The Post-Spawning Ecology of Iteroparous Salmonids: Basis of Variability in Migratory Behaviour and Survival, Ecological Importance and Conservation Implications

by

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Ma thèse est dédiée à mes parents, qui m'ont élevé avec amour, et qui, dès mon jeune âge, m'ont donné les outils nécessaires pour développer ma curiosité et persévérer dans le doute. À mon grand-père, Normand, qui m'a appris à faire d'une passion ma carrière. Et particulièrement à mon grand amour, grâce à qui tout est devenu si clair. Finalement, à notre fils, Lucas, né entre « deadlines » et promenades sur la côte, à qui je léguerai ma passion pour le monde naturel dans toute sa beauté, sa complexité et sa fragilité.

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Abstract

The overarching objective of my thesis is to shed light on a poorly understood life history stage of salmonid fish species, by quantifying spatio-temporal variation in the ecological importance of iteroparity (i.e. repeated breeding), as well as the factors influencing the movement ecology and survival of post-spawners, in freshwater, estuaries, and at sea. To do so, I used a variety of methods, including the analysis of long-term empirical data series, in addition to acoustic telemetry and physiological sampling, which I applied at various spatial and temporal scales and for two different but related iteroparous salmonid species – Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). The work identified some of the potential causes of inter-individual variation in migratory decisions and success, as well as the consequences for population-level processes. Throughout my studies, I consistently observed that, after spawning, nutritionally depleted (i.e. low body condition factor and/or plasma triglyceride concentration) or highly stressed individuals (i.e. high plasma cortisol and glucose concentrations) opted for riskier migratory tactics, which might reflect their higher energetic requirements and the necessity to accept greater risks in trying to offset these and recondition for future spawning attempts. While I showed that post-spawning migratory decisions, survival, and ultimately the degree of iteroparity are at least partly mediated by endogenous constraints related to the costs of reproduction, I also documented the consequences of additional anthropogenic stressors that are likely limiting repeat spawning potential in some regions. Collectively, my thesis provides valuable biological insights into the factors currently limiting repeat spawning ability and highlights the potential for increases in iteroparity to occur when anthropogenic threats are mitigated, with quantified benefits to population resilience. Moreover, considering that iteroparity is a bet-hedging strategy allowing individuals to spread the risk of reproductive failure over multiple years, addressing these issues is of particular importance for the management of declining salmonid populations, especially under increasing environmental variability associated with climate change.

List of Abbreviations Used

1SW	One sea-winter
2SW	Two sea-winter
AIC	Akaike information criterion
AICc	Corrected Akaike information criterion
ANCOVA	Analysis of covariance
BCI	Body condition index
°C	Degree Celsius
CI	Confidence interval
cm	Centimeter
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
DFA	Dynamic Factor Analysis
DFO	Department of Fisheries and Oceans Canada
DMR	Maine Department of Marine Resources
DNA	Deoxyribonucleic acid
DPS	Distinct Population Segment
DU	Designatable Unit
ELISA	Enzyme-linked immunosorbent assay
FL	Fork length
FRQNT	Fonds de recherche du Québec – Nature et technologies
g	Gram
g	Gravitational constant
h	Hour
HCL	Hydrogen chloride
HPI	Hypothalamic-pituitary-interrenal axis
ICES	International Council for the Exploration of the Sea
kg	Kilogram
kHz	Kilohertz

km	Kilometer
L	Liter
m	Meter
MFFP	Ministère des Forêts, de la Faune et des Parcs du Québec
min	Minute
ml	Milliliter
mm	Millimeter
mmol	Millimole
MS222	Tricaine methanesulphonate
MSW	Multi sea-winter
n	Sample size
NASCO	North Atlantic Salmon Conservation Organization
ng	Nanogram
nm	Nanometer
NSERC	Natural Sciences and Engineering Research Council of Canada
NTNU	Norwegian University of Science and Technology
OTN	Ocean Tracking Network
P	Proportion
p	*p*-value
PCR	Polymerase chain reaction
pg	Picogram
PGE_2	Plasma prostaglandin E_2
ppt	Parts per thousand
r	Correlation coefficient
R^2	Coefficient of determination
RS	Repeat spawner
s	Second
SD	Standard deviation
SW	Sea-age at maturity

t	Time step
TRIG	Plasma triglyceride concentration
µl	Microliter
UNESCO	United Nations Educational, Scientific and Cultural Organization
WGNAS	Working Group on North Atlantic Salmon

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Chapter 1

Introduction

In the face of global declines of wild animal populations caused by expanding natural and anthropogenic stressors (Ceballos *et al.*, 2017; Bar-On *et al.*, 2018), a key aspect of population persistence involves the capacity of members of the population to reproduce and maintain sufficient recruitment to compensate for increasing mortality risks. This poses additional challenges for marine and anadromous migratory species that can undertake long-distance migration to distant oceanic feeding grounds, in addition to the added management complexity surrounding conflicting perception of their ecological, socio-cultural, and economic worth (Lascelles *et al.*, 2014; Runge *et al.*, 2014). Confronted by this global crisis, new tools are becoming available to help us document aquatic animal movements in the ocean. As such, the recent development of electronic tracking technologies (Hussey *et al.*, 2015) and globally-linked tracking infrastructure such as that operated by the Ocean Tracking Network (Iverson *et al.*, 2019), now enables trans-boundary research aiming at better understanding the factors influencing the migratory behaviour and survival of aquatic migratory species, especially during their previously hidden marine phase.

In recent decades, many populations of anadromous salmonid fishes, that can undertake long distance migrations from home rivers to feeding pastures at sea and return to their natal sites for spawning, have experienced declines. While many factors are believed to have contributed to these declines, including over-exploitation, anthropogenic alteration of freshwater and coastal habitats, as well as changes in oceanographic conditions (Parrish *et al.*, 1998; Welch *et al.*, 2000; Nehlsen *et al.*, 2004; Chaput, 2012; ICES, 2013, 2018; Lehnert *et al.*, 2019), the magnitude of the factors responsible for high variability in marine survival rates remain mostly unknown (Friedland *et al.*, 2014). Significant research efforts have been directed at understanding the factors influencing the behaviour and survival of young salmonids (termed “smolts”)

during the early portion of their first migration to sea (Thorstad *et al.*, 2011; Drenner *et al.*, 2012). However, very little is known about the ecology and importance of the post-spawning (or kelt) life history stage of iteroparous salmonid species, which can reproduce multiple times during their lifespan (Halttunen, 2011; Thorstad *et al.*, 2011; Drenner *et al.*, 2012). As with any iteroparous species, understanding population demography and recovery potential requires knowledge of the natural and anthropogenic factors influencing the extent of the reproductive lifespan of individuals and their lifetime reproductive contributions. Moreover, with increasing variability in the survival of offspring, natural selection should theoretically favor life histories that spread the risk of reproductive failure over time (Murphy, 1968; Stearns, 1976). As such, the ecological importance of iteroparity might be particularly salient under increasing environmental variability associated with climate change (Stenseth *et al.*, 2002).

In this context, my thesis sheds light on the ecology of the poorly understood post-spawning and reconditioning life history stage of salmonid fish species, by quantifying spatio-temporal variation in the ecological importance of iteroparity. It also documents the endogenous and additional anthropogenic factors influencing the movement ecology and survival of post-spawners in freshwater, estuaries, and at sea. These are key aspects currently limiting our understanding of the resilience of declining iteroparous salmonid populations. Below, I present an overview of the endogenous and ecological considerations that can ultimately affect the reproductive lifespan of iteroparous salmonid species. While migratory decisions are at least partially based on an individual's condition and needs which are associated with physiological capacities and processes (reviewed in Hinch et *al.*, 2005), the level of resources invested into reproduction affects the post-spawning energetic condition of individuals (i.e. costs of reproduction). The level of reproductive investments then have implications for migratory decisions and success, ultimately affecting repeat-spawning potential.

1.1 The Costs of Reproduction

Throughout the branches of life, organismal fitness is constrained by life history trade-offs in the form of competitive allocation of limited resources towards one life history trait at the expense of another. For example, limited energy supplies must be partitioned among the competing functions of reproduction, growth, maintenance, storage and survival (Stearns, 1989). A predominant life history trade-off involves the differential investment of energy reserves into current reproduction versus those required for self-maintenance, survival, and/or future reproductive potential (Stearns, 1989). In sexually reproducing organisms, this trade-off is particularly important for capital breeders, which rely on somatic energy reserves accrued prior to breeding to power migrations to breeding areas, produce gametes, and support the behaviour necessary for successful courtship and mating (Stearns, 1989; Jager *et al.*, 2008). While high reproductive investment should increase current reproductive success, it can imply costs in terms of post-breeding mortality and a reduced likelihood of future reproduction (i.e. costs of reproduction; Williams 1996). At one end of the spectrum, maximum investment into a single life-time reproductive event (termed semelparity) is favored where there is low variability in juvenile survival and low post-breeding survival (Murphy, 1968). At the other end of the spectrum, species have evolved to conserve resources to favor a higher probability of breeding more than once (termed iteroparity) (Cole, 1954; Murphy, 1968). With increasing variability in the survival of offspring, natural selection favors life histories that spread the risk of reproductive failure over time (i.e. iteroparity), if post-breeding survival probability is sufficiently high (Murphy, 1968; Stearns, 1976).

Within salmonids, evolution has favored the development of contrasting investment strategies among and within species. As such, semelparity and iteroparity can exist as a continuum, as manifested by intra-specific variability in the occurrence of iteroparity, as described among populations of anadromous salmonid fish species such as Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), Arctic charr (*Salvelinus alpinus*), brook trout (*Salvelinus fontinalis*), Dolly Varden charr (*Salvelinus malma*),

rainbow / steelhead trout (*Oncorhynchus mykiss*), cutthroat trout (*Oncorhynchus clarki*) (reviewed in Fleming, 1998), as well as Chinook salmon (*Oncorhynchus tshawytscha*) (Barry *et al.*, 2001). In contrast, other salmonid species such as sockeye salmon (*Oncorhynchus nerka)*, coho salmon (*Oncorhynchus kisutch*), chum salmon (*Oncorhynchus keta*), and pink salmon (*Oncorhynchus gorbuscha*) are strictly semelparous (reviewed in Fleming, 1998). The life history trade-off between current reproduction and survival is well illustrated within the semelparity – iteroparity continuum of salmonid fishes, where high total energy expenditure during reproduction is negatively associated with the probability of future (repeat) breeding (i.e. highest energetic investment and lowest survival to future spawning (0 %) in semelparous species, followed by Atlantic salmon and steelhead trout which make intermediate investments in spawning and have a 10 – 11 % proportion of repeat spawners, and finally the brown trout and Arctic charr which have the lowest energy investments but the highest proportions of repeat spawners of 34 – 41 %) (Fleming, 1998; Fleming and Reynolds, 2004). This continuum can also manifest among populations of the same species, as illustrated in Atlantic salmon, where the average total energy expenditure by individuals for reproduction was negatively correlated with the average post-spawning survival rate of the population (Jonsson *et al.*, 1997).

While inter-population differences in the post-spawning survival of salmonids can partly result from differences in habitat (Jonsson *et al.*, 1991) and/or anthropogenic disturbances (e.g. Nyqvist *et al.*, 2016; Maynard *et al.*, 2017), these inter-population differences are also associated with variation in other life-history traits such sea-age at first maturity and body size that are known to influence individual reproductive investment, subsequent post-spawning survival, and population demographics (Fleming and Reynolds 2004, Jonsson and Jonsson 2011a). In general, smaller early-maturing salmon (termed one sea winter, or 1SW) invest proportionally less into reproduction (40 – 60 % of total energy reserves) than larger multi sea winter (MSW) individuals (up to 70 % of total energy reserves), and show higher post-spawning survival (Jonsson *et al.*, 1991, 1997; Fleming, 1998; Jonsson and Jonsson, 2003, 2011a). A recent study identified

a genotypic co-inheritance between sea-age at maturity and iteroparity in Atlantic salmon, with iteroparity being more likely in smaller, earlier-maturing salmon that generally invest proportionally less into reproduction (Aykanat *et al.*, 2019), showing the trait is heritable. In addition to body size considerations, reproductive investment should also vary among individuals due to differences in pre-breeding energetic reserves resulting from inter-individual variability in feeding success and lipid storage efficiency prior to reproduction, as well as for the potential of some individuals to hold back on reproductive investment for a higher probability of future spawning (Christie *et al.*, 2018).

Due to the high energy expenditure required for their spawning migration and investment into current reproductive efforts, post-spawned salmonids (or "kelts") are energetically and nutritionally depleted (Jonsson *et al.*, 1997; Fleming and Reynolds, 2004). In combination with sparse feeding opportunities in freshwater through the winter months, kelts depend on remaining somatic lipid reserves to survive (Jonsson *et al.*, 1997; Jonsson and Jonsson, 2011a). At the cellular level, when energy expenditure surpasses energy intake, lipids that were stored in adipose and muscle tissues during the feeding season are mobilized into circulation as triglycerides. Triglycerides are then hydrolyzed (lipolysis) to produce glycerol and free fatty acids, the major energy substrate in fish (Sargent *et al.*, 2002). During starvation, as energy stores are exhausted, plasma triglyceride concentration diminishes as the animal struggles to sustain basal metabolic processes (Kakizawa *et al.*, 1995). As such, plasma triglyceride concentration has been shown to be a useful, non-lethal indicator of nutritional status in many taxa, including wild salmonids (Boel *et al.*, 2014; Gauthey *et al.*, 2015), and is therefore a good candidate parameter for testing hypotheses about condition-dependent models of migratory behaviour in wild animals. While the costs of reproduction ultimately affects the probability of repeated breeding, it remains unclear how post-spawning condition affects aspects of the spatio-temporal habitat use and survival of reconditioning salmonid fishes, especially at sea.

1.2 Implications of Post-Spawning Condition for Migratory Decisions

From an evolutionary point of view, migration can be regarded as an individual adaptation to changing life history requirements and resource availability, allowing animals to exploit heterogeneous environments by travelling among different habitats at specific stages of their life cycles (Dingle, 2006). As an individually expressed trait, migration can also be viewed as a syndrome, shaped by natural selection, wherein correlated behavioural, physiological, morphological and other traits work together to maximize fitness within a life-history context (Dingle, 2006). Migration tendency also varies, among individuals, populations and species. For example, within-population migratory-dimorphism, or "partial migration", has been described in many species of invertebrates, fishes, amphibians, birds, and mammals, in which a certain proportion of a population remains resident (Chapman *et al.*, 2011), whereas others move to varying degrees among different habitats. However, little is known about the proximate control mechanisms of inter-individual variation in migratory tendency (Chapman *et al.*, 2011; Lennox *et al.*, 2019), as well as the associated consequences for population-level processes. While differences in migratory tendency can have both environmental and genetic links (Pulido, 2011), the degree to which these contribute can vary widely (Ferguson *et al.*, 2019). According to the conditional strategy concept, different tactics regulated by the same genotype can be maintained within populations (Gross and Repka, 1998). This can occur when the migratory decisions and fitness gained from alternative tactics depend primarily on individual phenotype (e.g. age, size, sex, energetic state, etc.; Repka and Gross, 1995; Gross and Repka, 1998). For example, in anadromous brown trout, phenotypic expression related to lipid biosynthesis and metabolism differ markedly between migratory and resident individuals living sympatrically (Wysujack *et al.*, 2009). By mediating the relationships between organism and their environment, physiological processes related to metabolism, nutrition and thermal relationships (Ricklefs and Wikleski, 2002) are increasingly being recognized as key to explaining animal variation in life-history traits and behaviour (Hinch *et al.*, 2005). The coupling of physiological sampling techniques with rapidly developing electronic

tracking technology has set a new course in the study of inter-individual variability, helping us to understand the environmental and anthropogenic factors affecting animal behaviour and survival (Cooke *et al.*, 2008, 2012).

Among migratory animals, the salmonid fishes (sub-family Salmoninae) are excellent models for the study of life history variation due to the high adaptability and phenotypic plasticity they exhibit, in combination with the prior scientific knowledge that has illuminated many aspects of their ecology and evolution (Hendry and Stearns, 2004). Salmonids display high variability in reproductive investment strategy (i.e. semelparity – iteroparity continuum) and migratory tendency and behaviour (Fleming and Reynolds, 2004; Hendry *et al.*, 2004; Jonsson and Jonsson, 2011b; Thorstad *et al.*, 2011). Despite high levels of reproductive investment (discussed above), iteroparous anadromous salmonids (e.g. Atlantic salmon and brown trout), have the capacity to survive a first spawning episode, and make return migrations to foraging areas to grow (increasing potential reproductive output) and to restore somatic energy reserves for future attempts (Jonsson and Jonsson, 2011b; Thorstad *et al.*, 2011). However, for energetically depleted kelts, their post-spawning energetic condition is believed to be an important mediator of migratory decision making and subsequent survival (Belding, 1934; Jonsson *et al.*, 1997; Halttunen *et al.*, 2013; Thorstad *et al.*, 2016).

After spawning in late fall, the extent to which post-spawned salmonids use their natal watercourses as overwintering habitat depends on the species and the availability of key hydrological features such as the presence of deep pools or accessible lakes that offer secure habitat (Cunjak *et al.*, 1998; Olsen *et al.*, 2006). But even when these are present, both post-spawned Atlantic salmon and brown trout exhibit strong individual variability in out-river migration timing, with some individuals of a population leaving shortly after spawning (late fall/early winter) and others exiting in the spring (summarized in Jonsson and Jonsson, 2011; Thorstad *et al.*, 2016). Although overwintering in fresh water is a common strategy for kelts, the winter months offer poor feeding opportunities. Kelts must therefore rely primarily on somatic lipid reserves to sustain basic metabolic costs (Jonsson *et al.*, 1997; Jonsson and Jonsson, 1998),

pointing towards the importance of post-spawning energetic condition in mediating migratory decisions and survival. As such, Halttunen *et al.* (2013) reported that Atlantic salmon kelts with low body condition exited freshwater soon after spawning in an attempt to restore their depleted state via estuarine or marine foraging, while kelts in better condition delayed migration until the spring (i.e. when foraging conditions at sea were near seasonal peaks). The presumed benefits of staying in fresh water were probably related to a low metabolic cost due to colder temperatures in the fresh water compared to the sea in southern and mid-latitudinal regions (Jobling, 1994) or to avoid < 0°C seawater at higher latitudes, as well as decreased predation risk (Gross *et al.*, 1988). The energy lost during migration and spawning is roughly proportional to fish length (Jonsson *et al.*, 1997), which likely explains the fairly common trend observed in anadromous brown trout and Atlantic salmon kelts where larger fish usually migrate out sooner (Bendall *et al.*, 2005; Halttunen *et al.*, 2013; Thorstad *et al.*, 2016).

Once they have left freshwater, residency and habitat use in estuaries and near shore marine areas can also be highly variable among and within anadromous salmonid populations. Environmental cues (e.g. river discharge, water temperature, photoperiod) can predict the timing of seawater entry of juvenile salmonid smolts, which tends to occur each year within a narrow window of opportunity (e.g. few weeks to a month) (Jensen *et al.*, 2012; Otero *et al.*, 2014; Thorstad *et al.*, 2016). However, for kelts, the temporal window for migration is wide (e.g. autumn and spring migrants) and less predictable, and does not appear to be linked to discreet environmental cues (e.g. Halttunen *et al.*, 2013), suggesting an increased importance of endogenous factors in mediating post-spawning migratory decisions. For example, inter-individual variation in the estuarine residency of Atlantic salmon kelts can range from a few days (Hubley *et al.*, 2008) to upwards of several weeks (Hedger *et al.*, 2009), which might be associated with a period of feeding in response to the requirement to improve somatic reserves for seaward migration (Hedger *et al.*, 2009) and/or to facilitate osmoregulatory acclimation to sea-water (Hubley *et al.*, 2008). Once at sea, Atlantic salmon kelts can spend as little as a few months to more than a year for reconditioning, before coming back to spawn as

consecutive or alternate repeat spawners, respectively (Jonsson *et al.*, 1991; Fleming, 1996). While the great majority of Atlantic salmon repeat spawners only survive to reproduce twice, the maximum number of reproductive cycles reported for an adult Atlantic salmon is seven (Chaput and Jones, 2006).

In the Canadian Maritime region there appears to be two migratory strategies for Atlantic salmon kelts: short-distance migrants residing in coastal waters for a short (< 1 year) period of time (i.e. salmon first maturing after one-sea-winter [1SW] and consecutive repeat spawners); and longer-distance migration to oceanic feeding grounds of the Labrador Sea and West Greenland (salmon first maturing after multiple-sea-winters [MSW] and alternate repeat spawners) (Ritter, 1989; Hubley *et al.*, 2008; Chaput and Benoit, 2012; Lacroix, 2013; Strøm *et al.*, 2017). While the timing of downriver migration to the marine environment, and to some extent the overwinter survival of Atlantic salmon kelts have been linked to nutritional condition and stress state (Belding, 1934; Halttunen *et al.*, 2013; Birnie-Gauvin *et al.*, 2019), the few previous telemetry studies documenting natural variation in post-spawning condition and its influence on the migratory behaviour and survival of post-spawned Atlantic salmon were limited in time and space (i.e. to ocean entry; Halttunen *et al.*, 2013; Birnie-Gauvin *et al.*, 2019). As such, it remains unclear how post-spawning condition and the initial downstream migratory decision then affect the marine migratory behaviour and longer-term survival of Atlantic salmon kelts that may return to spawn again.

