmon in Fundy National Park [Case study]. University of Waterloo, School of Environment, Resources and Sustainability. <https://onlineacademiccommunity.uvic.ca/ecorestoration/>
- McDonald, D. G., Milligan, C. L., McFarlane, W. J., Croke, S., Currie, S., Hooke, B., Angus, R. B., Tufts, B. L., & Davidson, K. (1998). Condition and performance of juvenile Atlantic salmon (*Salmo salar*): Effects of rearing practices on hatchery fish and comparison with wild fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(5), 1208–1219. <https://doi.org/10.1139/f98-003>
- McKinnell, S., Lundqvist, H., & Johansson, H. (1994). Biological characteristics of the upstream migration of naturally and hatchery-reared Baltic salmon, *Salmo salar* L. *Aquaculture Research*, 25(S2), 45–63. <https://doi.org/10.1111/are.1994.25.s2.45>
- McMillan, J. R., Morrison, B., Chambers, N., Ruggerone, G., Bernatchez, L., Stanford, J., & Neville, H. (2023). A global synthesis of peer-reviewed research on the effects of hatchery salmonids on wild salmonids. *Fisheries Management and Ecology*, 30(5), 446–463. <https://doi.org/10.1111/fme.12643>
- Melnchuk, M. C., Korman, J., Hausch, S., Welch, D. W., McCubbing, D. J. F., & Walters, C. J. (2014). Marine survival difference between wild and hatchery-reared steelhead trout determined during early downstream migration. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(6), 831–846. <https://doi.org/10.1139/cjfas-2013-0165>
- Mensingher, M. A., Casey, A. N., Mortelliti, A., & Zydlewski, J. D. (2025). Smallmouth bass (*Micropterus dolomieu*) and chain pickerel (*Esox niger*) identified as Atlantic salmon (*Salmo salar*) smolt predators in a reservoir system. *Canadian Journal of Fisheries and Aquatic Sciences*, 82, 1–15. <https://doi.org/10.1139/cjfas-2024-0416>
- Midwood, J. D., Larsen, M. H., Boel, M., Aarestrup, K., & Cooke, S. J. (2015). An experimental field evaluation of winter carryover effects in semi-anadromous brown trout (*Salmo trutta*). *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, 323(9), 645–654. <https://doi.org/10.1002/jez.1955>
- Mills, K. E., Pershing, A. J., Sheehan, T. F., & Mountain, D. (2013). Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations. *Global Change Biology*, 19(10), 3046–3061. <https://doi.org/10.1111/gcb.12298>
- Milot, E., Perrier, C., Papillon, L., Dodson, J. J., & Bernatchez, L. (2013). Reduced fitness of Atlantic salmon released in the wild after one generation of captive breeding. *Evolutionary Applications*, 6(3), 472–485. <https://doi.org/10.1111/eva.12028>
- Murphy, M. H., Connerton, M. J., & Stewart, D. J. (2006). Evaluation of Winter Severity on Growth of Young-of-the-Year Atlantic Salmon. *Transactions of the American Fisheries Society*, 135(2), 420–430. <https://doi.org/10.1577/T04-109.1>
- Naish, K. A., Taylor, J. E., Levin, P. S., Quinn, T. P., Winton, J. R., Huppert, D., & Hilborn, R. (2007). An Evaluation of the Effects of Conservation and Fishery Enhancement Hatcheries on Wild Populations of Salmon. In *Advances in Marine Biology* (Vol. 53, pp. 61–194). Academic Press. [https://doi.org/10.1016/S0065-2881\(07\)53002-6](https://doi.org/10.1016/S0065-2881(07)53002-6)

- Näslund, J., Rosengren, M., Del Villar, D., Gansel, L., Norrgård, J. R., Persson, L., Winkowski, J. J., & Kvingedal, E. (2013). Hatchery tank enrichment affects cortisol levels and shelter-seeking in Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 70(4), 585–590. <https://doi.org/10.1139/cjfas-2012-0302>
- Nason, J. S. J. (2023). An assessment of Inner Bay of Fundy Atlantic salmon (*Salmo salar*) spawning success in Fundy National Park (Unpublished honours thesis). University of New Brunswick.
- Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, 105(49), 19052–19059. <https://doi.org/10.1073/pnas.0800375105>
- Nieland, J. L., Sheehan, T. F., & Saunders, R. (2015). Assessing demographic effects of dams on diadromous fish: A case study for Atlantic salmon in the Penobscot River, Maine. *ICES Journal of Marine Science*, 72(8), 2423–2437. <https://doi.org/10.1093/icesjms/fsv083>
- Nilsen, C. I., Vollset, K. W., Velle, G., Barlaup, B. T., Normann, E. S., Stöger, E., & Lennox, R. J. (2023). Atlantic salmon of wild and hatchery origin have different migration patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, 80(4), 690–699. <https://doi.org/10.1139/cjfas-2022-0120>
- Nowak, B. V. R., Bowen, W. D., Whoriskey, K., Lidgard, D. C., Mills Flemming, J. E., & Iverson, S. J. (2020). Foraging behaviour of a continental shelf marine predator, the grey seal (*Halichoerus grypus*), is associated with in situ, subsurface oceanographic conditions. *Movement Ecology*, 8(1), 41. <https://doi.org/10.1186/s40462-020-00225-7>
- Økland, F., Erkinaro, J., Moen, K., Niemelä, E., Fiske, P., McKinley, R. s., & Thorstab, E. B. (2001). Return migration of Atlantic Salmon in the River Tana: Phases of migratory behaviour. *Journal of Fish Biology*, 59(4), 862–874. <https://doi.org/10.1111/j.1095-8649.2001.tb00157.x>
- Olla, B. L., Davis, M. W., & Ryer, C. H. (1998). Understanding how the Hatchery Environment Represses or Promotes the Development of Behavioral Survival Skills [Text]. University of Miami - Rosenstiel School of Marine, Atmospheric & Earth Science. <https://www.ingentaconnect.com/content/umrsmas/bullmar/1998/00000062/00000002/art00016#>
- O'Neil, S.F., Harvie, C.J., Longard, D.A. (1997). Stock status of Atlantic salmon (*Salmo salar*) on the eastern shore of Nova Scotia, Salmon Fishing Area 20, in 1997. DFO Canadian Stock Assessment Secretariat Research Document 98/37.
- O'Reilly, P., Rafferty, S., and Gibson, A.J.F. 2013. Within- and among-population genetic variation in Eastern Cape Breton Atlantic salmon and the prioritization of populations for conservation (*Salmo salar* L.). DFO Can. Sci. Advis. Sec. Res. Doc. 2013/076. vi + 25 p.
- Osterback, A.-M. K., Frechette, D. M., Shelton, A. O., Hayes, S. A., Bond, M. H., Shaffer, S. A., & Moore, J. W. (2013). High predation on small populations: Avian predation on imperiled salmonids. *Ecosphere*, 4(9), art116. <https://doi.org/10.1890/ES13-00100.1>