In comparison with Atlantic salmon, anadromous brown trout mostly feed in estuarine or coastal areas (Jonsson and Jonsson, 1993), exhibiting higher variability in marine residency times (i.e. between 43 and 362 days; Piggins, 1964) and distance from home watercourse (i.e. from a few hundred meters to more than 600 km; as summarized in Jonsson and Jonsson, 2011b), and partial migration is common in the species. As such, brown trout shows complex variation in its migratory tactics, ranging from highly localized freshwater residency, to potamodromy (migration between freshwater habitats), estuarine migration (Cucherousset *et al.*, 2005; Boel *et al.*, 2014), and to short- and long-distance coastal migration (del Villar-Guerra *et al.*, 2014; Eldøy *et*

al., 2015; Flaten *et al.*, 2016). While the drivers of the different migratory tactics remain obscure, especially for the marine migrations of kelts (Drenner *et al.*, 2012; Thorstad *et al.*, 2016), previous studies of first-time migrants suggest that the choice of migratory tactic is a plastic response to individual physiological state, metabolic rate, and food availability (Wysujack *et al.*, 2009). A recent telemetry study of the marine migrations of brown trout kelts suggested that migratory decisions were likely influenced by body condition (energetics) (Eldøy *et al.*, 2015). However, the link between individual post-spawning / pre-migratory nutritional state and the spatio-temporal extent of subsequent marine habitat use by brown trout has not been well-defined (Aldvén and Davidsen, 2017). By providing enhanced growth opportunities, the marine environment is believed to support higher abundances and more productive brown trout populations (Thorstad *et al.*, 2016). Marine foraging, especially in areas where rich feeding opportunities are present (e.g. pelagic fish species; Davidsen *et al.*, 2017), typically allows anadromous individuals to attain larger sizes than their freshwater resident counterparts. For females, this translates into a higher fecundity-at-age (Jonsson and Jonsson, 1993). Coupled with the higher prevalence of anadromy in females (as increased size represents a more direct fitness gain for females), it is likely that anadromous brown trout make very important contributions to the species' population dynamics (Thorstad *et al.*, 2016), although this has yet to be fully investigated. With the recent increase in marine mortality and decreased growth of anadromous brown trout due to anthropogenic impacts on marine habitats (e.g. Thorstad *et al.*, 2015), researchers have speculated that a reduction in the benefits of anadromy might favour selection for freshwater residency (Hendry *et al.*, 2004; Thorstad *et al.*, 2016). Better knowledge about the whereabouts of brown trout at sea and the endogenous factors affecting the extent of the marine migrations (e.g. distance and duration) will contribute to a fuller understanding of the drivers of marine habitat use of this important life-history stage.

1.3 Significance

Salmonids are cold-water adapted fishes native to the northern hemisphere that have been introduced to the cold water regions around the world due to their high value for commercial fisheries, aquaculture, as well as for recreational purposes (Welcomme, 1988). However, the global distribution of salmonids belies the fact that many populations are declining throughout their native range. Many Atlantic salmon populations, for example, have decreased significantly throughout their range in eastern Canada (Chaput, 2012; Lehnert *et al.*, 2019), prompting the Committee on the Status of Endangered Wildlife in Canada to classify many populations located mostly in the southern portion of the species Canadian range as endangered (COSEWIC, 2010). In Europe, Atlantic salmon and brown trout populations are also declining, especially in southern areas (ICES, 2013, 2018), and important drops in catches of adult brown trout (i.e. from 23 to 66 % over the course of the past two decades) have been observed in Norwegian populations, with a much steeper decline over the past 10 years (ICES, 2013). A number of factors are believed to have contributed to these declines, including over-exploitation, anthropogenic alteration of freshwater and coastal habitats, and changes in oceanographic conditions. While migratory decisions have important implications for individual fitness and population processes by affecting growth, survival, and reproductive output, little is known about the factors influencing the spatio-temporal aspects of the freshwater and marine habitat use of individual anadromous salmonids. These are important considerations as inter-individual variability in marine habitat use might result in differential levels of exposure and vulnerability to increasing anthropogenic perturbations in coastal areas. This is especially true for the post-spawning life-history stage of iteroparous salmonids for which we lack fundamental information about their biology and movement ecology (Halttunen, 2011; Thorstad *et al.*, 2011, 2016; Drenner *et al.*, 2012; Aldvén and Davidsen, 2017), as well as on the factors ultimately limiting repeat-spawning potential.

Despite their relatively low occurrence (especially in Atlantic salmon and steelhead trout, Fleming 1998), repeat spawners can make considerable contributions to

annual egg deposition, especially females via their comparatively large body size and high fecundity, thus contributing to population viability (Keefer *et al.*, 2009; Seamons and Quinn, 2010; Halttunen, 2011; Reid and Chaput, 2012; Lawrence *et al.*, 2016; Christie *et al.*, 2018). In addition to a direct contribution to recruitment, repeat spawning also maintains genetic diversity via a genetic contribution of one year-class to several other age-classes (Saunders and Schom, 1985; Palstra *et al.*, 2009). However, in the Atlantic salmon literature, and for iteroparous salmonid fishes more broadly, information on the occurrence of iteroparity and its potential ecological importance is sparse and often speculative. Despite the volumes of data collected annually on the composition of Atlantic salmon returns throughout the species' global range, as well as a growing number of studies assessing some aspects of the biology and ecology of post-spawners (e.g. Jonsson *et al.*, 1991; Niemelä *et al.*, 2006; Chaput and Benoit, 2012; Halttunen *et al.*, 2013), there have been limited attempts to quantify the contributions of repeat spawners to population-level processes (Halttunen, 2011; Lawrence *et al.*, 2016). Moreover, whether the degree of iteroparity is mainly constrained by endogenous factors (i.e. costs of reproduction) or the extent to which it is maintained at lower levels by additional anthropogenic stressors, are key questions limiting our understanding of the importance of iteroparity for population viability and recovery potential.

1.4 Thesis Objectives and Structure

To address these knowledge gaps, my thesis aims at quantifying the ecological importance of iteroparity, as well as examining the endogenous and anthropogenic factors influencing the migratory behaviour and survival of post-spawners in freshwater, estuaries, and at sea. To do so, I used a variety of methods, including the analysis of long-term empirical data series, acoustic telemetry, and physiological sampling. These were applied at various spatial and temporal scales and for two related iteroparous salmonid species – Atlantic salmon and brown trout. By combining telemetry and

physiology, I tested the overarching hypothesis that variation in post-spawning physiological state (i.e. nutritional and stress states) was associated with differences in the migratory behaviour and survival of kelts. Ultimately, I identified some of the causes of differential post-spawning migratory decisions and success, as well as the consequences for population level processes.

In Chapter 2, I initiated and led a national collaborative effort to quantify the ecological importance of iteroparity and describe spatio-temporal variation in the occurrence of repeat-spawning at the continental scale. In collaboration with scientists from the Department of Fisheries and Ocean Canada and Quebec's Ministère des Forêts, de la Faune et des Parcs, I compiled multi-decadal time series on the spawning history composition of Atlantic salmon annual returns across ten populations of the Northwest Atlantic (Canada and U.S.) in addition to West Greenland mixed-stock fishery landings to: i. describe spatio-temporal patterns of iteroparity at the continental scale; ii. quantify the reproductive contributions of repeat spawners; and iii. test the hypothesis that iteroparity acts as a population-level "safeguard" by making important reproductive contributions during periods of low recruitment. In this chapter, I also describe broad-scale, spatio-temporal shifts in iteroparity that occurred in the early 1990s across Atlantic salmon populations of the Northwest Atlantic and discuss the potential factors limiting repeat-spawning potential in some areas. This work laid the foundations for following thesis chapters.

In Chapters 3 and 4, I then combined acoustic telemetry and physiology to further assess factors influencing the migratory behaviour, individual fitness, and the repeat-spawning potential of Atlantic salmon kelts. As such, I documented the effect of endogenous (i.e. nutritional state, Chapter 3) and additional anthropogenic factors (i.e. captive breeding programs, Chapter 4) on spatio-temporal aspects of habitat use and survival prospects of Atlantic salmon kelts in the freshwater, estuarine, and marine environments. While Chapter 3 also provided previously lacking information on the habitat use patterns of adult Atlantic salmon in endangered populations migrating through the unique inland brackish sea formed by the Bras d'Or Lakes, Nova Scotia,

Chapter 4 provides scientific guidance on the importance of mitigating captivity stress imposed on reproductive individuals through broodstock collection programs so that these fish have higher probabilities of surviving to spawn again.

In Chapter 5, I used similar methods to those employed in Chapter 3 (i.e. acoustic telemetry and physiology) to address similar questions on the potential role of endogenous considerations (i.e. post-spawning / pre-migratory nutritional state) in driving inter-individual variation within the migratory continuum of anadromous brown trout in a coastal fjord system of northern Norway. Together, the findings from Chapters 3 and 5 highlight the role of nutritional condition in mediating the post-spawning migratory behaviour and survival of salmonid kelts. This suggests that initial differences in post-spawning condition, likely determined by individual variation in reproductive investment, are in some instances carried throughout their return migration to sea and ultimately affecting repeat-spawning potential. Furthermore, this chapter has led to my current involvement in ongoing international collaborative projects on the movement ecology of anadromous brown trout in contrasting ecological contexts: i. expanding research on the cause and consequences of the migratory continuum in native anadromous brown trout populations in Norway (detailed in Chapter 6); and ii. studying the exploration behaviour and colonization dynamics of anadromous salmonids introduced to the sub-Antarctic Kerguelen Archipelago, French Southern and Antarctic Lands.

Chapter 2

Spatio-Temporal Trends in the Importance of Iteroparity Across Atlantic Salmon Populations of the Northwest Atlantic [1]

2.1 Abstract

Iteroparity is a bet-hedging strategy where individuals spread the risk of reproductive failure over time. The occurrence of iteroparity (i.e. proportion of repeat spawners in annual returns) varies among Atlantic salmon (*Salmo salar*) populations, yet information on its ecological importance is limited. I compiled multi-decadal time series on the spawning history composition of Atlantic salmon annual returns across ten populations of the Northwest Atlantic and West Greenland mixed-stock fishery landings to: 1) describe spatio-temporal patterns of iteroparity at the continental scale; 2) quantify the reproductive contributions of repeat spawners; and 3) test the hypothesis that iteroparity acts as a population safeguard during periods of low recruitment through repeat spawners' contributions. Despite high variability in the representation of repeat spawners among populations and years (range: 0-24.7 %; average: 5.0 %), I identified broad-scale spatio-temporal shifts in iteroparity, with increases in mid-latitudinal and northern populations (from 3.1 % to 7.6 %) and declines in southern

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areas (from 4.1 % to 2.7 %), between the 1971-1992 and 1993-2017 periods. The current findings highlight the potential for increased prevalence of iteroparity when threats are mitigated (e.g. fishing pressure), with measurable benefits to population processes manifested by the high reproductive contributions of repeat spawners, especially in years of low maiden spawner abundance.

2.2 Introduction

One of the central assumptions of life-history theory is that reproduction is costly and involves a trade-off between reproductive effort and adult survival (Stearns, 1976). Across sexually reproducing organisms, breeding systems are classified as semelparous (i.e. single life-time reproductive event followed by death) or iteroparous (i.e. two or more life-time reproductive events) as strategies to maximize lifetime fitness (Cole, 1954; Murphy, 1968). With increasing variability in the survival of offspring, and increasing survival of adults, natural selection favors life histories that spread the risk of reproductive failure over space or time (Murphy, 1968; Stearns, 1976). Semelparity and iteroparity can exist as a continuum as manifested by intra-specific variability in the occurrence of iteroparity. Examples include populations of capelin (*Mallotus villosus*, Christiansen *et al.,* 2008) and American shad (*Alosa sapidissma*, Leggett and Carscadden, 1978). Various degrees of iteroparity have also been observed in anadromous salmonid species such as Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), Arctic charr (*Salvelinus alpinus*), brook trout (*Salvelinus fontinalis*), Dolly Varden charr (*Salvelinus malma*), rainbow / steelhead trout (*Oncorhynchus mykiss*), cutthroat trout (*Oncorhynchus clarki*) (reviewed in Fleming, 1998), as well as Chinook salmon (*Oncorhynchus tshawytscha*) (Barry *et al.*, 2001).

Whether semelparous or iteroparous, most salmonids are capital breeders, fasting during their extended spawning periods and instead relying on somatic energy reserves accrued prior to breeding to power migrations to natal spawning areas, produce gametes, develop secondary sexual characteristics, and support reproductive behaviours (Fleming and Reynolds, 2004; Jager *et al.*, 2008). The evolutionary trade-off

between reproductive investment and survival has received much attention in iteroparous salmonids, with spawning investment (i.e. total energy loss of 46-70 %) being negatively correlated with post-spawning survival (Fleming, 1996, 1998; Jonsson *et al.*, 1997; Fleming and Reynolds, 2004), reflective of a bet hedging strategy (Slatkin, 1974). This was further corroborated by a recent study that identified a genotypic co-inheritance between sea-age at maturity and iteroparity in Atlantic salmon, with iteroparity being more likely in smaller, earlier-maturing salmon that invest proportionally less into reproduction (Aykanat *et al.*, 2019). In Atlantic salmon and iteroparous salmonids more broadly, constraints imposed by capital breeding and by environmental conditions that affect somatic reconditioning are known to affect the post-spawning survival and the potential for repeat spawning (Belding, 1934; Fleming and Reynolds, 2004; Chaput and Benoit, 2012), both of which affect population demographics. However, anthropogenic factors such as exploitation and migration challenges posed by hydroelectric dams can also affect the survival of juvenile and adult salmon, inducing demographic changes and modifying life-history traits through size-selective mortality (Dempson *et al.*, 2004; Nyqvist *et al.*, 2016; Maynard *et al.*, 2017; Erkinaro *et al.*, 2019).

Atlantic salmon returns have generally declined throughout the North Atlantic stock complex over the past 50 years (ICES, 2018). Nonetheless, broad temporal fluctuations in the degree of iteroparity have been documented in different regions of the species' global range, with recent increases in some populations (Dempson *et al.*, 2004; Chaput and Benoit, 2012; Erkinaro *et al.*, 2019) and declines in others (Hubley and Gibson, 2011; Maynard *et al.*, 2017). Repeat spawners in Atlantic salmon represent on average 11 % of all spawners (range: 1-43 %), and similarly 10 % on average in steelhead trout (range: 1-31 %), compared to an average of 20-41 % in other anadromous iteroparous salmonids (range 5-69 %) (Fleming, 1998). Atlantic salmon can mature and migrate back to freshwater to spawn after feeding at sea for one (one-sea-winter, 1SW) or more years (multi-sea-winter). Similarly to variation in sea-age at maturity, Atlantic salmon can repeat spawn in consecutive or alternate years (up to seven times in rare

cases, Chaput and Jones, 2006), spending as little as a few months at sea to more than a year for reconditioning, respectively (Jonsson *et al.*, 1991; Fleming, 1996). Maiden (first-time) 1SW spawners and consecutive repeat spawners generally exhibit shorter feeding migrations (e.g. Gulf of St. Lawrence or Bay of Fundy) than maiden MSW (mostly 2SW) spawners and alternate repeat spawners that mostly migrate to distant feeding grounds (e.g. Labrador Sea and West Greenland) (Hubley *et al.*, 2008; Chaput and Benoit, 2012; Lacroix, 2013; Strøm *et al.*, 2017).

Despite their generally low occurrence (especially in Atlantic salmon and steelhead trout: Fleming, 1998), repeat spawners can make considerable contributions to annual reproduction, especially females via their comparatively large body size which translates into high fecundity, thus contributing to population viability (Keefer *et al.*, 2009; Seamons and Quinn, 2010; Halttunen, 2011; Reid and Chaput, 2012; Lawrence *et al.*, 2016). In addition to a direct contribution to recruitment, repeat spawning also plays a role in maintaining genetic diversity via a genetic contribution of one year-class to several other age-classes (Saunders and Schom, 1985; Palstra *et al.*, 2009). However, in the Atlantic salmon literature, and for iteroparous salmonid fishes more broadly, information on the occurrence of iteroparity and its potential ecological importance is sparse and often speculative. Despite the volume of data collected annually on the composition of Atlantic salmon returns throughout their global range, as well as a growing number of studies assessing some aspects of the biology and ecology of post-spawners (e.g. Jonsson *et al.*, 1991; Niemelä *et al.*, 2006a; Chaput and Benoit, 2012; Halttunen *et al.*, 2013), limited attempts have been made to quantify the contributions of repeat spawners to population processes (Halttunen, 2011; Lawrence *et al.*, 2016). Moreover, no previous study has specifically assessed spatio-temporal patterns in iteroparity levels at the continental scale of the species' distribution, nor empirically tested the circumstances in which iteroparity may act as a safeguard against low recruitment periods.

Here, I compiled multi-decadal time series on the sea-age and spawning history composition of Atlantic salmon returns for ten North American populations in addition

to mixed-stock fishery landings from West Greenland to: 1) assess spatio-temporal patterns of iteroparity at the continental scale; 2) quantify the relative reproductive contributions of repeat spawners across varying population contexts (i.e. different latitude and sea-age at maturity composition); and 3) evaluate the extent to which repeat spawners can compensate for losses in total reproductive output (i.e. increased relative importance of repeat spawners) during periods of low maiden spawner returns.

2.3 Methods

2.3.1 Data Sources

To describe sea-age at maturity and spawning history composition of Atlantic salmon annual returns, I compiled published and unpublished long-term data series from a total of ten populations in Newfoundland and Labrador (3), Quebec (2), New Brunswick (3), Nova Scotia (1), Maine (1), in addition to mixed-stock fishery landings from West Greenland to quantify the degree of iteroparity from a suite of North American populations across a latitudinal gradient. The data were collected by the Department of Fisheries and Oceans Canada (DFO), Quebec's Ministère des Forêts, de la Faune et des Parcs (MFFP), the Maine Department of Marine Resources (DMR; Maynard *et al.*, 2017), and ICES Working Group on North Atlantic Salmon (WGNAS; ICES, 2018), between 1971 and 2017 and ranged from 21 to 47 years (Table 2.1). Biological information and annual return estimates were collected at estuarine trapnets, fishways or counting fences for all populations except for the Rivière Saint Jean (Gaspé, QC), where biological information was collected on salmon captured as part of the recreational fishery and annual returns were assessed from counts made by snorkel surveys (Cauchon and April, 2017). Data on the composition of West Greenland fisheries was assessed from biological information collected on fishery landings (available in ICES, 2018). I summarized spawning history groups in three categories based on scale readings (White and Medcof, 1968): maiden-1SW (salmon returning to freshwater for the first time after a single winter at sea), maiden-2SW+ (salmon returning to freshwater for the first time after two or more winters at sea), and repeat spawners (including all

salmon returning to freshwater that spawned in previous years, as indicated by the presence of spawning marks on the scales). For West Greenland fishery landings, I assigned fish that had spent at least one winter at sea but still present in the area as maiden-2SW+ (as they would have not returned to freshwater as maiden-1SW salmon), and salmon with previous spawning marks as previously spawned / potential repeat spawners. These numbers exclude precocious maturation in freshwater by males as there is currently no way to empirically identify whether male spawners returning from the sea had previously matured as juveniles. For the purpose of this study, we thus defined repeat spawners as anadromous migrants that had spawned at least once in previous year(s) (based on the presence of previous spawning marks on scales: White and Medcof, 1968), excluding potential previous spawning as precocious parr.

Because only a subset of returning individuals were sampled for biological information (i.e. interpretation of scale patterns for age and previous spawning history, morphometrics, and sex) adjustments have been made to ensure that datasets are representative of the whole population. The spawning history characteristics of populations' annual return were derived by accounting for the biological data sampling design which was generally specific to the size group of salmon (small salmon < 63 cm fork length, large salmon >= 63 cm fork length) and weighting by the estimated size group in annual return to each river:

$$p_{r,y,a} = \left. \sum_s \left(\frac{n_{r,y,s,a}}{n_{r,y,s}} * N_{r,y,s} \right) \right/ \sum_s N_{r,y,s} \qquad (1)$$

with $p_{r,y,a}$ the proportion of the annual return in river r in year y of spawning history a; $n_{r,y,s,a}$ the number of samples aged for river r, year y, in size groups of spawning history a; $n_{r,y,s}$ the total number of samples processed; $N_{r,y,s}$ the total estimated return of salmon for corresponding river and year for size groups; s is size group as small salmon or large salmon; and a is spawning history as maiden-1SW, maiden-2SW+, or repeat spawner.

2.3.2 Spatio-Temporal Trends in Iteroparity

I conducted a Dynamic Factor Analysis (DFA) to assess the extent of spatial coherence in the temporal trends of iteroparity across populations of Atlantic salmon in different geographic areas. DFA is a multivariate statistical technique that can be used to identify common trends shared among multiple time series (Zuur *et al.*, 2003), and more recently to assess demographic changes in life-history traits at a continental, multi-population scale (Mills *et al.*, 2013; Ohlberger *et al.*, 2018). Using the spawning history composition estimates of Atlantic salmon annual returns, I constructed population specific time series of the proportion of repeat spawners across ten populations of the northwest Atlantic and West Greenland mixed-stock fishery landings. I then transformed the proportions on the logit scale ($-\infty$, $+\infty$) and calculated z-scores for the time series to remove inter-population differences in mean and variance (Ohlberger *et al.*, 2018). DFA was then implemented in a maximum likelihood framework using a multivariate autoregressive state-space modelling approach with the *MARSS* package (Holmes *et al.*, 2012) in *R* v.3.5.0 (R Development Core Team 2018). In simple terms, time series are modelled as a linear combination of "common trends" and factor loadings, plus a noise component (i.e. residual errors) (Zuur *et al.*, 2003). To allow for potential temporal patterns in iteroparity to vary across different geographic regions, I compared a suite of models based on a varying number of common trends (i.e. m=1 to 3 in "MARSS" function). In addition, I tested four different structures of the variance-covariance matrix of residual errors: same or different variances and no covariances (R="diagonal and equal" or "diagonal and unequal" in *MARSS* function), same variances and same covariances ("equalvarcov"), and different variances and different covariances ("unconstrained") (Holmes *et al.*, 2012). A total of 12 models were computed and model selection was based on AICc, an adjustment of the Akaike Information Criterion developed to avoid overfitting of small sample sizes (Hurvich and Tsai, 1989). At equivalent performances (i.e. ΔAICc < 1.0), models with a single "common" trend were preferred over more complex structures. See Zuur et al. (2003) or Holmes *et al.* (2012) for more information on the mathematics underlying DFA.

2.3.3 Reproductive Contributions of Repeat Spawners

To quantify the reproductive contributions of repeat spawners among varying populations (measured as eggs produced), I first quantified the adjusted spawning history composition of annual returns for females alone. From this I calculated the proportion of eggs laid by females of different spawning history groups based on the annual average length of each group and population specific fecundity-length relationships (Table 2.2), which included various spawning history types (e.g. 1SW, 2SW and repeat spawners). Due to data limitation, I restricted this analysis to four populations that had adequate data for this analysis, which were also located in different parts of the species' North American range: Conne, NL; Trinité, QC; Miramichi, NB; and LaHave, NS. While further research is needed to clarify to the effect of spawning history on the reproductive contributions of iteroparous salmonid species, I followed conclusions from a limited number of previous studies indicating that the fecundity-length relationship did not differ significantly between maiden and repeat spawners (Quinn *et al.*, 2011; Reid and Chaput, 2012).

Given the variability in available biological information among populations, I used two different approaches to quantify the composition of annual returns for females and the proportion of eggs contributed by females of different spawning history groups to estimated population total egg depositions. For the Miramichi (NB) and LaHave (NS) populations, which had adequate sampling (median of 346 and range of 23 – 1850 females sampled annually), the annual number of female returns by spawning history were quantified similarly to the method described (equation 1) using only female data. For these two populations, I then calculated the average annual fork length of each female spawning history group based on the individual biological information available and the average annual fecundity of each group based on a population specific fecundity-length relationship (Table 2.2). Finally, based on the adjusted composition of annual female returns and the average fecundity of each spawning history group, I calculated the proportion of eggs deposited by each spawning history group.

For the Conne (NL) and Trinité (QC) populations, I could not directly describe the annual composition of female returns due to limited annual sampling (median of 42 and range: 1 – 628 females sampled annually). For these rivers, I estimated the annual composition of female returns based on the proportion of females in both small and large groups averaged over multiple years. In addition, the average annual fecundity of each spawning history group was calculated from the average annual fork length of each class from all samples available (i.e. both sexes) and using population specific fecundity-length relationships (Table 2.2). The respective contributions of the different spawning history groups to total egg deposition were then calculated similarly to the method described above.

The identification of females was based on internal examination for the Conne (NL), but relied on external sex determination for the other three populations (Trinité, QC; Miramichi, NB; LaHave, NS). While external sex determination is a standard procedure for Atlantic salmon, I recognize that current research efforts using genetic sexing could provide greater accuracy in the future. Early results from the LaHave (NS) population indicate that, for this population at least, both methods achieved similar performance for estimating total egg depositions (A. Levy, Unpubl. data).

2.3.4 Safeguard Against Low Recruitment Periods

To assess the extent to which repeat spawners can compensate for losses in total reproductive output during years of low maiden spawner abundance, I assessed the relationship between brief fluctuations in the proportion of repeat spawners in annual returns against annual maiden spawner counts. More precisely, I tested the prediction that the relative importance of repeat spawners (i.e. proportion of repeat spawners in annual return) would be higher in years of low maiden spawner returns, which would not be the case if the returns of repeat and maiden spawners were similarly affected in bad years. To test this, I first detrended the data to remove large-scale temporal trends (lower frequency variability component) present in the time-series by fitting locally weighted regressions (or loess) using the *loess* function of the *stats* package in *R*

(Cleveland and Devlin, 1988) using a relatively high common smoothing factor of "span=0.8" (fit of individual time series can be found in Appendix 1). I then assessed potential correlations between the residuals of these loess regressions (or de-trended time series) of the proportion of repeat spawners in annual returns against that of maiden spawner annual counts at the population level by computing parametric Pearson's correlation coefficient based on meeting the assumption of normality. I performed these analyses on the same subset of populations used to describe the reproductive contributions of repeat spawners (as described above; Conne, NL; Trinite, QC; Miramichi, NB; and LaHave, NS). As for other analyses, a logit transformation was applied to proportional data on the representation of repeat spawners in annual returns. In addition, maiden spawner counts were log transformed to achieve the normality of distributions. Finally, both de-trended time series were z-score transformed and plotted on the same axes to better visualize the relationships between the proportion of repeat spawners in annual returns and maiden spawner counts in each population.

2.4 Results

2.4.1 Spatio-Temporal Trends in Iteroparity

The proportion of repeat spawners varied greatly among populations and years, ranging from 0.0 to 24.7 %, and averaging 5.0 ± 5.0 % over all populations and years (Fig. 2.2). Despite large inter-annual fluctuations in the proportions of repeat spawners, broader temporal changes in iteroparity were apparent across multiple populations. Dynamic Factor Analysis revealed spatial coherence in the temporal trends of iteroparity across populations of Atlantic salmon of the northwest Atlantic. The most parsimonious model (i.e. lowest AICc value) identified a single "common trend" shared among time series and correlated process errors with the same variance and covariances (R="equalvarcov", Table 2.3). Based on the output of the DFA (Fig. 2.3a and b), some loadings are strongly positive and other strongly negative, indicating that populations

experienced two opposite temporal tendencies, an increasing one and a decreasing one. In fact, most populations at the mid-latitudinal and northern part of the species' northwest Atlantic distribution (including West Greenland fishery landings since the vast majority of these fish, >85 % since 1970, originate from mid-latitudinal and northern populations: Bradbury *et al.*, 2016) have shown increases in the proportion of repeat spawners through time (i.e. high positive loadings for Sand Hill, NL; Western Arm Brook, NL; Trinité QC; and Miramichi, NB), while most southern populations have shown declines (i.e. high negative loadings for Saint John, NB; LaHave, NS; and Penobscot, ME) (Fig. 2.3b). Considering these contrasting temporal patterns, additional DFAs were computed for mid-latitudinal and northern populations combined and then separately for southern populations. Model selection was conducted as described in the Methods section and results are presented in Table 2.3 and Fig. 2.3c, d. Regions' specific DFA only included a single "common trend" for both models, with different variances and no covariances (R= "diagonal and unequal") for mid-latitudinal and northern populations, and correlated process errors with different variances and different covariances (R="unconstrained") for southern populations (Table 2.3). The common tendency shared among mid-latitudinal and northern populations (Gulf of St. Lawrence and Labrador Sea) was divided in three distinct periods (Fig. 2.3c). From a generally low proportion of repeat spawners in the 1971-1987 period, the proportion of repeat spawners increased after 1987 with the steepest increase from 1993-1997 peaking in 1998, and remaining at higher levels up to 2017 (with brief peaks in 1998, 2006, and 2013, Fig. 2.3c). In contrast, the common tendency exhibited in southern populations (Scotian Shelf, Bay of Fundy, and Gulf of Maine) was a general decline in the proportion of repeat spawners beginning in the early 1980s and continuing to the present time, with a brief increase around 2012 (Fig. 2.3d) apparent in all southern populations except the Penobscot (ME) (Fig. 2.4).

To assess the statistical significance of broad temporal changes in the degree of iteroparity, I compared the 1971-1992 period to the 1993-2017 period, based on findings from the Dynamic Factor Analysis that changes in iteroparity were steepest after 1992 (Fig. 2.3a). Across all ten populations and the West Greenland fisheries,

repeat spawners represented on average 3.5 ± 3.2 % of annual returns (or of landings in West Greenland) during the 1971-1992 period with population averages ranging from 0.4 – 7.5 % (Table 2.4). In contrast, during the 1993-2017 period, the overall occurrence of iteroparity averaged 5.8 ± 5.6 % (range: 1.0 – 13.6 %) over all populations and years (Table 2.4). The recent period showed not only a higher occurrence of iteroparity but also differences among broader geographical regions. In the mid-latitudinal and northern part of the species' northwest Atlantic range (Gulf of St. Lawrence and Labrador Sea), the average proportion of repeat spawners in annual returns increased from 3.1 to 7.6 % (a 2.5-fold increase, *p*-value ≤ 0.001), with five out of seven individual time series showing a significant increase (Table 2.4; Welch Two Sample t-tests). During the same period, southern populations of the Scotian Shelf, Bay of Fundy, and Gulf of Maine showed the opposite trend. For these populations, the average occurrence of iteroparity decreased significantly from 4.1 to 2.7 % (a 1.5-fold decrease, *p*-value = 0.007), with two of four individual time series showing a significant decrease (Table 2.4; Welch Two Sample t-tests). While the proportion of repeat spawners in populations of these two broader geographic regions did not statistically differ in the 1971-1992 period (4.1 *vs.* 3.1 %, *p*-value = 0.079), in recent decades, southern populations exhibited lower occurrence of iteroparity than mid-latitudinal and northern populations (2.7 *vs.* 7.6 %, *p*-value ≤ 0.001, Welch Two Sample t-tests).

Also worthy of interest, comparing the 1971-1992 and the 1993-2017 periods, the proportion of MSW in annual maiden spawner returns (i.e. similar to sea-age at first maturity) increased in the Sand Hill (NL; 7.0 to 15.2 %, $p = 0.002$) and the Trinité (QC; 25.9 to 34.5 %, $p = 0.045$), while it decreased in the Saint Jean (QC; 77.5 to 67.6 %, $p = 0.022$), the Nashwaak (NB; 59.9 to 26.0 %, $p = 0.056$) and the Saint John (NB; 44.9 to 29.3 %, $p = 0.006$) populations (Welch Two Sample t-tests). No statistically significant changes occurred in the other populations considered ($p > 0.125$).

2.4.2 Reproductive Contributions of Repeat Spawners

Given that a greater proportion of repeat spawners are females and that these are generally larger than their younger maiden counterparts (Table 2.2), the estimated egg contributions by repeat spawners were disproportionately higher than their proportions by number (Fig. 2.5). For the Trinité (QC) between 1993 and 2017, repeat spawners represented on average 9.8 % of the annual return of both sexes combined, 20.5 % of all females, and these females contributed to 27.0 % of total annual egg deposition. For the same time period in the Miramichi (NB), repeat spawners composed on average 13.6 % of both sexes combined, 21.8 % of females, and repeat females contributed to 28.1 % of eggs deposited annually. Considering their contributions to annual egg deposition, the influence of repeat spawners was 2.8-fold (i.e. 9.8 % of annual returns producing 27.0 % of eggs in the Trinité, QC) and 2.1-fold greater (i.e. 13.6 % of annual returns producing 28.1 % of eggs in the Miramichi, NB) than assessments based solely on their relative occurrence in the annual returns of both sexes combined. Of similar magnitude (2.2-fold) but at lower occurrences, repeat spawners in the LaHave River (NS) represented 3.2 % of all returning salmon, 4.5 % of females, and contributed 7.1 % of eggs deposited, on average. Of lower magnitude for Conne (NL) (1.4-fold), an average of 10.9 % of repeat spawners in the total annual return, represented 11.6 % of females, and contributed 15.3 % of annual eggs deposited. The smaller difference between the proportion of repeat spawners in annual returns and the proportion of eggs contributed by female repeat spawners for the Conne (NL) (i.e. 1.4-fold) is mainly due to maiden spawners being mostly comprised of females in a 1SW dominated river, and by female repeat spawners being dominated by 1SW-consecutive spawners of similar sizes (Fig. 2.5 and Table 2.2). However, in other populations with a higher proportion of males in maiden spawners, and more variability in sea-age at maturity and reconditioning strategy, such as the Trinite (QC), Miramichi (NB), and LaHave (NS) (Table 2.2), findings indicate that the proportion of repeat spawners by number in the annual return underestimated their relative contribution to annual egg deposition (Fig. 2.5).

2.4.3 Safeguard Against Low Recruitment Periods

Brief temporal fluctuations (higher frequency variation component) in the proportion of repeat spawners in annual returns were negatively correlated with estimated abundances of maiden spawners across populations (Fig. 2.6). Pearson's correlation coefficients ranged from -0.35 to -0.56 and negative relationships were statistically significant for all (p-values ≤ 0.002) but the Conne (NL) (p-value = 0.056, Fig. 2.6b). These relationships indicate that the relative importance of iteroparity (i.e. increase in the representation of repeat spawners in annual returns) was emphasized in periods of low maiden spawner abundance, which would not have been the case if repeat spawners were equally affected in bad years.

To illustrate this point, the most recent decrease in maiden spawner returns occurred in all years of the 2012-2014 period for Trinité, QC and Miramichi, NB or in some of those years for LaHave, NS (2012) and Conne, NL (2014) (Fig. 2.6; see also Appendix 1). During this period, in the Trinité (QC), Miramichi (NB), and LaHave (NS) populations, repeat spawners represented respectively 12.4, 16.3, and 11.9 % of annual returns, and contributed to 33.7, 28.8, and 18.2 % of the total annual egg deposition in those years. This emphasizes the importance of repeat spawners for future population recruitment. Other important declines in maiden spawner returns have occurred in the Trinité (QC) in 2001 (the lowest count of maiden salmon return recorded for the entire time series, at 237 individuals), and in the Miramichi (NB) during the 1997-1999 period (the lowest counts of maiden salmon return estimated prior to 2009, at between 26 049 to 31 268 individuals) (Fig. 2.6). During these years of low recruitment, repeat spawners represented on average 17.2 to 20.6 % of all spawners, and 26.9 to 41.8 % of total annual egg deposition, respectively, for the Trinité (QC) and Miramichi (NB) populations (Fig. 2.5). These findings provide evidence of iteroparity acting as a stabilizing force against periods of low maiden recruitment associated with higher post-smolt mortality at sea.

2.5 Discussion

While the occurrence of iteroparity (i.e. proportion of repeat spawners in annual returns) shows considerable variability within and among Atlantic salmon populations, my findings revealed broad-scale spatio-temporal shifts in iteroparity across populations of the northwest Atlantic. Through the analysis of time series spanning approximately 50 years, I documented increases in iteroparity, starting in the late 1980s or early 1990s, for populations situated in the mid-latitudinal and northern part of their range (Gulf of St. Lawrence and Labrador Sea) as well as in previously spawned salmon in the mixed-stock West Greenland fisheries. This broad-scale spatio-temporal pattern is further corroborated by recently documented changes in the northeast Atlantic part of the species' range. These included a 3.8-fold increase in the proportion of previously spawned, European-origin salmon in the West Greenland fishery landings starting in the mid-2000s (1985-2004 average of 0.4 *vs.* 1.5 % for the 2005-2017 period; ICES, 2018) and an increase in iteroparity in the River Teno system (Finland), with a 4.0-fold increase in the proportion of female repeat spawners since the early 2000s (1975-2000 average of 3.6 *vs.* 14.4 % for the 2001-2014 period, Erkinaro *et al.*, 2019). In contrast, starting in the late 1980s, I documented declines in iteroparity in southern populations (i.e. Scotian Shelf, Bay of Fundy, and Gulf of Maine). More broadly, this latitudinal pattern is also reflected in overall annual returns and trends in marine survival, which have declined more severely in the southern most regions of the species' range (Chaput, 2012), and as exemplified by their conservation status (Table 2.1; COSEWIC, 2010). Many factors might have contributed to recent demographic changes across Atlantic salmon's global range. Most noticeably, important changes in oceanic conditions (e.g. marine climate regime shifts; Drinkwater, 2000) might be either directly or indirectly responsible for a substantial reduction in post-smolt marine survival and overall productivity of Atlantic salmon (Dempson *et al.*, 2004; Chaput, 2012; Friedland *et al.*, 2014). In addition, closures of commercial Atlantic salmon fisheries in different parts of Canada implemented through the 1980s and early 1990s, and large reductions in harvests in the West Greenland fishery over the same time period, have reduced size-selective fishing

mortality of large salmon (i.e. particularly MSW and repeat spawners) (Moore *et al.*, 1995; Dempson *et al.*, 2004; Chaput, 2012).

While fluctuations in the abundance and relative importance of consecutive *vs.* alternate repeat spawning strategies would require further investigation, data on the composition of West Greenland mixed-stock fishery landings indicate increasing proportions of previously spawned salmon (potential alternate repeat spawners in this case) in the North Atlantic complex. This complements findings from Chaput and Benoit (2012) that increasing occurrence of iteroparity was dominated by consecutive repeat spawners in the Miramichi River (NB), suggesting that both repeat spawning strategies became more frequent since the early 90s in the mid-latitudinal and northern part of the species' North Atlantic Ocean range. The seemingly improved post-spawning reconditioning prospects in the Gulf of St. Lawrence attributed to an increased biomass of forage fish species (Chaput and Benoit, 2012), and removal of size-selective fishing pressures in distant and local fisheries (Moore *et al.*, 1995; Dempson *et al.*, 2004), are believed to have favored iteroparity and survival of MSW salmon. Interestingly, while earlier sea age at first maturity (i.e. 1SW) has recently been liked to iteroparity at the genotypic level (Aykanat *et al.*, 2019), I documented increases in iteroparity that occurred along with increasing proportions of MSW in maiden spawner returns (or later sea-age at first maturity) in some mid-latitudinal and northern populations. These observations are consistent with expectations associated with the closure of commercial fisheries (Dempson *et al.*, 2004) and rules out the possibility for observed increases in iteroparity to have been driven by a reduction in sea age at first maturity.

In contrast, in some southern populations, the degree of iteroparity decreased along with the proportion of MSW in maiden spawners and overall population returns. However, despite the seemingly improved survival prospects of post-spawners in common feeding areas, the declines in iteroparity that I documented in southern populations suggest that regional factors (e.g. environmental and anthropogenic threats) may have been limiting iteroparity in southern areas. Recent studies revealed size-selective pressure exerted by both upstream and downstream fish passage facilities

against large-bodied fish, which raises concerns about the effects of an artificially reduced potential for repeat spawning in regulated rivers, such as the Penobscot (Maine, US) and Saint John (NB) rivers (Nyqvist *et al.*, 2016; Maynard *et al.*, 2017). The contrast in the occurrence of iteroparity between populations of the Saint John, NB (above Mactaquac Dam: 1.2 %) and the adjacent, dam-free Nashwaak tributary, NB (5.3 %) provides further evidence of these anthropogenic factors affecting post-spawning survival (Chaput and Jones, 2006). In addition, hatchery supplementation programs, where captively held wild-origin, local broodstock are subjected to the stress of captivity and artificial spawning, can compromise post-spawning survival of broodstock upon their return to the wild and reduce their potential for repeat spawning (Bordeleau *et al.*, 2018b). These potential population-level impacts are likely amplified in large-scale hatchery programs (Bordeleau *et al.*, 2018b), such as the Penobscot River (Maine, US), where the majority of returning salmon are spawned at the hatchery and released back to the wild after many months in captivity (Kincaid and Stanley, 1989; Maynard *et al.*, 2017). Furthermore, hatchery reared juveniles could have different life-history traits that could affect the maturity schedule (Fleming and Petersson, 2001) and potentially iteroparity of populations with hatchery supplementation programs. In addition to these direct anthropogenic threats, reduced post-spawning survival due to higher energy expenditure imposed by warmer river temperatures (Glebe and Leggett, 2010; Lennox *et al.*, 2018a) might be of particular importance in southern areas of the Atlantic salmon's range. Moreover, since repeat spawners are the survivors of maiden spawners, their abundance depends primarily on the survival of post-smolts some years before (Niemelä *et al.*, 2006). As such, the potential for iteroparity to limit population declines is conditional on maintaining sufficient recruitment of maiden spawners. However, as survival decreases and fewer adults remain in the population, the potential for iteroparity to limit further population declines may be compromised, a situation which might be occurring in the southernmost regions examined in the current study.