- O’Sullivan, R. J., Aykanat, T., Johnston, S. E., Rogan, G., Poole, R., Prodöhl, P. A., de Eyto, E., Primmer, C. R., McGinnity, P., & Reed, T. E. (2020). Captive-bred Atlantic salmon released into the wild have fewer offspring than wild-bred fish and decrease population productivity. *Proceedings of the Royal Society B: Biological Sciences*, 287(1937), 20201671. <https://doi.org/10.1098/rspb.2020.1671>
- Pardo, S. A., Bolstad, G. H., Dempson, J. B., April, J., Jones, R. A., Raab, D., & Hutchings, J. A. (2021). Trends in marine survival of Atlantic salmon populations in eastern Canada. *ICES Journal of Marine Science*, 78(7), 2460–2473. <https://doi.org/10.1093/icesjms/fsab118>
- Pedersen, L.-F., Koed, A., & Malte, H. (2008). Swimming performance of wild and F1-hatchery-reared Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) smolts. *Ecology of Freshwater Fish*, 17(3), 425–431. <https://doi.org/10.1111/j.1600-0633.2008.00293.x>
- Pickering, A. D., & Pottinger, T. G. (1988). Lymphocytopenia and the overwinter survival of Atlantic salmon parr, *Salmo salar* L. *Journal of Fish Biology*, 32(5), 689–697. <https://doi.org/10.1111/j.1095-8649.1988.tb05409.x>
- Power, J. H., & McCleave, J. D. (1980). Riverine movements of hatchery-reared Atlantic salmon (*Salmo salar*) upon return as adults. *Environmental Biology of Fishes*, 5(1), 3–13. <https://doi.org/10.1007/BF00000945>
- Prevost, A. D. (2018). Assessing reproductive success of Atlantic salmon in two restoration programs (Unpublished master's thesis). Concordia University.
- Quinn, T. P. (1993). A review of homing and straying of wild and hatchery-produced salmon. *Fisheries Research*, 18(1), 29–44. [https://doi.org/10.1016/0165-7836\(93\)90038-9](https://doi.org/10.1016/0165-7836(93)90038-9)
- Raab, D., Taylor, A.D., Hardie, D.C., and Brunsdon, E.B. (2024). Updated Information on Atlantic Salmon (*Salmo salar*) Populations in Nova Scotia’s Southern Upland (SU; Salmon Fishing Areas 20, 21, and Part of 22) of Relevance to the Development of a 2nd COSEWIC Status Report. DFO Can. Sci. Advis. Sec. Res. Doc. 2024/050. v + 65 p.
- R Core Team. (2024). R: A language and environment for statistical computing. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Reddin, D. G., and W. H. Lear. 1990. Summary of marine tagging studies of Atlantic salmon (*Salmo salar* L.) in the Northwest Atlantic area. Can. Tech. Rep. Fish. Aquat.~ 1737: iv + 115 p.
- Reisenbichler, R., Rubin, S., Wetzel, L., & Phelps, S. (2004). Natural Selection After Release from a Hatchery Leads to Domestication in Steelhead, *Oncorhynchus mykiss*. In *Stock Enhancement and Sea Ranching* (pp. 371–384). John Wiley & Sons, Ltd. <https://doi.org/10.1002/9780470751329.ch27>
- Remen, M., Solstorm, F., Bui, S., Klebert, P., Vågseth, T., Solstorm, D., Hvas, M., & Oppedal, F. (2016). Critical swimming speed in groups of Atlantic salmon *Salmo salar*. *Aquaculture Environment Interactions*, 8. <https://doi.org/10.3354/aei00207>
- Ritter, J. (1997). The contribution of Atlantic salmon (*Salmo salar* L.) enhancement to a sustainable resource. *ICES Journal of Marine Science*, 54(6), 1177–1187. [https://doi.org/10.1016/S1054-3139\(97\)80025-2](https://doi.org/10.1016/S1054-3139(97)80025-2)