While the closure of commercial fisheries and increases in the occurrence of iteroparity have not prevented broad-scale declines in Atlantic salmon populations since

the 1980s, my findings emphasize the importance of iteroparity as a buffer during periods of low post-smolt survival and recruitment. Female repeat spawners produced a relatively high number of eggs, particularly at times of low maiden spawner returns. In these low return periods (e.g. 2001, 2012-2014 in Trinité, QC; 1997-1999, 2012-2014 in Miramichi, NB; and 2012 in LaHave, NS), on average repeat spawners accounted for 11.9 – 18.5 % of all spawners, and the repeat spawning females contributed 18.2 – 35.3 % of all eggs estimated to have been produced by populations. During the period when population abundances were sharply decreasing across the North Atlantic (particularly in the 1980s; ICES, 2018), the marked increase in iteroparity starting in the early 1990s (as described here in many mid-latitudinal and northern populations) coincided with decreases and levelling off of population abundances (Appendix 1). While I cannot attribute this exclusively to the increased relative importance of repeat spawners as other important changes also occurred (e.g. commercial fisheries closure: Moore *et al.*, 1995; Dempson *et al.*, 2004; and marine climate regime shifts: Drinkwater, 2000), increases in iteroparity likely contributed to the slowing of declines, with repeat spawners contributing, on average, 15.3 to 28.1 % of annual egg deposition during the 1993-2017 period in different mid-latitudinal populations (Conne, NL; Trinite, QC; and Miramichi, NB). As Atlantic salmon post-smolts are more susceptible to marine environmental conditions during their first few months at sea due to size-mediated survival, resulting in lower survival during the first year than in additional years (Friedland *et al.*, 2000; Chaput, 2003; Chaput *et al.*, 2018), my findings reinforce the premise that larger iteroparous individuals can act as a safeguard against low recruitment periods and mitigate some of the effects of variability in the marine survival of juvenile salmon (as previously suggested by Saunders and Schom, 1985; Niemelä *et al.*, 2006a).

2.5.1 Broader Perspectives

Quantifying the composition of spawners in annual returns, and especially the contributions of different spawning history groups to total egg deposition, provides

valuable information for estimating the importance of iteroparity to population dynamics. However, the importance of iteroparity likely goes beyond the relative proportion of eggs that are laid by female repeat spawners. Intergenerational effects passed by experienced breeders, via maternal effects, could confer currently unquantified benefits to offspring fitness (Fleming and Einum, 2011). While female size is positively associated with fecundity in salmonids as well as egg size, egg energy content, egg survival, and offspring survival in the wild (Fleming, 1996, 1998; Garant *et al.*, 2001, 2003), the nature of these relationships with respect to repeat spawning is unclear. In Atlantic salmon, recent hatchery-based work suggests that egg quality might depend on reconditioning strategies, with generally higher benefits to the alternate repeat spawners *vs.* maiden spawners, but lower for the consecutive repeat spawning strategy (Reid and Chaput, 2012). While this is a ripe area for future research, individual differences in spawning location and timing conferred by females' size and life experience could translate into higher competitive abilities and survival (and hence fitness) of repeat spawners' offspring in the wild. These behavioral maternal effects, not considered in hatchery-based studies, include higher digging capacity, deeper egg deposition, and lower susceptibility to redd superimposition (as correlated with size; reviewed in Quinn, 2005), higher competitive ability and access to preferred sites (as correlated with size; reviewed in Fleming and Einum, 2011), and optimal run timing (as correlated with previous spawning experience; Niemelä *et al.*, 2006b). Furthermore, other studies suggest a higher tolerance of repeat spawners than maiden spawners to environmental disturbances such as increased thermal resilience and lower vulnerability to thermally-induced reproductive inhibition (cultured Tasmanian Atlantic salmon; Pankhurst *et al.*, 2011; Anderson *et al.*, 2012), and greater tolerance of eggs to hypoxic conditions (cultured Tasmanian Atlantic salmon; Polymeropoulos *et al.*, 2016). More recently, Lennox *et al.* (2018a) showed that larger body size in Atlantic salmon resulted in less relative energy depletion and greater resilience to increases in pre-spawning temperature, an advantage which may also be attributed to repeat spawners. Predicting species' responses to climate change presents many challenges (Aas *et al.*, 2011; Comte

et al., 2013), yet these recent studies suggest further behavioural and physiological mechanisms by which iteroparity can positively influence Atlantic salmon population resilience. As more empirical information becomes available on the reproductive output and offspring fitness of maiden *vs.* repeat spawners, additional fitness consequences of iteroparity to salmon population dynamics should be examined, as well as addressing the life-history implications of consecutive and alternate repeat spawning strategies (Reid and Chaput, 2012).

Considering declines in marine survival (i.e. low probability of breeding once) and the poor post-spawning survival prospects of Atlantic salmon accentuated by the more severe anthropogenic stressors present in southern regions (i.e. low probability of survival between spawning events), there is potential for selection pressure to favor semelparity over iteroparity (Stearns, 1976). While iteroparity is a bet-hedging strategy allowing individuals to spread the risk of reproductive failure over multiple years (Slatkin, 1974), with the ongoing decrease in the incidence of iteroparity in southernmost regions and the potential for this decrease to become widespread is of particular concern for the viability and recovery potential of Atlantic salmon populations, particularly under increasing environmental variability associated with climate change (Stenseth *et al.*, 2002). As such, the importance of iteroparity should be considered in recovery actions, and mitigation measures should be envisioned to reduce post-spawning mortality as it relates to current anthropogenic threats occurring in freshwater (summarized in Keefer *et al.*, 2008). Efforts should be directed at improving the design of dams to minimize downstream passage mortality for large post-spawners (Kraabøl *et al.*, 2009; Nyqvist *et al.*, 2016) and mitigating the many stressors and associated fitness consequences that wild-origin broodstock experience in current hatchery programs (Bordeleau *et al.*, 2018b).

Whether iteroparity is generally occurring to a low degree in Atlantic salmon due to physiological constraints (i.e. trade-offs between current breeding investments and survival probability to future breeding), or whether it is maintained at a reduced level by anthropogenic activities, are key questions limiting our understanding of the importance

of iteroparity for population viability and recovery potential. While the degree of iteroparity is likely driven by both natural and anthropogenic factors, the spatio-temporal trends presented here highlight the potential for increases in iteroparity to occur when anthropogenic threats are mitigated, with known benefits to population resilience.

2.6 Acknowledgments

I would like to thank the numerous people involved in the collection and compilation of Atlantic salmon annual returns since the 1970s through the Department of Fisheries and Oceans Canada (DFO), Quebec's Ministère des Forêts, de la Faune et des Parcs (MFFP), the Maine Department of Marine Resources (DMR), ICES Working Group on North Atlantic Salmon (WGNAS), as well as from other organisations. Further, I would like to thank George A. Maynard for additional details on the data provided in Maynard et al. (2017). I would also like to thank Jan G. Davidsen, Christophe Herbinger, Ian Fleming, and Laura Weir for providing valuable feedback, as well as Rui Zhang for his early input into this research question, in addition to the ideasOTN committee of the Ocean Tracking Network. X.B. was supported by a graduate scholarship from the Fonds de recherche du Québec – Nature et technologies (FRQNT) and from the Natural Sciences and Engineering Research Council of Canada (NSERC). Additional support was provided from NSERC with a Discovery Grant to G.T.C. Finally, I would like to thank Tom Quinn and Bror Jonsson, in addition to another anonymous reviewer for their constructive and insightful feedback.

Table 2.1. Information on the location and extent of time series included in this study, with ten populations across the Northwest Atlantic range and West Greenland mixed-stock fishery landings.

Population	Population segment (DU / DPS [1])	Conservation Status	Geographic Coordinates	Time series extent	Data source
West Greenland fishery landings	---	---	N 64.161 W 51.819	1985-2017	WGNAS [4] ICES (2018)
Sand Hill, NL	Central Labrador	Not at risk [1]	N 53.511 W 56.490	1971-2016	DFO [5]
Western Arm Brook, NL	West coast of Newfoundland	Not at risk [1]	N 51.189 W 56.758	1974-2016	DFO
Trinite, QC	Quebec western north shore	Special concern [1]	N 49.411 W 67.337	1980-2017	MFFP [6]
Saint Jean, QC	Gaspé – southern Gulf of St. Lawrence	Special concern [1]	N 48.771 W 64.431	1981-2017	MFFP
Conne, NL	South coast of Newfoundland	Threatened [1]	N 47.915 W 55.688	1986-2016	DFO
Miramichi, NB	Gaspé – southern Gulf of St. Lawrence	Special concern [1]	N 46.980 W 65.569	1971-2017	DFO
Nashwaak, NB	Outer Bay of Fundy	Endangered [1]	N 45.957 W 66.620	1972-2017	DFO
Saint John, NB	Outer Bay of Fundy	Endangered [1]	N 45.952 W 66.875	1978-2017	DFO
LaHave, NS	Nova Scotia Southern uplands	Endangered [1]	N 44.536 W 64.713	1979-2017	DFO
Penobscot, ME	Gulf of Maine	Endangered [2]	N 44.832 W 68.701	1978-2013	DMR [7] Maynard et al. (2017)

[1] DU stands for Designatable Unit in Canada, the equivalent of Distinct Population Segment (DPS) in the United States; [2] Status assessment conducted by COSEWIC (2010); [3] Listed on the Endangered Species Act in 2000; [4] Working Group on North Atlantic Salmon of the International Council for the Exploration of the Sea; [5] Department of Fisheries and Ocean Canada; [6] "Ministère des Forêts, de la Faune et des Parcs du Québec"; [7] Maine Department of Marine Resources

Table 2.2. Average proportion of females, fork lengths, and fecundities of different spawning history groups (maiden-1SW, maiden-2SW+, as well as repeat spawners [RS]). Equations relating fecundity to length are given in the last column, along with their source.

Population	Prop. female			Fork length (cm)			Fecundity (eggs)			Fecundity-length relationship
	1SW	2SW+	RS	1SW	2SW+	RS	1SW	2SW+	RS	
Conne, NL	0.752	0.889	0.789	51.2	67.0	61.7	2102	4345	3476	$F_{(eggs)} = e^{0.7945} \times L_{(cm)}^{1.8326}$ O'Connell et al. (2008)
Trinité, QC	0.103	0.910	0.910	54.6	74.3	81.8	3349	6720	8340	$F_{(eggs)} = e^{-0.9099} \times L_{(cm)}^{2.2566}$ Based on data provided in Cauchon and April (2017)
Miramichi, NB	0.177	0.903	0.612	55.3	75.2	85.9	2583	5927	8489	$F_{(eggs)} = 0.051 \times L_{(cm)}^{2.700}$ Reid and Chaput (2012)
LaHave, NS	0.402	0.851	0.660	54.2	72.5	77.3	3180	6163	7318	$F_{(eggs)} = 446.54 \times e^{0.0363 \times L_{(cm)}}$ Cutting et al. (1987)

Table 2.3. Top three DFA models following model selection based on AICc for all populations combined (n=11), then separately for mid-latitudinal and northern populations (n=7), and southern populations (n=4). “m” stands for the number of common trends included in the model and “R” for the structure of the variance-covariance matrix of residual errors. Dashed boxes represent preferred models as detailed in the Methods section.

Rank	Model structure	AICc	ΔAICc
	All. pop		
1	m=1, R=equalvarcov	957.6	0.0
2	m=1, R=diagonal and equal	973.4	15.8
3	m=3, R=equalvarcov	974.8	17.2
	Mid-lat. and northern pop.		
1	m=2, R=diagonal and unequal	593.6	0.0
2	m=1, R=diagonal and unequal	594.2	0.6
3	m=1, R=equalvarcov	598.0	4.4
	Southern pop.		
1	m=1, R=unconstrained	375.4	0.0
2	m=1, R= equalvarcov	377.0	1.6
3	m=2, R= unconstrained	378.9	3.5

Table 2.4. Average proportions of repeat spawners in annual returns across Atlantic salmon populations of the northwest Atlantic Ocean, comparing the 1971-1992 and the 1993-2017 periods. *P*-values were computed using Welch Two Sample t-tests after the application of a logit transformation for proportional data. Means and standard errors are back-transformed from the logit scale. Populations are ordered by latitude with northern and mid-latitude (mid-lat.) populations on top, and southern populations below, with region-specific average proportions between dotted lines.

Population	1971-1992 average (± SD)	1993-2017 average (± SD)	Trend	*p*-value
Mid-lat. and northern pop.	0.031 (± 0.029)	0.076 (± 0.060)	↗	≤ 0.001*
West Greenland	0.010 (± 0.007)	0.033 (± 0.019)	↗	≤ 0.001*
Sand Hill, NL	0.015 (± 0.009)	0.050 (± 0.032)	↗	0.012*
Western Arm Brook, NL	0.004 (± 0.007)	0.046 (± 0.039)	↗	≤ 0.001*
Trinite, QC	0.024 (± 0.008)	0.098 (± 0.054)	↗	≤ 0.001*
Saint Jean, QC	0.054 (± 0.024)	0.043 (± 0.038)	—	0.129
Conne, NL	0.070 (± 0.019)	0.109 (± 0.070)	—	0.065
Miramichi, NB	0.046 (± 0.029)	0.136 (± 0.051)	↗	≤ 0.001*
Southern pop.	0.041 (± 0.035)	0.027 (± 0.031)	↘	0.007*
Nashwaak, NB	0.075 (± 0.050)	0.053 (± 0.041)	—	0.444
Saint John, NB	0.031 (± 0.019)	0.012 (± 0.011)	↘	≤ 0.001*
LaHave, NS	0.073 (± 0.036)	0.032 (± 0.025)	↘	≤ 0.001*
Penobscot, ME	0.016 (± 0.013)	0.010 (± 0.008)	—	0.110
All pop.	0.035 (± 0.032)	0.058 (± 0.056)	↗	≤ 0.001*

* $p < 0.05$

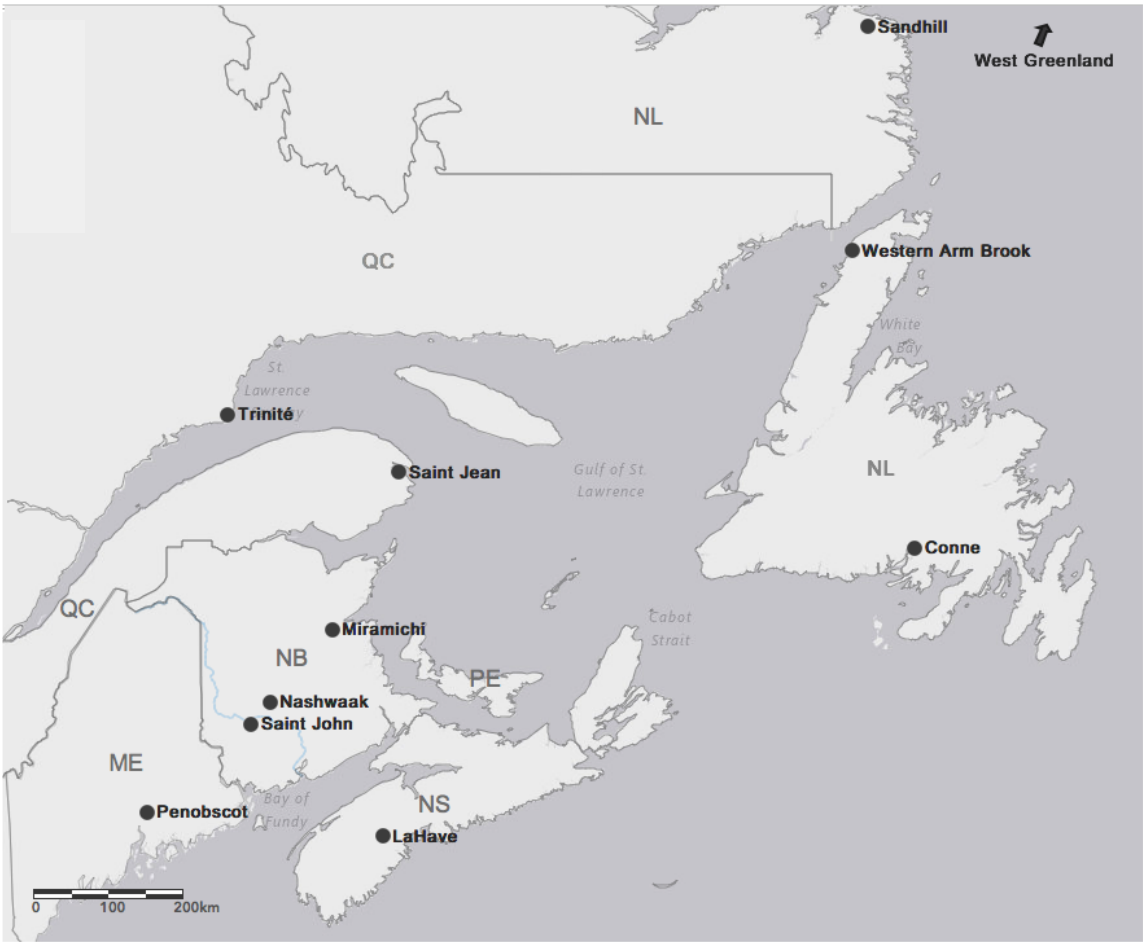


Fig. 2.1. Map of the Northwest Atlantic showing the location of Atlantic salmon populations with long-term monitoring programs that were included in this study (the map was produced using Esri, HERE, Garmin, NGA, USGS). Information on the extent of the time series is provided in Table 1.

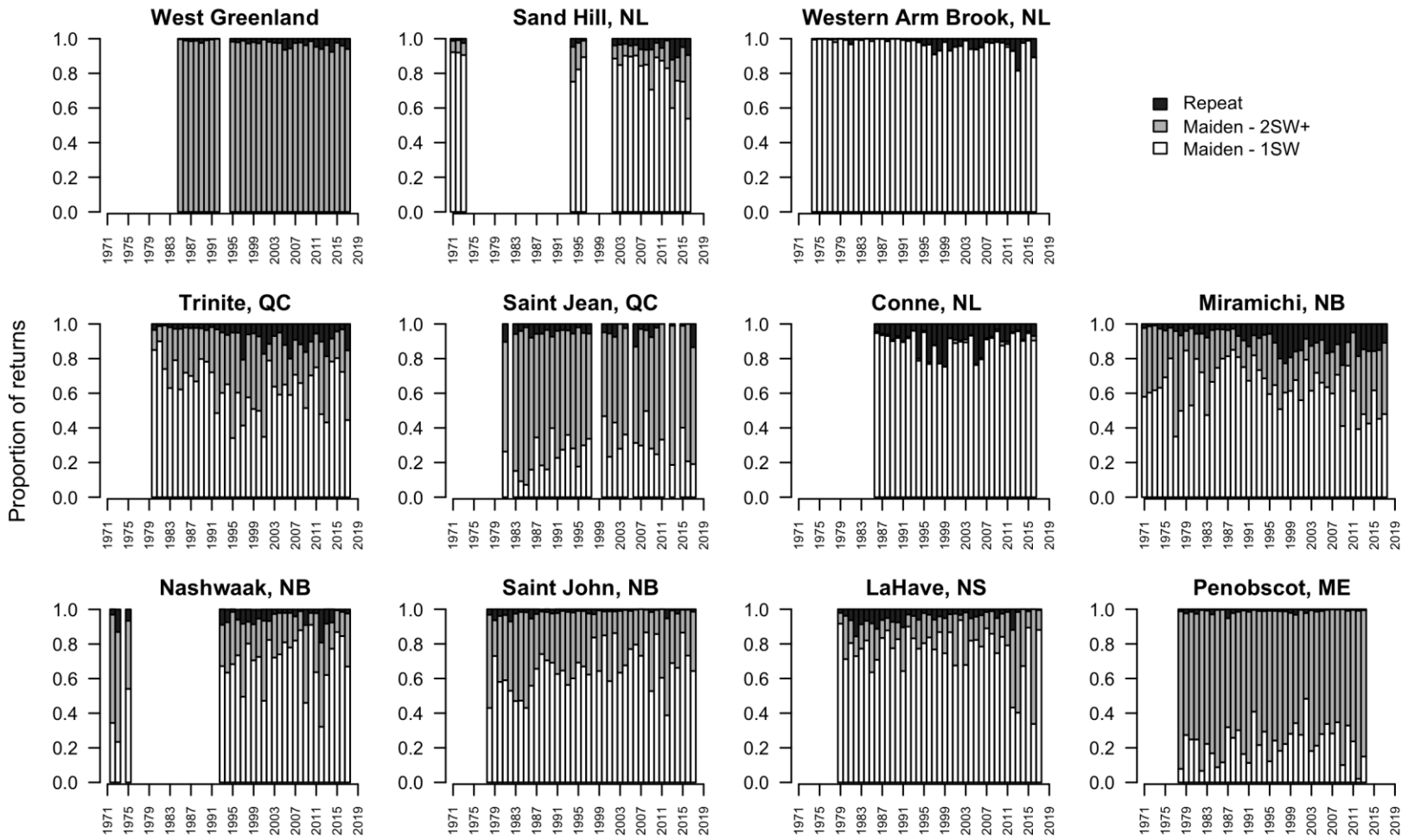


Fig. 2.2. Proportional spawning history composition of Atlantic salmon annual returns (sexes combined) across populations of the northwest Atlantic from 1971 to 2017, including the West Greenland fisheries. The proportions are represented for maiden-1SW in white, maiden-2SW+ in grey, and repeat spawners in black.

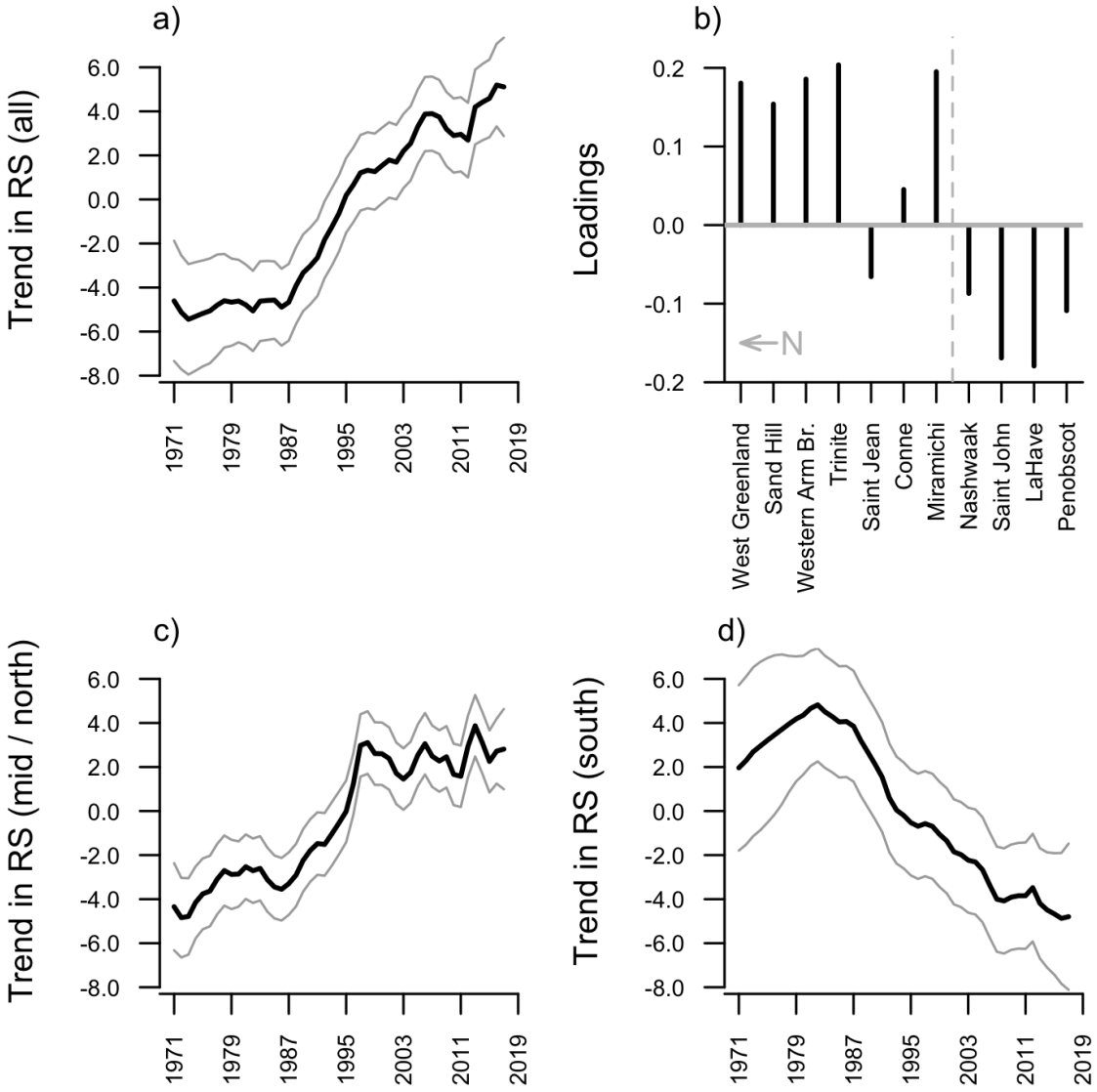


Fig. 2.3. Output of the Dynamic Factor Analysis (DFA) for the logit proportions of repeat spawners in annual returns (z-scored): a) the common temporal trend in repeat spawners across all 10 populations of the northwest Atlantic and West Greenland fishery landings (grey lines represent ± 2 standard errors); b) the average DFA loadings of each population on that common trend (ordered by latitude with northern most populations on the left, and southern populations right of the dotted line); c) the common temporal trend in repeat spawners across mid-latitudinal and northern populations (n = 7); and d) the common temporal trend in repeat spawners across southern populations (n = 4).

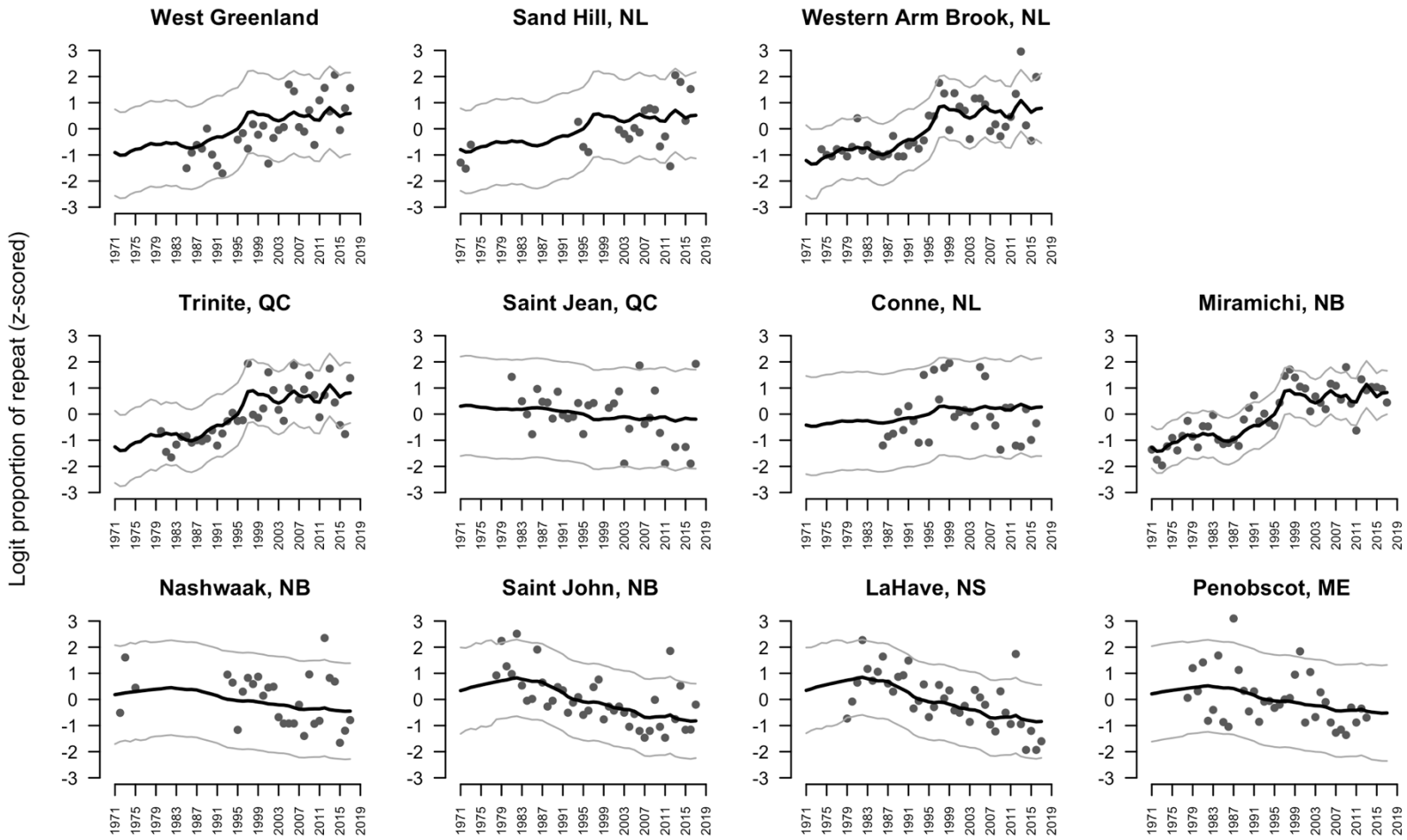


Fig. 2.4. Output of the Dynamic Factor Analysis (DFA) showing model fit to population's specific time series of the logit proportion of repeat spawners in annual returns (z-scored) (grey lines represent ± 2 standard errors). Mid-latitudinal / northern population time series (top two rows, n = 7) and southern populations (bottom row, n = 4) were fitted with the DFA trend common to these regions, presented respectively in Fig. 2.3c and Fig. 2.3d.

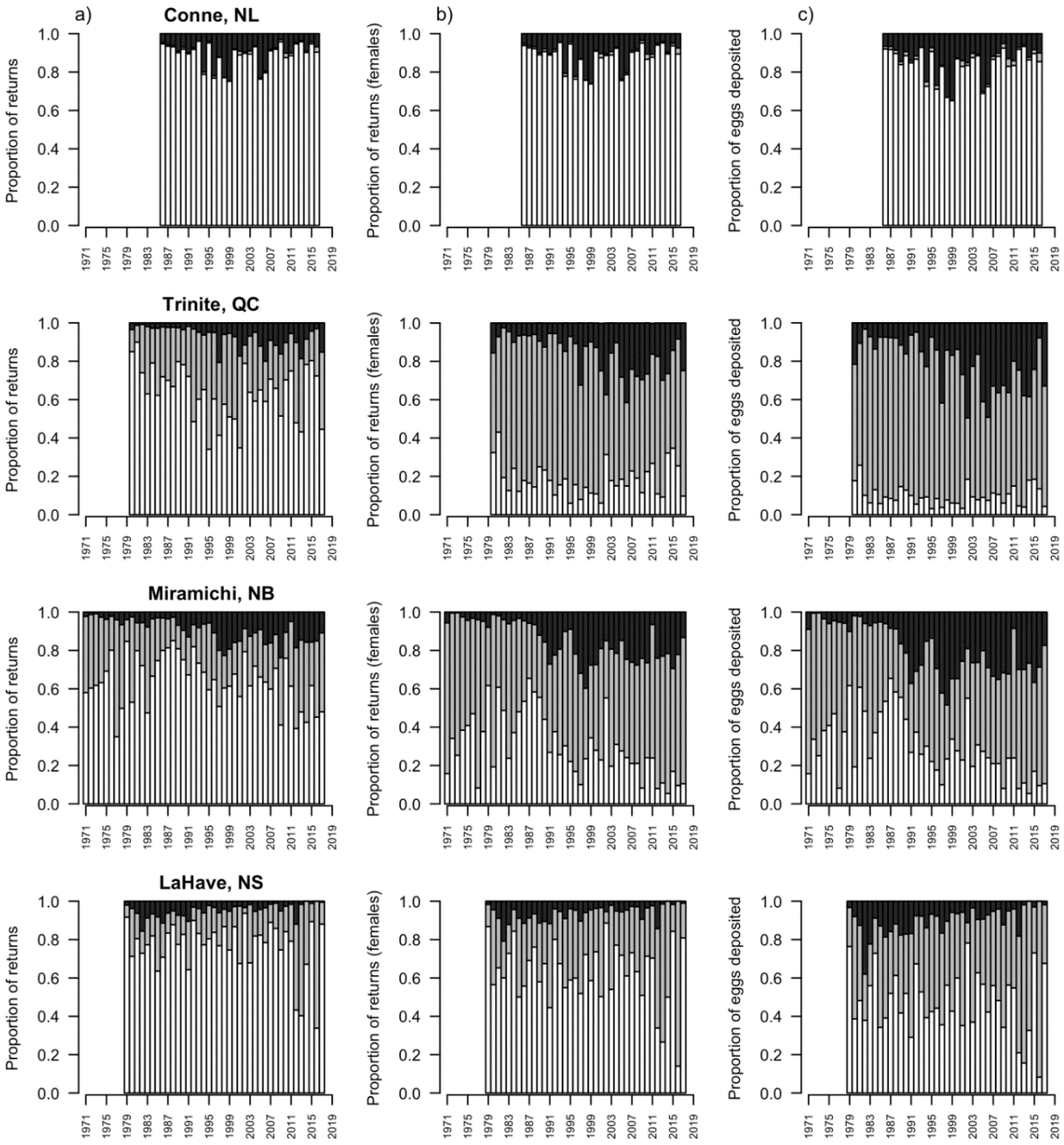


Fig. 2.5. Proportions by spawning history group of Atlantic salmon annual returns across four populations of the northwest Atlantic from 1971 to 2017; a) the proportions of all returns, sexes combined; b) the proportions for females only; and c) the proportions of the total annual egg deposition. The spawning history groups are maiden-1SW in white, maiden-2SW+ in grey, and repeat spawners in black.

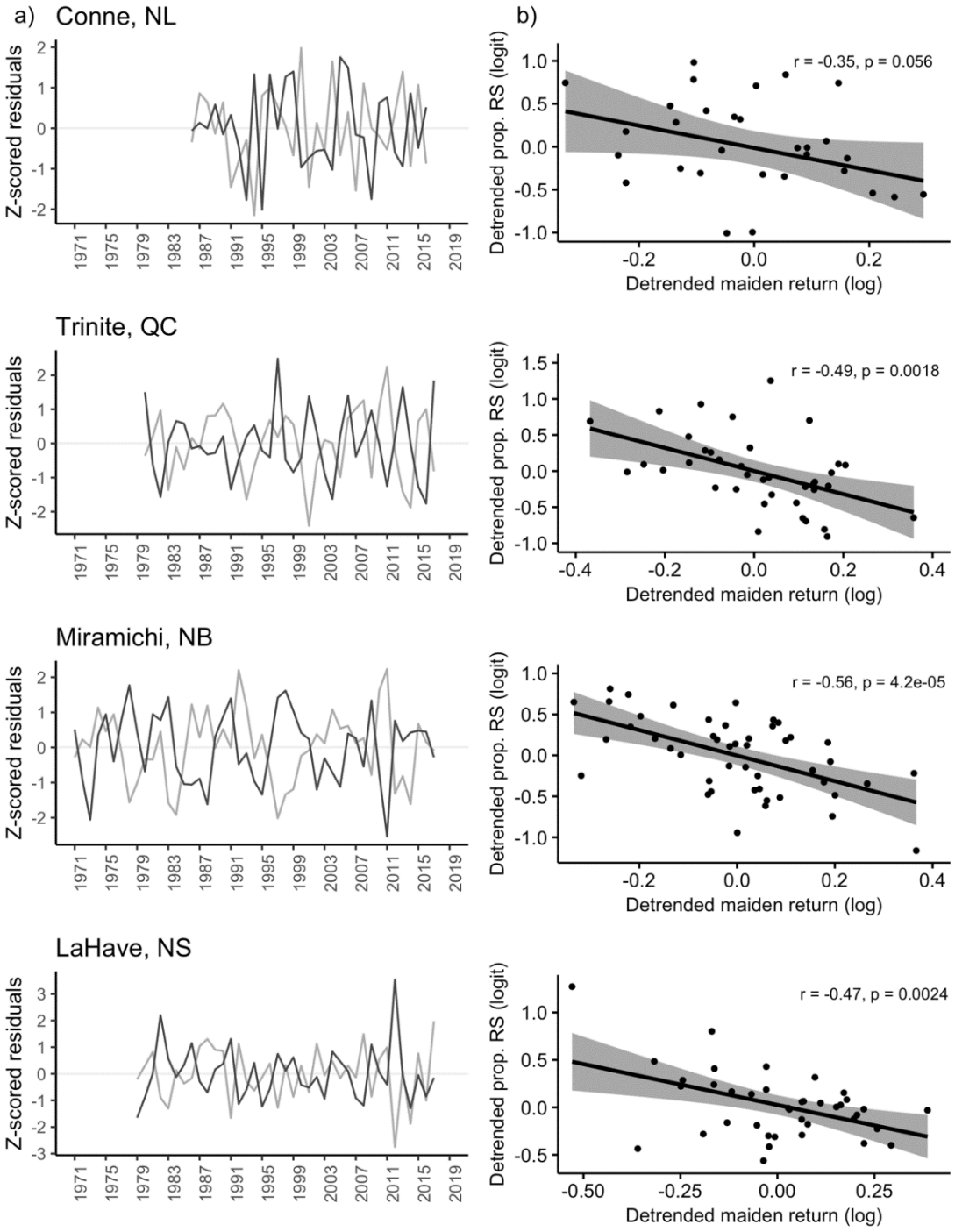
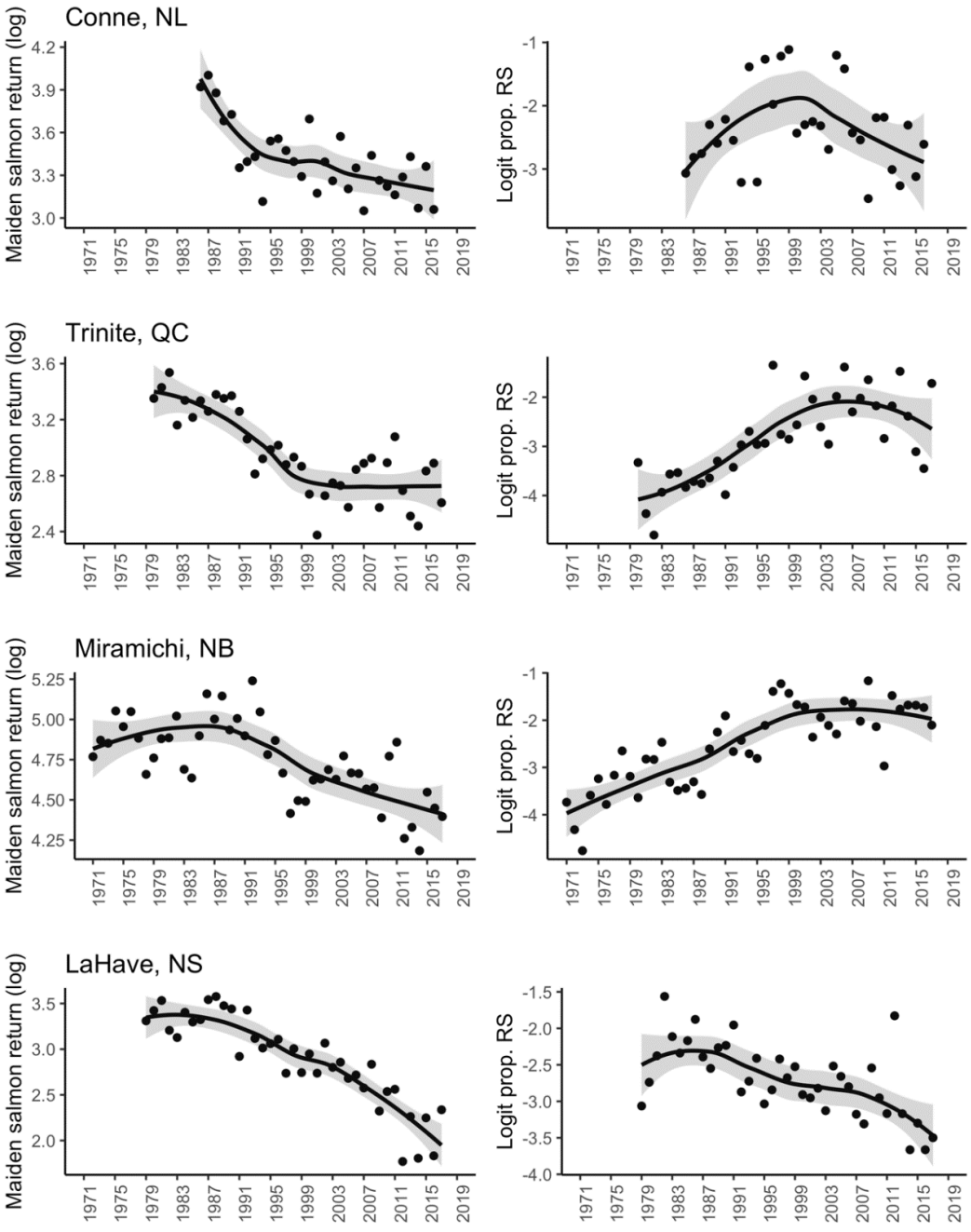


Fig. 2.6. Relationships between the de-trended proportion of repeat spawners (RS) in annual returns (logit transformed) and de-trended annual maiden salmon counts (log transformed): a) de-trended time series of the proportion of repeat spawner (black) and maiden salmon abundance (grey), z-score transformed; and b) correlation between the two de-trended time series with the Pearson correlation coefficient value and the *p*-value of the linear regression as inset text. The shaded area encompasses the 95 % CI of the slope.