- Rivinoja, P., McKinnell, S., & Lundqvist, H. (2001). Hindrances to upstream migration of atlantic salmon (*Salmo salar*) in a northern Swedish river caused by a hydroelectric power-station. *Regulated Rivers: Research & Management*, 17(2), 101–115. <https://doi.org/10.1002/rrr.607>
- Rosengren, M., Kvingedal, E., Näslund, J., Johnsson, J. I., & Sundell, K. (2017). Born to be wild: Effects of rearing density and environmental enrichment on stress, welfare, and smolt migration in hatchery-reared Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 74(3), 396–405. <https://doi.org/10.1139/cjfas-2015-0515>
- Rubenstein, S. R., Peterson, E., Christman, P., & Zydlewski, J. D. (2023). Adult Atlantic salmon (*Salmo salar*) delayed below dams rapidly deplete energy stores. *Canadian Journal of Fisheries and Aquatic Sciences*, 80(1), 170–182. <https://doi.org/10.1139/cjfas-2022-0008>
- Russell, I. C., Aprahamian, M. W., Barry, J., Davidson, I. C., Fiske, P., Ibbotson, A. T., Kennedy, R. J., Maclean, J. C., Moore, A., Otero, J., Potter, T. E. C. E., & Todd, C. D. (2012). The influence of the freshwater environment and the biological characteristics of Atlantic salmon smolts on their subsequent marine survival. *ICES Journal of Marine Science*, 69(9), 1563–1573. <https://doi.org/10.1093/icesjms/fsr208>
- Sabal, M. C., Merz, J. E., Alonzo, S. H., & Palkovacs, E. P. (2020). An escape theory model for directionally moving prey and an experimental test in juvenile Chinook salmon. *Journal of Animal Ecology*, 89(8), 1824–1836. <https://doi.org/10.1111/1365-2656.13233>
- Saloniemi, I., Jokikokko, E., Kallio-Nyberg, I., Jutila, E., & Pasanen, P. (2004). Survival of reared and wild Atlantic salmon smolts: Size matters more in bad years. *ICES Journal of Marine Science*, 61(5), 782–787. <https://doi.org/10.1016/j.icesjms.2004.03.032>
- Säterberg, T., Jacobson, P., Ovegård, M., Rask, J., Östergren, J., Jepsen, N., & Florin, A.-B. (2023). Species- and origin-specific susceptibility to bird predation among juvenile salmonids. *Ecosphere*, 14(12), e4724. <https://doi.org/10.1002/ecs2.4724>
- Sayer, C. 2024. *Salmo salar* (Europe assessment). The IUCN Red List of Threatened Species 2024: e.T19855A212864916. <https://dx.doi.org/10.2305/IUCN.UK.20242.RLTS.T19855A212864916.en>
- Schwinn, M., Baktoft, H., Aarestrup, K., & Koed, A. (2019). Artificial lakes delay the migration of brown trout (*Salmo trutta*) smolts: A comparison of migratory behaviour in a stream and through an artificial lake. *Journal of Fish Biology*, 94(5), 745–751. <https://doi.org/10.1111/jfb.13950>
- Seber, G. A. F. (1965). A Note on the Multiple-Recapture Census. *Biometrika*, 52(1/2), 249–259. <https://doi.org/10.2307/2333827>
- Smialek, N., Pander, J. & Geist, J. (2021) Environmental threats and conservation implications for Atlantic salmon and brown trout during their critical freshwater phases of spawning, egg development and juvenile emergence. *Fisheries Management and Ecology*, 28, 437–467. <https://doi.org/10.1111/fme.12507>
- Snyder, N. F. R., Derrickson, S. R., Beissinger, S. R., Wiley, J. W., Smith, T. B., Toone, W. D., & Miller, B. (1996). Limitations of Captive Breeding in Endangered Species Recovery. *Conservation Biology*, 10(2), 338–348. <https://doi.org/10.1046/j.1523-1739.1996.10020338.x>

- Stark, E. J., Atkinson, E. J., & Kozfkay, C. C. (2014). Captive rearing for Chinook salmon (*Oncorhynchus tshawytscha*) and Atlantic salmon (*Salmo salar*): The Idaho and Maine experiences. *Reviews in Fish Biology and Fisheries*, 24(3), 849–880. <https://doi.org/10.1007/s11160-014-9346-x>
- Thériault, V., Moyer, G. R., Jackson, L. S., Blouin, M. S., & Banks, M. A. (2011). Reduced reproductive success of hatchery coho salmon in the wild: Insights into most likely mechanisms. *Molecular Ecology*, 20(9), 1860–1869. <https://doi.org/10.1111/j.1365-294X.2011.05058.x>
- Therneau T (2024). A Package for Survival Analysis in R. (Version 3.6.4) [R package]. <https://CRAN.R-project.org/package=survival>.
- Thomas, K., Hansen, T., Brophy, D., Ó Maoiléidigh, N., & Fjelldal, P. G. (2019). Experimental investigation of the effects of temperature and feeding regime on scale growth in Atlantic salmon *Salmo salar* post-smolts. *Journal of Fish Biology*, 94(6), 896–908. <https://doi.org/10.1111/jfb.13971>
- Thorstad, E. B., Bliss, D., Breau, C., Damon-Randall, K., Sundt-Hansen, L. E., Hatfield, E. M. C., Horsburgh, G., Hansen, H., Maoiléidigh, N. Ó., Sheehan, T., & Sutton, S. G. (2021). Atlantic salmon in a rapidly changing environment—Facing the challenges of reduced marine survival and climate change. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31(9), 2654–2665. <https://doi.org/10.1002/aqc.3624>
- Thorstad, E. B., Økland, F., Aarestrup, K., & Heggberget, T. G. (2008). Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. *Reviews in Fish Biology and Fisheries*, 18(4), 345–371. <https://doi.org/10.1007/s11160-007-9076-4>
- Thorstad, E. B., Økland, F., Finstad, B., Sivertsgård, R., Plantalech, N., Bjørn, P. A., & McKinley, R. S. (2007). Fjord migration and survival of wild and hatchery-reared Atlantic salmon and wild brown trout post-smolts. In P. R. Almeida, B. R. Quintella, M. J. Costa, & A. Moore (Eds.), *Developments in Fish Telemetry* (pp. 99–107). Springer Netherlands. https://doi.org/10.1007/978-1-4020-6237-7_11
- Thorstad, E. B., Uglem, I., Arechavala-Lopez, P., Økland, F., & Finstad, B. (2011). Low survival of hatchery-released Atlantic salmon smolts during initial river and fjord migration. *Boreal environment research*, 16(2), 115.
- Thorstad, E. B., Uglem, I., Finstad, B., Chittenden, C. M., Nilsen, R., Økland, F., & Bjørn, P. A. (2012). Stocking location and predation by marine fishes affect survival of hatchery-reared Atlantic salmon smolts. *Fisheries Management and Ecology*, 19(5), 400–409. <https://doi.org/10.1111/j.1365-2400.2012.00854.x>
- Thorstad, E. B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H., & Finstad, B. (2012). A critical life stage of the Atlantic salmon *Salmo salar*: Behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*, 81(2), 500–542. <https://doi.org/10.1111/j.1095-8649.2012.03370.x>