2.7 Appendix

2.7.1 Appendix 1



Loess regression fits to de-trend the time series (maiden salmon returns on the left and annual proportion of repeat spawners on the right) used to isolate the high frequency variation component to test the hypothesis of iteroparity acting as a safeguard against low recruitment periods.

2.7.2 Appendix 2

Table with summary information on the proportional spawning history composition (maiden-1SW, maiden-2SW+, and repeat spawners) of Atlantic salmon annual returns (sexes combined) across nine populations of the northwest Atlantic from 1971 to 2017 (Sand Hill, NL; Western Arm Brook, NL; Conne, NL; Trinité, QC; Saint Jean, QC; Miramichi, NB; Nashwaak, NB; Saint John, NB; LaHave, NS). Published data on West Greenland fisheries landings and Penobscot (ME) can be found in ICES (2018) and Maynard et al. (2017).

Year	Sand Hill, NL					Western Arm Brook, NL					Conne, NL				
	P(1SW)	P(2SW+)	P(RS)	n small	n large	P(1SW)	P(2SW+)	P(RS)	n small	n large	P(1SW)	P(2SW+)	P(RS)	n small	n large
1971	0.923	0.065	0.012	392	78	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1972	0.920	0.071	0.009	412	64	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1973	0.906	0.069	0.025	951	227	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1974	NA	NA	NA	NA	NA	0.994	0.001	0.004	80	0*	NA	NA	NA	NA	NA
1975	NA	NA	NA	NA	NA	0.999	0.000	0.001	18	0*	NA	NA	NA	NA	NA
1976	NA	NA	NA	NA	NA	1.000	0.000	0.000	6	0*	NA	NA	NA	NA	NA
1977	NA	NA	NA	NA	NA	0.994	0.001	0.004	53	2*	NA	NA	NA	NA	NA
1978	NA	NA	NA	NA	NA	0.980	0.016	0.003	65	0*	NA	NA	NA	NA	NA
1979	NA	NA	NA	NA	NA	1.000	0.000	0.000	226	0*	NA	NA	NA	NA	NA
1980	NA	NA	NA	NA	NA	0.992	0.002	0.006	58	2*	NA	NA	NA	NA	NA
1981	NA	NA	NA	NA	NA	0.968	0.000	0.032	65	1*	NA	NA	NA	NA	NA
1982	NA	NA	NA	NA	NA	0.995	0.001	0.003	73	0*	NA	NA	NA	NA	NA
1983	NA	NA	NA	NA	NA	0.992	0.001	0.007	190	0*	NA	NA	NA	NA	NA
1984	NA	NA	NA	NA	NA	1.000	0.000	0.000	117	0*	NA	NA	NA	NA	NA
1985	NA	NA	NA	NA	NA	0.986	0.013	0.001	82	1*	NA	NA	NA	NA	NA
1986	NA	NA	NA	NA	NA	1.000	0.000	0.000	38	0*	0.947	0.017	0.035	360	1*
1987	NA	NA	NA	NA	NA	0.998	0.000	0.001	80	1*	0.935	0.018	0.047	405	0*
1988	NA	NA	NA	NA	NA	0.986	0.000	0.014	78	1*	0.931	0.017	0.051	808	3*
1989	NA	NA	NA	NA	NA	1.000	0.000	0.000	140	0*	0.901	0.008	0.091	146	15
1990	NA	NA	NA	NA	NA	1.000	0.000	0.000	46	1*	0.919	0.024	0.057	177	0*
1991	NA	NA	NA	NA	NA	0.993	0.001	0.007	224	1*	0.896	0.000	0.104	42	3*
1992	NA	NA	NA	NA	NA	0.986	0.005	0.009	408	3*	0.918	0.009	0.073	293	13

* Indicates the years during which a low number of large salmon were sampled. For these years, the composition of large salmon were calculated based on the mean composition of an extended time period (i.e. multiple years).

Appendix 2 (continued)

Year	Sand Hill, NL					Western Arm Brook, NL					Conne, NL				
	P(1SW)	P(2SW+)	P(RS)	n small	n large	P(1SW)	P(2SW+)	P(RS)	n small	n large	P(1SW)	P(2SW+)	P(RS)	n small	n large
1993	NA	NA	NA	NA	NA	0.990	0.005	0.005	251	4*	0.961	0.000	0.039	293	10
1994	0.752	0.201	0.047	157	20	0.979	0.010	0.010	103	6	0.788	0.012	0.200	87	5
1995	0.823	0.154	0.023	149	26	0.961	0.003	0.035	97	34	0.952	0.009	0.039	113	7
1996	0.892	0.088	0.019	166	3*	0.966	0.000	0.034	75	16	0.769	0.011	0.220	90	7
1997	NA	NA	NA	NA	NA	0.906	0.002	0.091	42	1*	0.876	0.002	0.122	685	26
1998	NA	NA	NA	NA	NA	0.931	0.000	0.069	103	12	0.772	0.000	0.228	159	32
1999	NA	NA	NA	NA	NA	0.980	0.000	0.019	6	0*	0.753	0.000	0.247	135	39
2000	NA	NA	NA	NA	NA	0.929	0.002	0.070	23	0*	0.917	0.002	0.081	202	19
2001	NA	NA	NA	NA	NA	0.953	0.000	0.047	29	7	0.890	0.019	0.091	183	6
2002	0.886	0.076	0.039	63	6	0.958	0.000	0.042	99	12	0.898	0.007	0.095	227	26
2003	0.849	0.117	0.034	131	24	0.989	0.000	0.011	146	14	0.894	0.015	0.091	157	0*
2004	0.901	0.069	0.030	235	40	0.940	0.000	0.060	69	12	0.932	0.004	0.064	242	22
2005	0.897	0.063	0.040	222	55	0.938	0.002	0.060	77	24	0.764	0.005	0.231	184	19
2006	0.903	0.061	0.036	299	42	0.949	0.000	0.051	54	6	0.796	0.009	0.195	171	20
2007	0.843	0.095	0.061	150	26	0.979	0.003	0.018	76	8	0.911	0.008	0.081	157	5
2008	0.850	0.086	0.064	133	69	0.975	0.000	0.025	56	3*	0.919	0.016	0.065	177	3*
2009	0.706	0.232	0.062	178	55	0.981	0.006	0.014	53	7	0.958	0.012	0.030	145	6
2010	0.892	0.084	0.024	155	16	0.977	0.000	0.023	59	41	0.875	0.024	0.101	126	6
2011	0.866	0.102	0.032	28	2*	0.952	0.014	0.033	78	11	0.886	0.013	0.101	139	7
2012	0.830	0.160	0.010	74	17	0.929	0.002	0.069	30	30	0.947	0.017	0.035	164	4*
2013	0.600	0.279	0.121	116	61	0.816	0.002	0.183	60	49	0.958	0.008	0.034	204	4*
2014	0.758	0.135	0.108	149	27	0.976	0.000	0.024	89	10	0.903	0.000	0.097	124	2*
2015	0.752	0.199	0.048	175	49	0.989	0.001	0.010	61	21	0.947	0.011	0.042	132	15
2016	0.538	0.367	0.094	111	66	0.892	0.003	0.105	58	51	0.904	0.027	0.069	156	5
2017	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Appendix 2 (continued)

Year	Trinité, QC					Saint Jean, QC					Miramichi, NB				
	P(1SW)	P(2SW+)	P(RS)	n small	n large	P(1SW)	P(2SW+)	P(RS)	n small	n large	P(1SW)	P(2SW+)	P(RS)	n small	n large
1971	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.580	0.397	0.023	257	314
1972	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.604	0.383	0.013	699	498
1973	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.617	0.374	0.008	744	724
1974	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.632	0.341	0.027	1378	569
1975	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.692	0.270	0.038	1020	338
1976	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.802	0.176	0.022	984	197
1977	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.350	0.610	0.041	421	514
1978	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.498	0.436	0.066	387	289
1979	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.847	0.114	0.040	743	97
1980	0.850	0.115	0.035	NA	39	NA	NA	NA	NA	NA	0.530	0.444	0.026	541	329
1981	0.900	0.088	0.013	NA	24	0.263	0.634	0.103	NA	50	0.799	0.145	0.056	607	52
1982	0.740	0.252	0.008	NA	64	NA	NA	NA	NA	4	0.721	0.223	0.056	527	86
1983	0.630	0.351	0.019	NA	77	0.152	0.790	0.058	NA	278	0.474	0.448	0.078	214	74
1984	0.791	0.181	0.028	NA	129	0.092	0.868	0.040	NA	317	0.666	0.299	0.035	237	96
1985	0.622	0.349	0.028	NA	253	0.071	0.909	0.020	NA	285	0.747	0.223	0.030	199	180
1986	0.719	0.260	0.021	NA	212	0.159	0.762	0.079	NA	214	0.800	0.169	0.031	424	284
1987	0.700	0.276	0.024	NA	126	0.345	0.598	0.057	NA	229	0.814	0.151	0.035	310	63
1988	0.668	0.309	0.023	NA	87	0.184	0.760	0.056	NA	467	0.851	0.122	0.027	326	249
1989	0.798	0.177	0.025	NA	111	0.160	0.805	0.035	NA	479	0.809	0.122	0.069	286	207
1990	0.782	0.182	0.036	NA	159	0.399	0.528	0.074	NA	245	0.751	0.153	0.095	243	402
1991	0.721	0.261	0.018	NA	122	0.227	0.734	0.039	NA	492	0.672	0.198	0.129	127	339
1992	0.485	0.483	0.032	NA	147	0.274	0.690	0.035	NA	597	0.819	0.115	0.065	662	1012

Appendix 2 (continued)

Year	Trinité, QC					Saint Jean, QC					Miramichi, NB				
	P(1SW)	P(2SW+)	P(RS)	n small	n large	P(1SW)	P(2SW+)	P(RS)	n small	n large	P(1SW)	P(2SW+)	P(RS)	n small	n large
1993	0.602	0.349	0.049	NA	57	0.360	0.603	0.037	NA	500	0.734	0.185	0.081	275	524
1994	0.652	0.285	0.063	NA	33	0.282	0.663	0.055	NA	572	0.686	0.251	0.062	927	1002
1995	0.342	0.609	0.049	NA	107	0.177	0.803	0.020	NA	418	0.595	0.348	0.057	602	1708
1996	0.604	0.346	0.050	NA	63	0.299	0.649	0.052	NA	364	0.647	0.244	0.108	585	996
1997	0.414	0.380	0.206	NA	54	0.337	0.608	0.055	NA	204	0.508	0.292	0.199	529	1257
1998	0.576	0.364	0.060	NA	78	NA	NA	NA	NA	NA	0.604	0.169	0.227	1187	635
1999	0.510	0.436	0.054	NA	45	NA	NA	NA	NA	NA	0.614	0.193	0.193	1641	1081
2000	0.499	0.429	0.072	NA	14	0.468	0.484	0.048	NA	44	0.677	0.165	0.158	725	1047
2001	0.348	0.479	0.172	NA	34	0.233	0.712	0.055	NA	98	0.560	0.288	0.152	949	2193
2002	0.789	0.096	0.115	NA	22	0.431	0.495	0.074	NA	23	0.794	0.120	0.086	2200	771
2003	0.638	0.293	0.069	NA	84	0.280	0.720	0.000	NA	52	0.615	0.259	0.126	1395	1371
2004	0.592	0.358	0.049	NA	33	0.362	0.614	0.025	NA	26	0.718	0.174	0.108	1638	1307
2005	0.650	0.229	0.121	NA	26	NA	NA	NA	NA	2	0.662	0.247	0.092	1231	1094
2006	0.591	0.209	0.200	NA	43	0.313	0.556	0.131	NA	42	0.635	0.196	0.169	2579	1203
2007	0.707	0.202	0.091	NA	93	0.298	0.672	0.029	NA	48	0.599	0.240	0.161	1857	924
2008	0.659	0.224	0.117	NA	64	0.498	0.467	0.036	NA	14	0.707	0.176	0.117	1635	402
2009	0.515	0.324	0.162	NA	18	0.281	0.643	0.076	NA	57	0.411	0.351	0.238	935	742
2010	0.703	0.195	0.102	NA	64	0.247	0.732	0.021	NA	109	0.759	0.135	0.106	2487	1070
2011	0.750	0.195	0.055	NA	68	0.333	0.667	0.000	NA	44	0.614	0.338	0.049	2031	1046
2012	0.479	0.419	0.102	NA	87	NA	NA	NA	NA	NA	0.393	0.421	0.186	676	691
2013	0.432	0.382	0.186	NA	64	0.186	0.804	0.010	NA	84	0.479	0.375	0.146	812	553
2014	0.783	0.132	0.084	NA	36	NA	NA	NA	NA	NA	0.425	0.418	0.157	0*	609
2015	0.803	0.154	0.043	NA	46	0.401	0.589	0.010	NA	61	0.617	0.227	0.157	0*	720
2016	0.723	0.246	0.031	NA	81	0.207	0.793	0.000	NA	74	0.452	0.397	0.150	0*	971
2017	0.445	0.403	0.152	NA	62	0.191	0.674	0.135	NA	12	0.480	0.411	0.109	0*	1029

Appendix 2 (continued)

Year	Nashwaak, NB					Saint John, NB					LaHave, NS				
	P(1SW)	P(2SW+)	P(RS)	n small	n large	P(1SW)	P(2SW+)	P(RS)	n small	n large	P(1SW)	P(2SW+)	P(RS)	n small	n large
1971	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1972	0.344	0.626	0.031	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1973	0.234	0.636	0.130	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1974	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1975	0.541	0.394	0.065	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1976	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1977	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1978	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1979	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.917	0.063	0.021	255	14
1980	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.712	0.250	0.038	141	113
1981	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.805	0.132	0.063	330	184
1982	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.729	0.115	0.156	67	40
1983	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.773	0.140	0.087	113	170
1984	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.820	0.114	0.066	33	137
1985	NA	NA	NA	NA	NA	0.430	0.538	0.032	NA	NA	0.636	0.282	0.082	218	429
1986	NA	NA	NA	NA	NA	0.730	0.207	0.063	NA	NA	0.708	0.178	0.113	264	487
1987	NA	NA	NA	NA	NA	0.581	0.380	0.039	NA	NA	0.834	0.104	0.062	661	416
1988	NA	NA	NA	NA	NA	0.590	0.376	0.033	NA	NA	0.878	0.072	0.050	849	362
1989	NA	NA	NA	NA	NA	0.529	0.399	0.071	NA	NA	0.775	0.152	0.073	939	456
1990	NA	NA	NA	NA	NA	0.470	0.504	0.025	NA	NA	0.827	0.097	0.075	783	405
1991	NA	NA	NA	NA	NA	0.473	0.511	0.016	NA	NA	0.643	0.253	0.104	246	291
1992	NA	NA	NA	NA	NA	0.430	0.553	0.017	NA	NA	0.900	0.070	0.030	1165	256

Appendix 2 (concluded)

Year	Nashwaak, NB					Saint John, NB					LaHave, NS				
	P(1SW)	P(2SW+)	P(RS)	n small	n large	P(1SW)	P(2SW+)	P(RS)	n small	n large	P(1SW)	P(2SW+)	P(RS)	n small	n large
1993	0.672	0.239	0.090	NA	NA	0.559	0.388	0.054	NA	NA	0.832	0.129	0.038	432	192
1994	0.635	0.291	0.074	NA	NA	0.657	0.317	0.027	NA	NA	0.773	0.167	0.060	202	231
1995	0.684	0.302	0.015	NA	NA	0.741	0.245	0.013	NA	NA	0.804	0.174	0.022	285	212
1996	0.735	0.206	0.058	NA	NA	0.705	0.279	0.016	NA	NA	0.838	0.131	0.032	238	184
1997	0.495	0.422	0.083	NA	NA	0.692	0.284	0.023	NA	NA	0.768	0.173	0.060	190	122
1998	0.803	0.126	0.071	NA	NA	0.626	0.351	0.022	NA	NA	0.868	0.091	0.041	360	133
1999	0.706	0.208	0.085	NA	NA	0.646	0.344	0.010	NA	NA	0.746	0.203	0.052	185	131
2000	0.726	0.221	0.052	NA	NA	0.564	0.422	0.015	NA	NA	0.867	0.104	0.028	250	117
2001	0.472	0.463	0.065	NA	NA	0.601	0.381	0.018	NA	NA	0.676	0.298	0.026	117	175
2002	0.824	0.109	0.067	NA	NA	0.693	0.298	0.009	NA	NA	0.938	0.029	0.033	222	68
2003	0.722	0.252	0.026	NA	NA	0.670	0.320	0.011	NA	NA	0.679	0.304	0.018	119	198
2004	0.740	0.240	0.020	NA	NA	0.623	0.353	0.024	NA	NA	0.819	0.129	0.052	82	116
2005	0.810	0.170	0.020	NA	NA	0.837	0.134	0.029	NA	NA	0.823	0.134	0.043	277	75
2006	0.780	0.200	0.020	NA	NA	0.644	0.349	0.007	NA	NA	0.785	0.181	0.034	358	107
2007	0.820	0.140	0.040	NA	NA	0.849	0.138	0.013	NA	NA	0.890	0.094	0.016	327	41
2008	0.880	0.110	0.010	NA	NA	0.585	0.404	0.011	NA	NA	0.858	0.131	0.011	585	92
2009	0.460	0.450	0.090	NA	NA	0.862	0.125	0.013	NA	NA	0.747	0.203	0.050	168	52
2010	0.911	0.069	0.020	NA	NA	0.634	0.356	0.010	NA	NA	0.841	0.133	0.026	294	52
2011	0.637	0.341	0.022	NA	NA	0.676	0.320	0.004	NA	NA	0.792	0.192	0.016	289	76
2012	0.322	0.487	0.191	NA	NA	0.770	0.220	0.009	NA	NA	0.433	0.448	0.119	28	39
2013	0.621	0.297	0.083	NA	NA	0.796	0.201	0.002	NA	NA	0.403	0.581	0.016	75	111
2014	0.773	0.152	0.076	NA	NA	0.732	0.268	0.000	NA	NA	0.672	0.328	0.000	43	21
2015	0.869	0.126	0.005	NA	NA	0.867	0.131	0.002	NA	NA	0.894	0.095	0.011	160	19
2016	0.846	0.140	0.014	NA	NA	0.527	0.456	0.017	NA	NA	0.338	0.662	0.000	23	45
2017	0.670	0.307	0.023	NA	NA	0.857	0.139	0.004	NA	NA	0.881	0.115	0.005	192	26

Chapter 3

Nutritional Correlates of the Overwintering Behaviour, Seaward Migration Timing, and Longer-Term Survival of Post-Spawning Atlantic Salmon [2]

3.1 Abstract

Despite the importance of iteroparity (i.e. repeated spawning) for the viability of Atlantic salmon populations, little is known about the factors influencing the migratory behaviour and survival prospects of post-spawned individuals (kelts). To test the hypothesis that post-spawning nutritional condition underlies differences in spatio-temporal aspects of the habitat use and survival of migrating Atlantic salmon kelts, I physiologically sampled and acoustically tagged 25 individuals from the Middle River, Nova Scotia in autumn 2015. Kelts were subsequently tracked within their natal river during the winter months, and as far as 650 km away along known migration pathways towards the Labrador Sea and Greenland. Some kelts were detected nearly 2 years later, upon their return to the natal river for repeat spawning. Overall, kelts in poor or depleted post-spawning nutritional state (i.e. low body condition index or plasma triglyceride level): i. initiated down-river migration earlier than higher condition kelts; ii. experienced higher overwinter mortality in the natal river; iii. tended to spend greater time in the estuary before moving to sea; and iv. did not progress as far in the marine

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Authors' contributions: XB and BGH collected the telemetry data with contributions from SD, and FGW; XB ran laboratory assays with contribution from DAP and GTC; XB analyzed the data; XB wrote the manuscript; SD, FGW, DAP and GTC contributed several ideas, comments, edits in the manuscript.

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environment, with a reduced probability of future repeat spawning. The current findings suggest that initial differences in post-spawning condition are carried through subsequent migratory stages, which can ultimately affect repeat-spawning potential. These results point to the importance of lipid storage and mobilisation in Atlantic salmon kelts for mediating post-spawning migratory behaviour and survival.

3.2 Introduction

A predominant life history trade-off involves the differential investment of energy reserves into current reproduction versus those required for self-maintenance, survival, and/or future reproductive potential (Stearns, 1989). In sexually reproducing organisms, this trade-off is particularly important for capital breeders, which rely on somatic energy reserves accrued prior to breeding to power migrations to breeding areas, produce gametes, and support the behaviour necessary for successful courtship and mating (Stearns, 1989; Jager *et al.*, 2008).

While high reproductive investment should increase the probability of current reproductive success, it can exact costs in terms of post-breeding mortality and a reduced likelihood of future reproduction (i.e. costs of reproduction; Williams 1996). At one end of the spectrum, the ultimate investment into a single life-time reproductive event (i.e. semelparity) is favored where there is low variability in juvenile survival and low post-breeding survival. However, in other circumstances there can be benefits to conserving resources to increase the probability of breeding more than once (i.e. iteroparity) (Cole, 1954; Murphy, 1968). As such, with increasing variability in the survival of offspring, natural selection favors life histories that spread the risk of reproductive failure over space or time (Murphy, 1968; Stearns, 1976).

The life history trade-off between current reproduction and survival is well illustrated within the semelparity – iteroparity continuum of salmonid fishes (family Salmonidae), where high total energy expenditure during reproduction is negatively associated with the probability of future (repeat) breeding (i.e. lowest in Atlantic

salmon, *Salmo salar*, and steelhead trout, *Oncorhynchus mykiss*, at 10 – 11 % and highest in brown trout, *Salmo trutta*, and Arctic charr, *Salvelinus alpinus*, at 34 – 41 %, among iteroparous species) (Fleming, 1998; Fleming and Reynolds, 2004). This continuum can also manifest within populations of the same species, as illustrated in Atlantic salmon where the average total energy expenditure for reproduction was negatively correlated with the average post-spawning survival rate of a population (Jonsson *et al.*, 1997). While inter-population differences in the post-spawning survival of salmonids can result from differences in habitat (Jonsson *et al.*, 1991) and/or anthropogenic disturbances (Maynard *et al.*, 2017; Bordeleau *et al.*, 2019b), these are at least partly caused by variation in life-history traits (e.g. sea-age at first maturity) and body size that influence reproductive investment, which then affect post-spawning survival and population demographics (Fleming and Reynolds 2004, Jonsson and Jonsson 2011a). As such, smaller, early-maturing salmon (i.e. one sea winter, or 1SW) that invest proportionally less into reproduction (40 – 60 % of total energy reserve) than larger multi sea winter (MSW) individuals (up to 70 % of total energy reserve) generally show higher post-spawning survival (Jonsson *et al.*, 1991, 1997; Fleming, 1998; Jonsson and Jonsson, 2003, 2011a). This was further corroborated by a recent study that identified a genotypic co-inheritance between sea-age at maturity and iteroparity in Atlantic salmon, with iteroparity being more likely in smaller, earlier-maturing salmon that invest proportionally less into reproduction (Aykanat *et al.*, 2019).

For iteroparous salmonids, post-spawning energetic condition is believed to be an important mediator of migratory decision-making and subsequent survival (Belding, 1934; Jonsson *et al.*, 1997; Halttunen *et al.*, 2013; Bordeleau *et al.*, 2018a). After spawning in the fall, energetically depleted Atlantic salmon kelts spend variable amounts of time in freshwater before initiating their seaward migration. Some may initiate seaward migration soon after spawning while others might overwinter in fresh water and delay migration until the spring (Jonsson and Jonsson 2011b). Although overwintering in fresh water is a common strategy for kelts, the winter months are generally lean with few feeding opportunities. Kelts must therefore rely primarily on

somatic lipid reserves to sustain basic metabolic costs (Jonsson *et al.*, 1997), pointing towards the importance of post-spawning energetic condition in mediating migratory decisions and survival. As such, Halttunen et al. (2013) reported that Atlantic salmon kelts with low body condition exited freshwater soon after spawning in an attempt to restore their depleted state via estuarine or marine foraging, while kelts in better condition delayed migration until the spring and opted for overwintering in freshwater. Once they have left freshwater, residency and habitat use in estuaries and near shore marine areas can also be highly variable among and within anadromous salmonid populations. For example, inter-individual variation in the estuarine residency of Atlantic salmon kelts can range from a few days (Hubley *et al.*, 2008) to upwards of several weeks (Hedger *et al.*, 2009), and even months (Bordeleau *et al.*, 2018b), with high inter-individual variability. Environmental cues (e.g. river discharge, water temperature, photoperiod) can predict the timing of seawater entry of juvenile salmonid smolts, which tends to occur each year within a narrow window (e.g. few weeks) (Jensen *et al.*, 2012; Otero *et al.*, 2014). However for kelts, the temporal window for migration is wide (e.g. autumn and spring migrants) and less predictable and does not appear to be linked to discreet environmental cues, suggesting an increased importance of endogenous factors in mediating post-spawning migratory decisions. When subjected to nutritional constraints, a major source of metabolic energy comes from the production of glycerol and free fatty acids via the hydrolysis of plasma triglycerides that were released into circulation from the catabolism of lipids stored in adipose and muscle tissue (Sargent *et al.*, 2002). During starvation, the concentration of triglycerides diminishes due to the energy demand imposed by basal metabolic processes (Kakizawa *et al.*, 1995). As such, plasma triglyceride concentration has been shown to be a useful, non-lethal indicator of nutritional status in many taxa, including wild salmonids (Boel *et al.*, 2014; Gauthey *et al.*, 2015; Bordeleau *et al.*, 2018a). Recently, triglyceride levels have been linked to inter-individual variation in the marine habitat use of post-spawned anadromous brown trout with depleted individuals remaining at sea for longer periods, in a presumed effort to offset higher nutritional needs (Bordeleau *et al.*, 2018a).

While the timing of downriver migration to the marine environment, and to some extent the overwinter survival of Atlantic salmon kelts, have both been linked to nutritional condition and stress state (Belding, 1934; Halttunen *et al.*, 2013; Bordeleau *et al.*, 2018b; Birnie-Gauvin *et al.*, 2019), the few previous telemetry studies documenting natural variation in post-spawning condition and its influence on the migratory behaviour and survival of post-spawned Atlantic salmon were limited in time and space (i.e. to Ocean entry; Halttunen *et al.*, 2013; Birnie-Gauvin *et al.*, 2019). As such, it remains unclear how post-spawning condition and the initial downstream migratory decision then affects the marine migratory behaviour and longer-term survival of Atlantic salmon kelts that either recondition at sea for from a few months (i.e. consecutive repeat spawners), or to more than a year (i.e. alternate repeat spawners).

In Atlantic salmon, and iteroparous salmonids more broadly, repeat spawners that are mostly constituted by large females, have an important ecological role contributing disproportionally to total annual egg deposition. For example in Atlantic salmon, 3.2 – 13.6 % repeat spawners in annual returns were estimated to contribute to 7.1 – 28.1 % of all eggs, an influence that was accentuated in years of low maiden spawner returns (Bordeleau *et al.*, 2019b). Combined with recent findings that iteroparity has been increasing in mid-latitudinal and northern parts of the Atlantic salmon's North American range, where repeat spawners have increased from 3.1 % (9971-1992) to 7.6 % (1993-2017) of annual returns (Bordeleau *et al.*, 2019b), identifying the factors influencing the habitat use and repeat-spawning potential of Atlantic salmon would benefit current and future conservation efforts in the face of declining populations. To address current knowledge gaps, I combined acoustic telemetry and physiological sampling to test the hypothesis that post-spawning nutritional condition underlies inter-individual differences in migratory behaviour and survival. As such, I physiologically sampled and acoustically tracked post-spawned Atlantic salmon kelts through their marine migrations (up to 650 km from the River mouth and over up to 654 days) until their eventual return as repeat spawners. I tested the predictions that individuals in depleted nutritional state (i.e. low body condition factor or plasma

triglyceride concentration) would: (i) initiate downstream migration earlier; (ii) experience greater overwinter mortality; (iii) spend greater time in the estuary; and (iv) have reduced probabilities of marine progression and repeat spawning.

3.3 Methods

3.3.1 Study System and Acoustic Receiver Array

I conducted the study on the Atlantic salmon population of the Middle River, Nova Scotia, draining into the vast estuarine habitat formed by the brackish Bras d'Or Lake system (~1100 km^2 in area, 45°51'37"N, 60°46'44"W; Fig. 3.1). Population numbers in this and surrounding rivers have been decreasing in recent decades, and while the Middle River supports the largest spawning runs remaining in the Eastern Cape Breton populations, annual returns are low (<350 on average, Gibson and Levy 2014). The declines prompted the Committee on the Status of Endangered Wildlife In Canada (COSEWIC, 2010) to recommend that the Eastern Cape Breton Atlantic salmon population segment be designated as endangered by the Canadian government.

For seaward migrating Atlantic salmon leaving the Middle River and migrating through the Bras d'Or Lakes system, the closest access to the Atlantic Ocean is located ~64 km away, either through the Great or Little Bras d'Or Channels (Fig. 3.1). In order to document the overwinter habitat use and seaward migrations of acoustically tagged Atlantic salmon kelts, a total of 30 VR2W acoustic receivers (Vemco Ltd., NS, Canada) were deployed throughout the Bras d'Or Lakes, forming acoustic detection gates that fish must cross en route to the Atlantic Ocean (Fig. 1; see Crossin et al. 2016 for additional details on the array). Once in the Atlantic Ocean, kelts could then be detected on two additional marine gates positioned across the Cabot Strait (i.e. to detect entry in the Gulf of St. Lawrence) and across the Strait of Belle Isle (i.e. the Northern exit of the Gulf of St. Lawrence towards the Labrador Sea: Fig. 3.1). To evaluate the detection efficiency of the acoustic array, I examined data from the 5 receiver gates the fish had to cross on their way to the Gulf of St Lawrence (i.e. river mouth, Nyanza Bay, two gates in

either the Great or Little Bras d'Or channels, and Cabot Strait: Fig. 3.1), and determined that all individuals that were detected on a given gate were also detected on the previous more inland/upstream gate. Thus, the detection efficiency of the array was high (Bordeleau *et al.*, 2018b).

3.3.2 Fish Capture, Blood Sampling and Tagging

A total of 25 post-spawned Atlantic salmon (51.1 – 95.0 cm FL) were captured on the Middle River by angling between Nov 26 – Dec 10, 2015. Immediately after capture, individual salmon were placed in a padded cradle supplied with ambient river water and blood was sampled. The average time from hooking to blood collection was 8:32 min (SD: 6:36 min, range: 2:49–30:49 min). Blood samples were placed in an ice-water slurry before centrifugation. Following blood sampling, fish were individually anesthetized, and then underwent surgical procedures at the site of capture for the implantation of 69 kHz V16-4H acoustic transmitter (16-mm diameter × 68 mm, 24 g in air, nominal delay of 20–70 s, estimated battery life of 1257 days; Vemco Ltd., NS, Canada). Transmitter mass relative to body mass averaged 1.0 % for kelts (range: 0.4 – 1.9 %), well within the tolerance limits for Atlantic salmon tag burden (Lacroix *et al.*, 2004). At the end of the tagging procedure, fork length and mass were recorded, scales were collected for ageing, and sex was determined morphologically. Body condition index was calculated from the residuals of the linear regression between $\log_e$ (mass in g) and $\log_e$ (fork length in mm) (i.e. residual mass, Kaufman et al. 2007). Sea age at first maturity was determined from scale readings (White and Medcof, 1968). Following sampling and tagging, kelts were placed in a recovery basin and later released at the capture site after regaining full equilibrium and swimming capacities (about 1 h later). While I also tagged wild-origin, hatchery-spawned kelts that had been captured for broodstock programs, these were excluded from the present study due to important anthropogenically-driven physiological, behavioral and survival differences with wild-spawned kelts (Bordeleau *et al.*, 2018b). Fish were handled in conformity with guidelines established by the Canadian Committee on Animal Care, approved by Dalhousie University and Cape Breton

University Animal Care Committees (protocol numbers: 14-105 and 1213-16, respectively). They were captured under the authority of a Scientific Fishing License granted by Fisheries and Ocean Canada (number: 340450).

3.3.3 Blood Processing and Triglyceride Assay

Within 3 h of blood sampling, samples were centrifuged at 1163g for 10 min and the resultant plasma was collected and flash-frozen at –80 °C. Plasma triglyceride levels were assayed in duplicate using a commercially available colorimetric kit (Cayman Chemical Company, USA) and read at 530 nm with a BioTek Synergy HTX microplate reader (BioTek Instruments, Inc., USA), according to the manufacturer's standard procedure. The mean coefficient of variation between duplicates was 6.7 %.

3.3.4 Data Analyses

To test the hypothesis that variation in the post-spawning nutritional state of individuals underlies differences in migratory behaviour and survival, different types of models were computed (i.e. binomial logistic regression, general linear regression, or Cox proportional hazards regression) depending on the nature of the response variable or aspect of interest. For each model, indices of nutritional state (i.e. plasma triglycerides level, body condition), fork length, sea-age at first maturity, sex, as well as simple interactions were considered as potential explanatory variables. Due to limited sample sizes, final statistical models were limited to the inclusion of a maximum of two explanatory variables for a minimum sample size of 20 individuals, and to a single explanatory variable for sample sizes lower than 20. The best fitting model was selected using a stepwise model building approach (based on AIC values and comparison with a null model; Anderson et al. 2001) using the *step* function in *R* v .3.5.0 (R Development Core Team 2018). Note that plasma triglyceride concentration and body condition index were not correlated (r = 0.08, Pearson correlation coefficient).

3.3.4.1 Overwintering Habitat Choice and Downstream Migration Timing

After being tagged in late fall, kelts spent various amount of time upstream before initiating their downstream migration to the Middle River mouth and adjacent estuary of Nyanza Bay (Fig 3.1). The initiation of downstream river migration and associated overwinter habitat choice was determined from the timing of individuals' first detection at the river mouth, which was bimodally distributed with autumn (i.e. before Jan-31) and spring downstream migrants (i.e. after Apr-1). All of the autumn migrating kelts were detected at the river mouth during the winter months and none of them were detected on the Nyanza Bay gate before spring, indicating that they ceased migration and overwintered in the lower section of the river or the upper estuary, as opposed to overwintering upstream for spring downstream migrants. To test the first prediction that the initiation of the downstream migration of post-spawned Atlantic salmon was related to individuals' nutritional condition, with kelts in poorer condition migrating down earlier, binomial logistic regression models (with two possible outcomes: autumn or spring downstream migrants) were computed in R. Model selection was conducted as previously described.

3.3.4.2 Overwinter Riverine Survival

Following the observation that no kelts were detected on estuarine receivers of the Bras d'Or Lakes or on marine gates before spring (i.e. earliest detection outside the river on Apr-24), the overwinter riverine survival of kelts tagged in late-November/early-December was calculated from the proportion of tagged individuals that reached the River mouth conditional to being detected on the first estuarine gate positioned in Nyanza Bay (indicating that individuals exited the Middle River). To test the second prediction that the overwinter riverine survival of post-spawned Atlantic salmon was related to individuals' nutritional condition, with kelts in poorer condition less likely to survive, binomial logistic regression models were computed in R. Model selection was conducted as previously described.

3.3.4.3 Estuarine Residency

For overwinter riverine survivors, the estuarine residency period of individuals started from the last detection at the river mouth receiver gate (estuarine entry) and ended at the first detection at an outermost receiver gate of either one of the Bras d'Or channels (estuarine exit or Ocean entry, Fig. 3.1). To test the hypothesis that the duration of the estuarine residency period of post-spawned Atlantic salmon was related to individuals' nutritional condition, with kelts in poorer condition spending more time reconditioning in the estuary before initiating their migration to oceanic feeding grounds, general linear regressions were computed in R. Model selection was conducted as previously described.

3.3.4.4 Marine Migration and Overall Survival

From the initial release site, kelts had to cross four acoustic receiver gates on their way to the Atlantic Ocean (i.e. Middle River mouth, Nyanza Bay and then two consecutive gates in either the Great or Little Bras d'Or channels, Fig 3.1.). Once at sea, kelts could then be detected on two additional marine gates, crossing the Cabot Strait to enter the Gulf of St. Lawrence and then crossing the Strait of Belle Isle to reach the Labrador Sea (Fig. 3.1). However, once in the Gulf of St. Lawrence, not all Atlantic salmon kelts migrate to the Labrador sea (Chaput and Benoit, 2012; Lacroix, 2013; Strøm *et al.*, 2017), therefore the probability of detection at the Strait of Belle Isle cannot be solely interpreted as survival as it is also confounded by the migratory decision of individuals. Finally, because of the long-lasting battery life of tags (> 4 years), potential repeat spawners could then be detected at mouth of the Middle River in following years. In total, kelts could be detected on six different acoustic gates and potentially back to the Middle River mouth in subsequent years. To test the hypothesis that the migratory progression and overall survival probability of kelts throughout the different stages of migration was influenced by individuals' nutritional condition, with kelts in better condition progressing further, Cox proportional hazards regressions were computed using the *coxph* and *Surv* function of the *survival* package in R. This method, originally

based on time-to-event analysis, was slightly modified by using a spatial variable (i.e. gate number, from 1 to 7) instead of time such that an individual that was detected at the last Bras d'Or gate (i.e. gate no 4) but not after was marked as to have survived until *t*(4) (Lennox *et al.*, 2018b). By adding explanatory variables in the model, this allowed us to evaluate the influence of nutritional condition and other covariates on the observed progression or survival pattern through the different stages of migration. Model selection was conducted as previously described and the proportional hazards assumption was verified using the *cox.zph* function of the *survival* package (testing the independence between Schoenfeld residuals and time/gate) (Grambsch and Therneau, 1994). Finally, I plotted Kaplan-Meier survival curves to visualize model output using the *survfit* function of the *survival* package in R.

3.3.4.5 Complementary Analysis

I used supplementary data provided by Gauthey *et al.* (2015) to conduct additional analyses on the relationship between post-spawning plasma triglyceride levels (i.e. as measured in this study) and reproductive investment. While the authors conducted their experiment on brown trout, their data provided a unique opportunity to gain further information on the biological relevance of measuring post-spawning concentration of plasma triglycerides as a metric reflective of a carryover effect from previous energy investment into reproduction in an iteroparous salmonid species closely related to Atlantic salmon. Following Gauthey *et al.* (2015) findings that high relative variation in plasma metabolites (e.g. variation of plasma triglycerides during the spawning season, between November and January) reflected high energy investment into reproduction, and high reproductive success (i.e. number of offspring produced), I tested whether the post-spawning (or final) triglycerides concentration alone was reflective of reproductive investment through the spawning season. More specifically, I tested the prediction that individuals with low post-spawning triglyceride levels were the ones that invested proportionally more resources into spawning, as indicated by a negative correlation between final triglyceride level and the relative variation of

triglycerides during spawning (more details on these metrics in Gauthey *et al.* 2015). To do so, from the original data set, I first excluded individuals with missing data on plasma triglyceride concentration or weight (n = 3) and individuals smaller than 120 g prior to spawning (n = 10). I then converted plasma triglyceride concentration in mmol L^{-1} to reflect current units (0.02 – 3.89 mmol L^{-1}, average: 0.85 mmol L^{-1}), before applying a square root transformation for normality and homoscedasticity purposes (final n = 36, 16 females and 20 males). To test the hypothesis, I then computed Pearson correlation coefficients in R.

3.4 Results

3.4.1 Overwintering Habitat Choice and Downstream Migration Timing

Among the 25 Atlantic salmon kelts (19 females, 6 males) that were tagged and released in the Middle River between Nov-26 to Dec-10, 2015, post-spawning downstream migratory timing was bimodally distributed. Eight individuals initiated downstream migration in late fall or early winter (termed autumn migrants), with first detections at the river mouth gate between Nov-29 and Jan-21 (average: Dec-12) depending on the individual. All of these autumn downstream migrants were detected at the river mouth during the winter months (until death or moving out in the spring) and none of them were detected on estuarine or marine receivers before spring and were therefore considered to have overwintered in the lower part of the Middle River or near its mouth. Twelve individuals spent the entire winter up-river, only initiating downstream migration in the spring (termed spring migrants) as first detected at the River mouth between Apr-23 and May-25 (average: May-9). A remaining 5 individuals were never detected at the river mouth or elsewhere in the acoustic array and were presumed to have died in the river.