- Thorstad, E. B., Whoriskey, F., Rikardsen, A. H., & Aarestrup, K. (2011). Aquatic nomads: the life and migrations of the Atlantic salmon. *Atlantic salmon ecology*, 1(6), 1-32.
- Thorstad, E.B., Økland, F., Finstad, B., Sivertsgård, R., Bjørn, P., & McKinley, R. (2004). Migration speeds and orientation of Atlantic salmon and sea trout post-smolts in a Norwegian fjord system. *Environmental Biology of Fishes*, 71(3), 305–311. <https://doi.org/10.1007/s10641-004-1264-7>
- Todd, C.D., Friedland, K.D., MacLean, J.C., Hazon, N., Jensen, A.J. (2011). Getting into Hot Water? Atlantic salmon responses to climate change in freshwater and marine environments. In Ø. Aas, S. Einum, A. Klemetsen, & J. Skurdal (Eds.), *Atlantic salmon ecology* (pp. 409–433). Wiley-Blackwell.
- Urke, H. A., Kristensen, T., Ulvund, J. B., & Alfredsen, J. A. (2013). Riverine and fjord migration of wild and hatchery-reared Atlantic salmon smolts. *Fisheries Management and Ecology*, 20(6), 544–552. <https://doi.org/10.1111/fme.12042>
- Vilhunen, S. (2006). Repeated antipredator conditioning: A pathway to habituation or to better avoidance? *Journal of Fish Biology*, 68(1), 25–43. <https://doi.org/10.1111/j.0022-1112.2006.00873.x>
- Vincent, R. E. (1960). Some influences of domestication upon three stocks of brook trout (*Salvelinus fontinalis* Mitchell). *Transactions of the American fisheries society*, 89(1), 35-52.
- Vollset, K., Urdal, K., Utne, K., Thorstad, E., Sægvog, H., Raunsgård, A., Skagseth, Ø., Lennox, R., Østborg, G., Ugedal, O., Jensen, A., Bolstad, G., & Fiske, P. (2022). Ecological regime shift in the Northeast Atlantic Ocean revealed from the unprecedented reduction in marine growth of Atlantic salmon. *Science Advances*, 8. <https://doi.org/10.1126/sciadv.abk2542>
- Waldman, J. R., & Quinn, T. P. (2022). North American diadromous fishes: Drivers of decline and potential for recovery in the Anthropocene. *Science Advances*, 8(4), eab15486. <https://doi.org/10.1126/sciadv.ab15486>
- Walsh, S. J., Jelks, H. L., & Burkhead, N. M. (2011). The decline of North American freshwater fishes. *Am Curr*, 36(4), 10-17.
- Watt, W. D. (1987). A summary of the impact of acid rain on Atlantic salmon (*Salmo salar*) in Canada. *Water, Air, and Soil Pollution*, 35(1), 27–35. <https://doi.org/10.1007/BF00183841>
- Webb, J. H., Verspoor, E., Aubin-Horth, N., Romakkaniemi, A., & Amiro, P. (2007). The Atlantic salmon. In E. Verspoor, L. Stradmeyer, & J. L. Nielsen (Eds.), *The Atlantic salmon: Genetics, conservation and management* (pp. 17–56). Blackwell Publishing.
- Weir, L. K., Hutchings, J. A., Fleming, I. A., & Einum, S. (2004). Dominance relationships and behavioural correlates of individual spawning success in farmed and wild male Atlantic salmon, *Salmo salar*. *Journal of Animal Ecology*, 73(6).
- World Wide Fund for Nature (WWF). (2001). WWF annual report 2000/2001. WWF International.
- Wood, S. N. (2024). mgcv: Mixed GAM computation vehicle with automatic smoothness estimation (Version 1.9.1) [R package]. [CRAN: Package mgcv](https://cran.r-project.org/web/packages/mgcv/index.html)

- Woodward, C. C., & Strange, R. J. (1987). Physiological Stress Responses in Wild and Hatchery-Reared Rainbow Trout. *Transactions of the American Fisheries Society*, 116(4), 574–579. [https://doi.org/10.1577/1548-8659\(1987\)116<574:PSRIWA>2.0.CO;2](https://doi.org/10.1577/1548-8659(1987)116<574:PSRIWA>2.0.CO;2)
- Young, K. A., Chaput, G., Knight, P., Russell, I., Sivertsen, A., Hutchinson, P., & Forero Segovia, S. L. (Eds.). (2017). Understanding the risks and benefits of hatchery and stocking activities to wild Atlantic salmon populations (NASCO Council Document CNL(17)61, 116 pp.). North Atlantic Salmon Conservation Organization.
- Zarate, J., & Bradley, T. M. (2003). Heat shock proteins are not sensitive indicators of hatchery stress in salmon. *Aquaculture*, 223(1), 175–187. [https://doi.org/10.1016/S0044-8486\(03\)00160-1](https://doi.org/10.1016/S0044-8486(03)00160-1)

APPENDIX A – CHAPTER 3 SUPPLEMENTARY MATERIAL

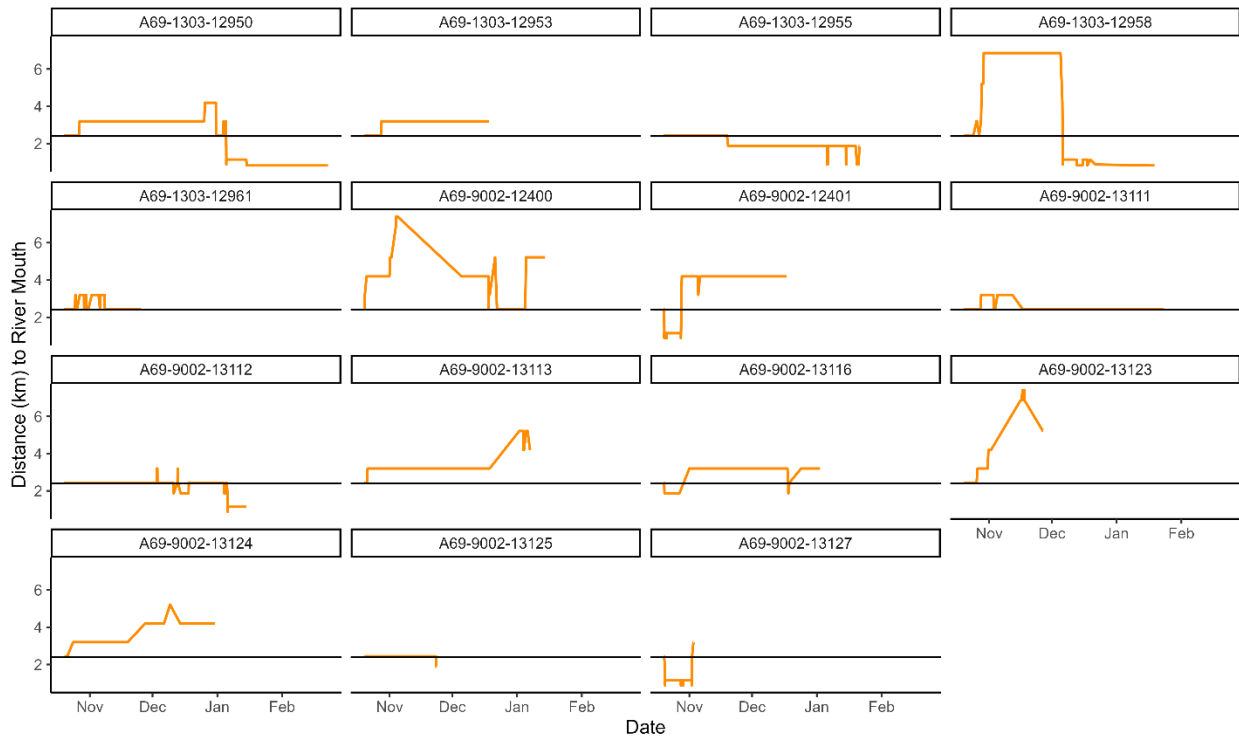


Figure 13. Graph portraying the river movement of smolt-to-adult supplemented (SAS) salmon that spent 1 year in captivity at the Aquatron Laboratory (SAS1) before being released into the Clyburn Brook in October 2023 (n=15). Each block is an individual fish and the black horizontal line represents the release point.

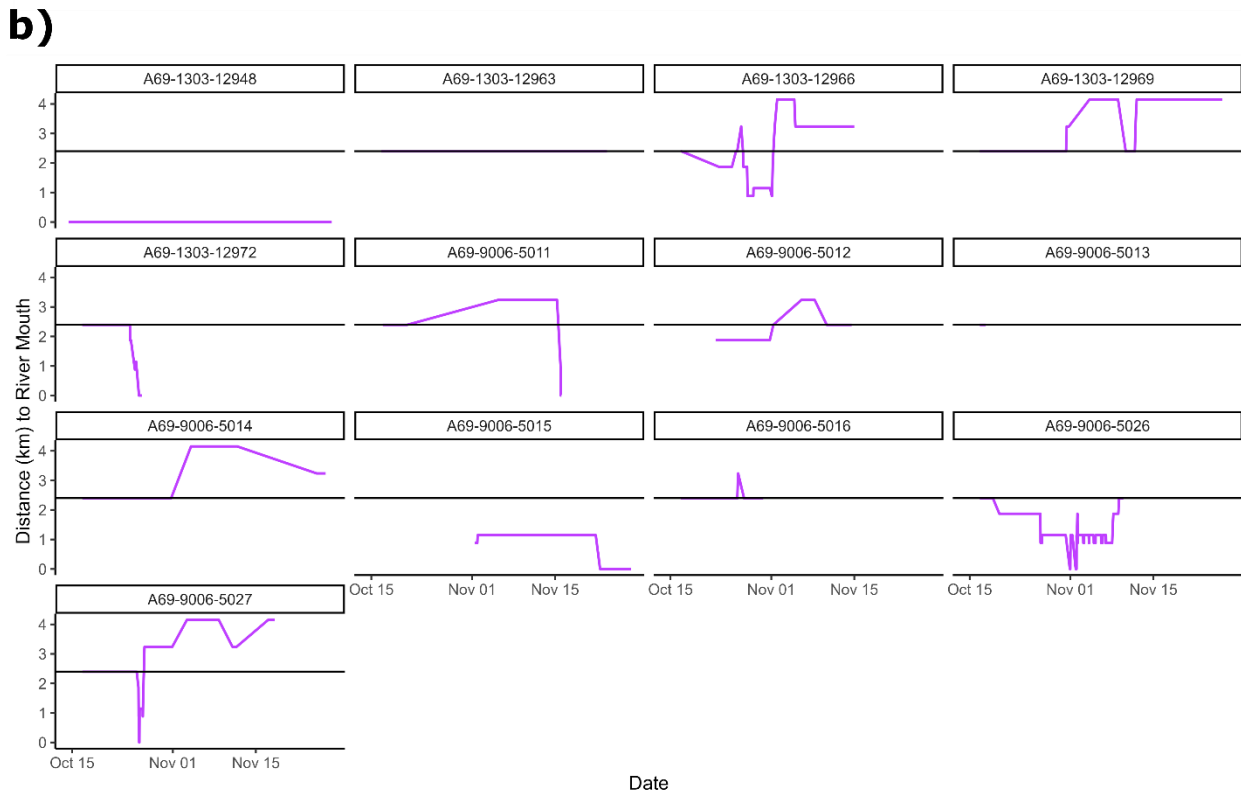
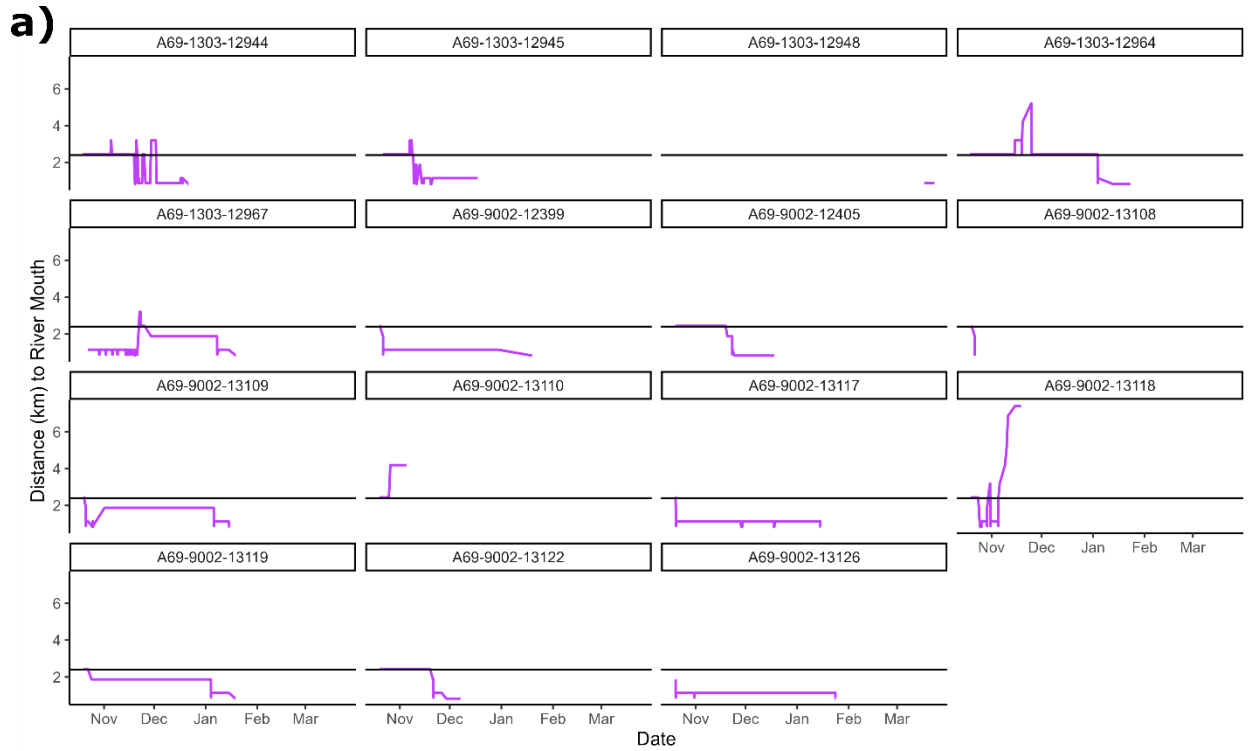


Figure 14. a) Graph portraying the river movement of smolt-to-adult supplemented (SAS) salmon that spent 2 years in captivity at the Aquatron Laboratory (SAS2) before being released into the Clyburn Brook in October 2023 (n=15). b) Graph portraying the river movement of smolt-to-adult supplemented (SAS) salmon that spent 2 years in captivity at the Aquatron Laboratory (SAS2) before being released into the Clyburn Brook in October 2024 (n=13). Each block is an individual fish and the black horizontal line represents the release point.

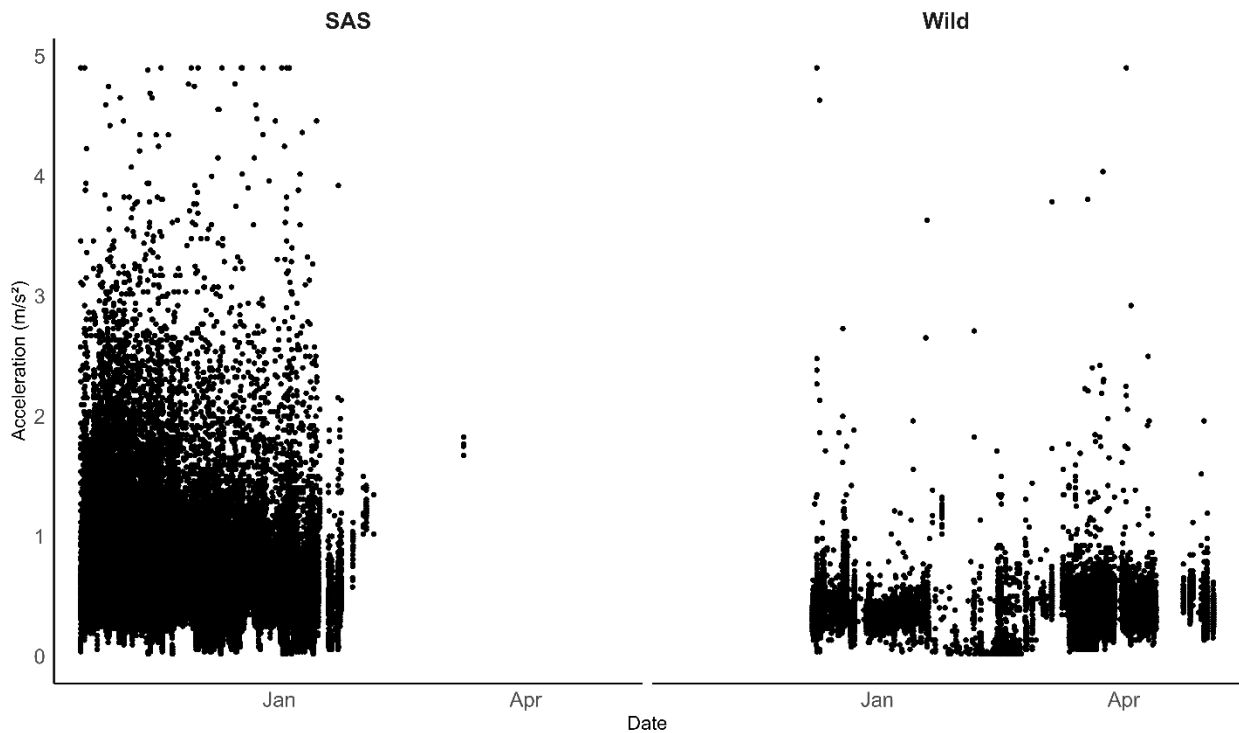


Figure 15. Comparison of raw acceleration detections (m/s^2) of SAS and wild salmon from October 2023 to May 2024 in Clyburn Brook and Chéticamp River respectively. Each point represents a single acceleration reading from an individual fish tag.

APPENDIX B – CHAPTER 2 R CODE ANALYSIS

```
library(Rmark)
library(glmmTMB)
library(emmeans)
library(adehabitatHR)
library(sp)

##### Cormack Jolly Seber Survival Analysis #####

# Convert detection timestamps to binary (1 = detected, 0 = not detected)

cjs_df <- cjs_df %>%
  select(-Transmitter, -Group) %>%
  mutate(across(everything(), ~ ifelse(is.na(.), 0, 1)))

# Create capture histories (CH strings like "110011...")

ch <- apply(cjs_df[, -(1:2)], 1, paste0, collapse = "")

# Process capture data for CJS model (group = wild/SAS)

smolt.proc <- process.data(cjs_marked_df, model = "CJS", groups = "Group")
smolt.ddl <- make.design.data(smolt.proc)

# Label each receiver interval for survival (Phi) and detection (p)

receiver_names <- c("A0", paste0("A", 1:16)) # Total 17 receivers (A0 to A16)

# Tag each interval with array names

smolt.ddl$Phi$array <- factor(smolt.ddl$Phi$time, labels = receiver_names[1:16])
smolt.ddl$p$array <- factor(smolt.ddl$p$time, levels = 1:17, labels = receiver_names)
```

```
# Model fitting
# Model 1: interaction between Group and array (for both survival and detection). Chosen model
used
```

```
mod1 <- mark(
  smolt.proc, smolt.ddl,
  model.parameters = list(
    Phi = list(formula = ~ Group * array),
    p = list(formula = ~ Group * array)
  ))
```

```
# Model 2: additive model (Group + array)
```

```
mod2 <- mark(
  smolt.proc, smolt.ddl,
  model.parameters = list(
    Phi = list(formula = ~ Group + array),
    p = list(formula = ~ Group + array)
  ))
```

```
# Model 3: survival by Group only; constant detection
```

```
mod3 <- mark(
  smolt.proc, smolt.ddl,
  model.parameters = list(
    Phi = list(formula = ~ Group),
    p = list(formula = ~ 1)
  ))
```

```
# Comparing models
```

```
models <- collect.models()
```

```
##### Migration Speed GLMM analysis #####
```

```
# creating body lengths / second dataset
```

```
blspeed <- glatevents_clean %>%
```

```

  arrange(animal_id, first_detection) %>% # arranging first detections at each receiver for
  each fish chronologically
  group_by(animal_id) %>%
  mutate(
    time_diff_sec = as.numeric(difftime(lead(first_detection), first_detection, units =
"secs")), # calculating the time difference between consecutive receivers for each fish in
seconds
    dist_diff_m = lead(distance_m) - distance_m, # calculating the difference between
each consecutive receiver station
    bl_per_sec = (dist_diff_m / time_diff_sec) / (length_cm / 100), # length in cm to m,
calculating body lengths per second for each fish and section by determining m/s and
then dividing by each fish body length to standardize for length.
    from_sec = Section,
    to_sec = lead(Section)
  ) %>%
  ungroup() %>%
  filter(!is.na(bl_per_sec), bl_per_sec > 0, is.finite(bl_per_sec))

```

glmm modelling

```

model_glmm <- glmmTMB(bl_per_sec ~ to_sec * group + weight_kg + releaseday +
  (1 | animal_id),
  data = blspeed,
  family = Gamma(link = "log"))

```

Ocean movement minimum convex polygons

Running 100% MCP

```
mcp_temp_lhv <- mcp(subset[, "uid"], percent = 100)
```

Flattening the spatial polygon into a data frame for plotting

```
mcp_fortified_lhv <- fortify(mcp_temp_lhv)
mcp_fortified_lhv$group <- g
```

Saving this MCP into my list

```

mcp_list[[paste(g, m, sep = "_")] <- mcp_fortified_lhv
}
} }

```

APPENDIX C – CHAPTER 3 R CODE ANALYSIS

```
library(survival)
```

```
library(mgcv)
```

```
library(stats)
```

```
library(adehabitatHR)
```

```
library(sp)
```

Cox Proportional Hazards Model for survival analysis

```
#Calculate time in days relative to study_start_date
```

```
time = as.numeric(difftime(fatedate, study_start_date, units = "days")), # Time in days
```

```
# code fate with 1 = death and 0 = survived
```

```
event = ifelse(is.na(fatedate) & fate == 1, 1, # 1 = death, but censored if no fatedate  
ifelse(is.na(fatedate), 0, 1)), # 0 = censored if no fatedate, 1 = death
```

```
# Fit Cox Proportional Hazards Model with group object representing SAS1 and SAS2 cohorts
```

```
cox_model <- coxph(Surv(time, event) ~ group + sex, data = fish_data)
```

Global acceleration level model analysis

```
# Fitting a GAMM (Generalized Additive Mixed Model) using 'bam'
```

```
# Response: trueaccel
```

```
# Predictors: group (fixed, wild and SAS salmon), hour_of_day (cyclical smooth), days (smooth  
by group)
```

```
# Random effect: transmitter_id (each fish)
```

```
# Family: Gamma (log link), acceleration is only positive continuous data
```

```
m1 <- bam(trueaccel ~ group + s(hour_of_day, bs = "cc", k = 5) + # Cyclical smooth for  
time of day
```

```
s(days, bs = "tp", k = 5, by = group) + # Group-specific smooth over days  
s(transmitter_id, bs = "re"), # Random effect for individual fish
```

```
family = Gamma(link = "log"), data = acc_hm3, method = "fREML", discrete = TRUE)
```

River exit linear regression analysis

```
#Linear Model
```

```

exited_only <- rexit_clean[rexit_clean$event == 1, ] # only including fish that were
detected exiting the river (event == 1 is confirmed exit)

lm_model <- lm(riverdays ~ group, data = exited_only) # wild vs SAS for group with
riverdays representing the number of days between release and river exit

##### Ocean movement minimum convex polygons #####
# Grabbing the month from detection datetime
oceanets$month <- month(oceanets$dt, label = TRUE)
# Just want Feb to July in a specific order for plotting later
month_order <- c("Feb", "Mar", "Apr", "May", "Jun", "Jul")
oceanets <- oceanets %>% filter(month %in% month_order) %>%
mutate(month = factor(month, levels = month_order))
#Making a list to store MCP polygons for each group in each month
mcp_list <- list()
# Going to loop through each month and group combo
for (m in unique(oceanets$month)) {
  for (g in unique(oceanets$group)) {
# Filter detections just for that month & group
subset <- oceanets %>%
  filter(month == m, group == g, !is.na(llon), !is.na(llat)) %>%
  select(llon, llat, transmitter_id)

# Only compute MCP if there's enough data (needs 5+ points)
if (nrow(subset) >= 5) {
coordinates(subset) <- ~llon + llat # Converting to spatial object for MCP calculation
proj4string(subset) <- CRS("+proj=longlat +datum=WGS84")

# Giving each group-month combo a unique ID for MCP
subset$uid <- paste(g, m, sep = "_")

# Running 100% MCP
mcp_temp <- mcp(subset[, "uid"], percent = 100)

# Flattening the spatial polygon into a data frame for plotting
mcp_fortified <- fortify(mcp_temp)
mcp_fortified$group <- g
mcp_fortified$month <- m

# Saving this MCP into my list

```

```
    mcp_list[[paste(g, m, sep = "_")] ] <- mcp_fortified
  }
} }
# Combine all the MCPs into one data frame for plotting
mcp_df_all <- bind_rows(mcp_list)
#Reorder months again just to be safe before plotting
mcp_df_all$month <- factor(mcp_df_all$month, levels = month_order)
```