In support of the first prediction, the best fitting (i.e. lowest AIC) binomial logistic regression model strictly included body condition index (BCI) (i.e. residual mass: Table 3.1), with kelts in lower condition having a higher probability of migrating soon after

spawning (i.e. in late fall or early winter) and spending the winter in the lower portion of the river (Fig. 3.2). In contrast, kelts in higher body condition initiated downstream migration later in the spring. With a 0.1 increase in BCI (representing a mass gain of 313 g for a fish of 719 mm in fork length, for a total mass of 3294 g), the odds of waiting for the spring to initiate downstream migration as opposed to migrating down in the autumn were 2.6 times greater, for a change in probability from 56 % (at BCI = -0.025) to 76 % (at BCI = 0.075) (Fig. 3.2). Body condition index was not a statistically significant single predictor of the probability of autumn *vs.* spring downstream migration timing (binomial logistic regression, $p = 0.104$, Fig. 3.2). However, dividing kelts in two equal groups based on body condition scores, kelts in lower body condition (<0.025) migrated down to the river mouth earlier than kelts in higher body condition (>0.025) with an average group difference of 84 days (i.e. Jan-28 *vs.* Apr-21). Considering body condition as a categorical variable (i.e. low or high body condition), body condition was a statistically significant single predictor of the probability of autumn *vs.* spring downstream migration timing (binomial logistic regression, $p = 0.016$, Table 3.2). This formulation provided the most parsimonious model (Table 3.1). Among the successful downstream migrants (n=20), 90 % (9/10) of kelts in the high body condition group spent the winter up-river and initiated their downstream migration in the spring, whereas only 30 % (3/10) of kelts in the low body condition group did so, with the majority of these fish (70 %) migrating down to the river mouth in the few weeks or months after spawning. The other explanatory variables, covariates and simple interactions considered (i.e. plasma triglycerides, sea-age at maturity, length, and sex) were not retained in the model during the stepwise process (Table 3.1).

3.4.2 Overwinter Riverine Survival

None of the tagged kelts were detected on estuarine receivers of the Bras d'Or Lakes or on marine gates before spring, meaning that they all overwintered in the Middle River or near its mouth before migrating out to enter the estuary between Apr-23 to May-25. Of the 25 individuals that were tagged, five kelts were never recorded at

the river mouth (i.e. presumed to have died up-river). Another three individuals that were detected arriving at the river mouth in the autumn, and detected there for a minimum of ~2 months, were then never detected elsewhere in the array and were presumed to have died in the lower part of the river. Thus, the combined riverine overwinter survival of kelts was estimated at 68.0 % (17/25).

In support of the second prediction, the best fitting (i.e. lowest AIC score) binomial logistic regression model included plasma triglyceride level and sea-age at maturity as important predictors of riverine overwinter survival probability (Table 3.1), with depleted 2SW kelts dying to a greater extent. While all 1SW kelts survived (6/6), compared to only 58 % (11/19) for 2SW kelts, the odds of overwinter survival for 2SW kelts increased by 9.9 times with a 0.50 mmol L^{-1} increase in plasma triglycerides concentration (p = 0.047, Table 3.2 and Fig. 3.3). At the time of tagging the average concentration of plasma triglycerides for 2SW kelts was 1.6-fold higher in kelts that survived overwinter (0.77 mmol L^{-1}) than in those that died in the few months after spawning (0.48 mmol L^{-1}) (p = 0.024, Welch Two Sample t-test). The other explanatory variables, covariates (i.e. body condition, length, and sex) and simple interactions considered were not retained in the model during the stepwise process. Because 1SW kelts were dominated by males (5 males, 1 female) and 2SW kelts by females (1 male, 18 females), the riverine overwinter survival probability of males (83 % or 5/6) was higher than for females (63 % or 12/19). However, I could not differentiate the effect of sex from the effect of sea-age at maturity due to strong correlation between these and relatively low sample sizes. The overwinter riverine survival of 1SW females (1/1) was equal to 1SW males (5/5). In contrast, the overwinter survival of 2SW females (11/18) appeared higher than that of 2SW males (0/1), although this remains uncertain due to low sample sizes.

3.4.3 Estuarine Survival and Residency

All survivors that overwintered in the river (n = 17) entered the vast estuary formed by the Bras d'Or Lakes between Apr-23 and May-25 (average: May-11). Among

the individuals that were detected entering the estuarine habitat of the Bras d'Or Lakes (i.e. as detected on the Nyanza Bay gate), all were subsequently detected on the next two estuarine receiver gates leaving the estuary and entering the Atlantic Ocean between May-9 and Jun-23 (average: Jun-8). Thus, the estuarine survival of kelts was 100 % (17/17). Bras d'Or or estuarine residency periods varied among individuals between 5.9 and 45.1 days (average: 28.8 days).

In partial support of the third prediction, the best fitting (i.e. lowest AIC score) general linear regression model only included body condition index (Table 3.1), indicating that depleted individuals tended to spend more time in the estuarine habitat of the Bras d'Or Lakes before migrating out to sea (6.2 extra days for each 0.1 decrease in body condition index, Table 3.2 and Fig. 3.4). However, despite being the most parsimonious model, body condition index was a marginally significant single predictor of the estuarine residency period of seaward migrating kelts (p = 0.057, Table 3.2). The other explanatory variables, covariates and simple interactions considered (i.e. plasma triglyceride, sea-age at maturity, length, and sex) were not retained in the model during the stepwise process (Table 3.1).

3.4.4 Marine Progression and Overall Survival Pattern

Of the 17 kelts that were detected leaving the Bras d'Or Lakes to enter the Atlantic Ocean between May-9 and Jun-26 (average: Jun-10), 13 were subsequently detected on the Cabot Strait receiver line between May-16 and Jun-29 (average: Jun-14), providing a minimum early marine survival estimate of 76 %. Six of these kelts were subsequently detected on the Strait of Belle Isle receiver array (located ~650 km from Middle River) between Jul-3 to Jul-15 (average: Jul-10), presumably migrating towards the Labrador Sea. Of the initial 25 kelts that were tagged after spawning in late fall 2015, two kelts returned as repeat spawners. Both of these fish were female, 2SW-maiden kelts at tagging and were tracked to the Strait of Belle Isle before coming back as alternate repeat spawners to the Middle River on Sep-7 and Sep-10, 2017, 489 and 504

days after having left the river in spring 2016. Thus, survival to repeat spawning was of 8 % (2/25) for both sexes combined and 11 % for females alone (2/19).

In support of the final prediction that the marine progression and overall survival probability would be reduced for nutritionally depleted individuals, the best fitting (i.e. lowest AIC score) Cox proportional hazards regression model included plasma triglycerides level, sea-age at maturity, and a simple interaction term between the two (Table 3.1). As such, the probability of progressing or surviving further through the different stages of migration (river, estuary, ocean, then back to the river to spawn again) increased with increasing plasma triglycerides level for 2SW kelts (p = 0.013, Table 3.2). And while post-spawning plasma triglycerides level was not a significant predictor of survival probability for 1SW kelts (considering the marginally significant interaction, p = 0.067: Table 3.2), 1SW kelts experienced higher overall survival than 2SW kelts as driven by their higher survival in the earlier stages of migration (Fig. 3.5). The other explanatory variables, covariates and simple interactions considered (i.e. body condition, estradiol, testosterone, length, and sex) were not retained in the model during the stepwise process.

Based on these findings on the link between the overall survival of 2SW kelts and triglyceride level and to facilitate the interpretation, I divided 2SW kelts into two groups based on plasma triglyceride concentration: kelts with low post-spawning levels between 0.21 – 0.62 mmol L^{-1}; and kelts with high levels between 0.68 – 1.27 mmol L^{-1}. I then plotted Kaplan-Meier survival curves to better visualize differences in the progression or survival probability of kelts throughout the different stages of migration among 1SW (n = 6), 2SW with high triglyceride level (n = 9), and 2SW kelts with low triglyceride level (n = 10) (Fig. 3.5). 1SW kelts (independently of their plasma triglyceride concentration) had the highest survival probability through the riverine and estuarine migration stages with 100 % of them surviving to reach the ocean (i.e. to BC2 gate, Fig. 3.1), followed by 2SW kelts with high triglyceride level at 78 % survival, and by 2SW kelts with depleted triglyceride level at a reduced 40 % survival probability (Fig. 3.5).

Once in the marine environment, the vast majority of 1SW kelts (5/6) and depleted 2SW kelts (4/4) that survived to enter the ocean, subsequently survived to cross the Cabot Strait. While the early marine survival of both of these groups was high, the probability of progressing further (i.e. to cross the Strait of Belle Isle and enter the Labrador Sea) declined abruptly, with a reduced apparent overall survival of 33 % (2/6) for 1SW kelts and 0 % (0/10) for low triglyceride 2SW kelts (13 % combined (2/16) (Fig. 3.5). Moreover, none of these individuals returned to the Middle River to spawn again. In contrast, 44 % (4/9) of 2SW kelts with high plasma triglyceride level survived to reach the Labrador Sea, with 22 % (2/9) of them returning to the Middle River as alternate repeat spawners. These two individuals were 2SW females that had higher (i.e. 1.7-fold) post-spawning plasma triglyceride concentration than 2SW kelts that did not survive to spawn again (averages of 1.01 mmol L^{-1} *vs.* 0.60 mmol L^{-1}, respectively).

3.4.5 Complementary Analysis

From additional analyses computed using the supplementary data provided in Gauthey et al. (2015), as hypothesized, post-spawning plasma triglyceride concentration (square root transformed) was negatively correlated with the relative variation of triglycerides during spawning ($r = -0.61$, $p < 0.001$, $R^2 = 0.37$), which was in turn positively correlated with reproductive success (i.e. number of offspring assigned; Gauthey et al. 2015). As such, individuals with depleted post-spawning levels of triglycerides invested more energy into reproduction.

3.5 Discussion

Our findings support the hypothesis that inter-individual differences in post-spawning nutritional condition underlie differential migratory decisions and survival propensity for Atlantic salmon kelts. I identified nutritional correlates of spatio-temporal variation in the habitat use and survival of kelts through their winter in river, during their seaward migration, and on their way back to spawn in subsequent years. Overall, kelts in

depleted nutritional condition (i.e. low body condition index or plasma triglyceride level): i. initiated downstream river migration sooner; ii. experienced higher overwinter riverine mortality; iii. tended to spend greater time in the estuary before moving back to sea; and iv. did not progress as far in the marine environment and had a reduced probability of surviving to reproduce again than kelts in better nutritional condition.

After spawning, kelts in poor body condition had an increased probability of initiating downstream migration in the autumn to overwinter in the lower section of the river compared to animals with better body condition which mostly overwintered up-river and only migrated down in the spring. Similar condition-dependent migration timing of Atlantic salmon kelts, with depleted individuals initiating downstream movement soon after spawning, was previously described by Halttunen *et al.* (2013). In addition to a lower body condition factor in autumn migrating Atlantic salmon kelts (Halttunen *et al.*, 2013), Birnie-Gauvin *et al.* (2019) reported that early migrants tended to have higher baseline plasma cortisol levels compared to spring migrating kelts. This might suggest that kelts perceive low nutritional state and low resource availability as a stressful stimuli which might trigger the upregulation of cortisol levels for feeding and preparation for salt water. Although the majority of kelts with low body condition initiated downstream migration in the autumn, in contrast with previous studies (i.e. Halttunen *et al.*, 2013; Birnie-Gauvin *et al.*, 2019), no kelts from the current study entered the sea before spring and instead decided to overwinter in the lower section of the Middle River or near its mouth. Complementary to my findings on the condition-dependent downstream migration timing of kelts, nutritional status was also linked to overwinter riverine survival so that the survival probability of 2SW kelts decreased with decreasing post-spawning triglyceride concentration (i.e. an important source of energy for metabolic maintenance during starvation; Sargent et al. 2002). In addition, all 1SW kelts survived through the winter months as expected given their lower metabolic costs due to proportionally lower reproductive investment (Jonsson et al. 1991, 1997, Fleming 1996). Among the kelts that successfully migrated down to the river mouth (either in the autumn or the spring) the only individuals that did not survive to reach the first

estuarine gate were three 2SW females that had migrated down in the autumn. I believe this migratory decision about overwinter habitat choice reflects a trade-off between the safety of overwintering in freshwater and the more numerous feeding opportunities of the lower river section and adjacent estuarine habitat incurring greater risks, such as predation (as suggested by Halttunen *et al.*, 2013). While no wild-spawned kelts in the current study exited the river before spring, the risk of premature seaward migration was further exemplified in a recent study in the same system where the survival probability of wild-origin, hatchery-spawned kelts (i.e. high stress group) released back to the river after being stripped of gametes and which migrated to the estuary in the autumn was only 33 % (Bordeleau *et al.*, 2018b). Together these findings suggest that depleted kelts are less likely to survive through the winter, likely due to a combination of higher nutritional requirements to sustain basal metabolic processes and the necessity to migrate to a risker habitat in trying to offset these. The overwinter riverine survival probability of kelts reported in this study (i.e. 68 %) was of similar magnitude to that reported from the Alta River, northern Norway (63 %) (Halttunen *et al.* 2013).

In addition to the apparent role of nutritional condition in mediating the post-spawning downstream migration timing and overwinter riverine survival of Atlantic salmon kelts, I also identified nutritional correlates of spatio-temporal variation in the habitat use and survival of kelts through the estuarine and marine migration stages. As such, the estuarine residency period of kelts (of up to 45 days) was negatively correlated with body condition factor such that depleted kelts tended to spend more time in the brackish Bras d'Or Lakes before migrating to sea. With important numbers of rainbow smelt, *Osmerus mordax*, a preferred prey species for Atlantic salmon kelts (Cunjak *et al.*, 1998) present in the Middle River and the Bras d'Or Lakes in the winter and spring (S. Denny, unpublished), I believe this provides the opportunity for an initial period of feeding needed to partially restore somatic reserves prior to oceanic migration (as suggested by Hedger et al. 2009). Differential nutritional needs might explain the longer estuarine residency periods of kelts in lower body condition. Similarly, the marine residency period of adult anadromous brown trout was also negatively correlated with

pre-migratory nutritional condition (i.e. plasma triglycerides, expressed at similar concentration to those in the current study) with depleted individuals spending more time feeding at sea, potentially reflecting higher energetic requirements (Bordeleau *et al.*, 2018a). Although no Atlantic salmon kelts that I tagged from the Middle River were detected in the brackish inland sea formed by the Bras d'Or Lakes after the month of June, the estuarine residency periods observed were substantial (i.e. up to 45 days in wild-spawned kelts; and even to 191 days in early migrating hatchery-spawned kelts, Bordeleau et al. 2018b). This points out the ecological importance of this unique system for reconditioning Atlantic salmon, as suggested by Mi'kmaq traditional ecological knowledge (see Crossin et al. 2016).

In this study, the survival of kelts through the estuary and the early marine migration phase (i.e. to cross the Cabot Strait and enter the Gulf of St. Lawrence) was 76 %, which agrees with previous findings that these phases of the migration of Atlantic salmon kelts are characterized by high survival (range: 70 – 92 %; Hubley et al. 2008, Halttunen et al. 2009, Hedger et al. 2009). Moreover, while the early marine survival of kelts was high, the probability of them reaching the Labrador Sea declined abruptly to 35 % (i.e. similar to that observed by Hedger et al. 2009 at 32 %). This decline in the progression probability of kelts in the later phase of their marine migration was especially important for 1SW kelts and 2SW kelts with depleted triglyceride levels, compared to 2SW kelts with high triglyceride levels. While this also seems to point out to the role of post-spawning nutritional condition in mediating longer-term migratory behaviour and survival of 2SW, this is not evident for 1SW that also experienced reduced progression probability in the marine environment. However, this might not solely reflect differences in survival as it might also have been partly driven by smaller (e.g. 1SW) and depleted kelts more likely to adopt a shorter distance migratory strategy to feed in the Gulf of St. Lawrence instead of migrating towards the Labrador Sea and the West coast of Greenland (Chaput and Benoit, 2012; Strøm *et al.*, 2017). In conjunction, it is also possible that smaller (e.g. 1SW) and depleted kelts experienced higher predation risks, which might be especially important in the Gulf of St. Lawrence (Strøm *et al.*,

2019). Nonetheless, among 2SW it is perhaps unsurprising to note that the only two individuals that survived to repeat spawning were two 2SW female kelts with high post-spawning triglyceride levels. These two individuals were tracked all the way up to the Strait of Belle Isle before coming back to spawn as alternate repeat-spawners a few years after tagging.

Additional analyses I conducted on supplementary data provided in Gauthey et al. (2015) confirmed that post-spawning levels of plasma triglycerides were reflective of the relative variation of this metabolite during the spawning season, a measure of energy investment into reproduction which was in turn positively correlated with reproductive success. While I could not directly quantify total reproductive investment in this study, findings are consistent with expectations from the life history trade-off between current reproduction and survival in which larger and more depleted individuals experienced higher post-spawning mortality as a result of higher energy investment into spawning (Jonsson *et al.*, 1991, 1997; Fleming, 1996; Aykanat *et al.*, 2019). This offers additional support for the biological relevance of measuring post-spawning plasma triglyceride concentration as a valuable and relatively simple non-lethal indicator of nutritional condition, and indicator of a potential reproductive carryover effect on post-spawn survival (as suggested by Bordeleau et al. 2018a). While additional research is needed to further clarify the link between total reproductive investment and post-spawning metabolites level, this might present future research opportunities in study designs, such as ours, were repeated sampling is not possible.

Collectively my findings highlight the role of nutritional condition in mediating the post-spawning migratory behaviour and survival of Atlantic salmon kelts. As such, indices of nutritional condition were correlated with spatio-temporal variation in the habitat use and survival of kelts throughout their entire migration (overwinter period, seaward migration, and eventual return as repeat-spawners). This suggests that initial differences in post-spawning condition, likely determined by individual variation in reproductive investment, can be carried throughout their migration and ultimately affect repeat-spawning potential. Moreover, by providing valuable information on some

of the endogenous mechanisms at play, these findings will inform current and future management and conservation efforts directed at improving the survival prospects and future breeding potential of post-spawners. This is especially important considering recent findings on the ecological importance of repeat spawners to the viability of Atlantic salmon populations and the broad-scale spatio-temporal shifts in iteroparity that have been occurring over the last few decades across populations of the northwest Atlantic (Bordeleau *et al.*, 2019b).

3.6 Acknowledgments

I would like to thank Tyson Paul and Emma Garden from the Unama'ki Institute of Natural Resources; Jesse MacDougall and Joel Hayes from Cape Breton University; Leah Strople and Danny Farrar from Dalhousie University; as well as Greg Lovely, Bill Haley, and Leonard Forsyth from the Margaree Salmon Association for their assistance in the field. I also thank Alex Levy and Greg Stevens from Fisheries and Ocean Canada for their input on the study design. The staff of the Ocean Tracking Network, especially within the data system, provided valuable assistance with acoustic tag detections.

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Table 3.1. Model selection process and composition of the best three fitting regression models (i.e. lowest AIC) for each migratory components. BCI stands for body condition index (i.e. residual mass) as either a continuous or categorical variable (i.e. low and high body condition group as detailed above). SW stands for sea-age at maturity (i.e. 1SW or 2SW) and TRIG for plasma triglyceride concentration.

Rank	Model structure	AIC	ΔAIC
i. Downstream migration timing *(binomial logistic)*			
1	~ BCI (cat.)	22.7	0.0
2	~ BCI	27.9	5.3
3	~ 1	28.9	6.2
ii. Overwinter riverine survival *(binomial logistic)*			
1	~ SW + TRIG	26.4	0.0
2	~ SW	29.9	3.5
3	~ SW + BCI (cat.)	30.2	3.8
iii. Estuarine residency period *(general linear)*			
1	~ BCI	83.1	0.0
2	~ BCI (cat.)	84.8	1.7
3	~ 1	85.4	2.3
iv. Marine progression and overall survival *(Cox proportional hazards)*			
1	~ SW + TRIG + SW:TRIG	114.4	0.0
2	~ SW + TRIG	115.2	0.8
3	~ 1	116.0	1.6

Table 3.2. Composition of the best fitting regression models (i.e. lowest AIC) for each migratory components. BCI stands for body condition index (i.e. residual mass) as either a continuous or categorical variable (i.e. low and high body condition group as detailed above). SW stands for sea-age at maturity (i.e. 1SW or 2SW) and TRIG for plasma triglyceride concentration.

Variable	Coefficient	SE	*p*-value
i. Downstream migration timing *(binomial logistic)*			
Intercept	2.20	1.05	---
BCI (cat. = low)	-3.05	1.26	0.016 *
ii. Overwinter riverine survival *(binomial logistic)*			
Intercept	-2.49	1.45	---
TRIG	4.58	2.31	0.047 *
SW (1SW)	21.08	---	0.999
iii. Estuarine residency period *(general linear)*			
Intercept	29.13	2.65	---
BCI	-61.54	29.81	0.057 .
iv. Marine progression and overall survival *(Cox proportional hazards)*			
TRIG	-2.52	1.01	0.013 *
SW (1SW)	-2.14	0.88	0.015 *
TRIG:SW (1SW)	2.83	1.54	0.067 .

* $p < 0.05$; . $p < 0.07$

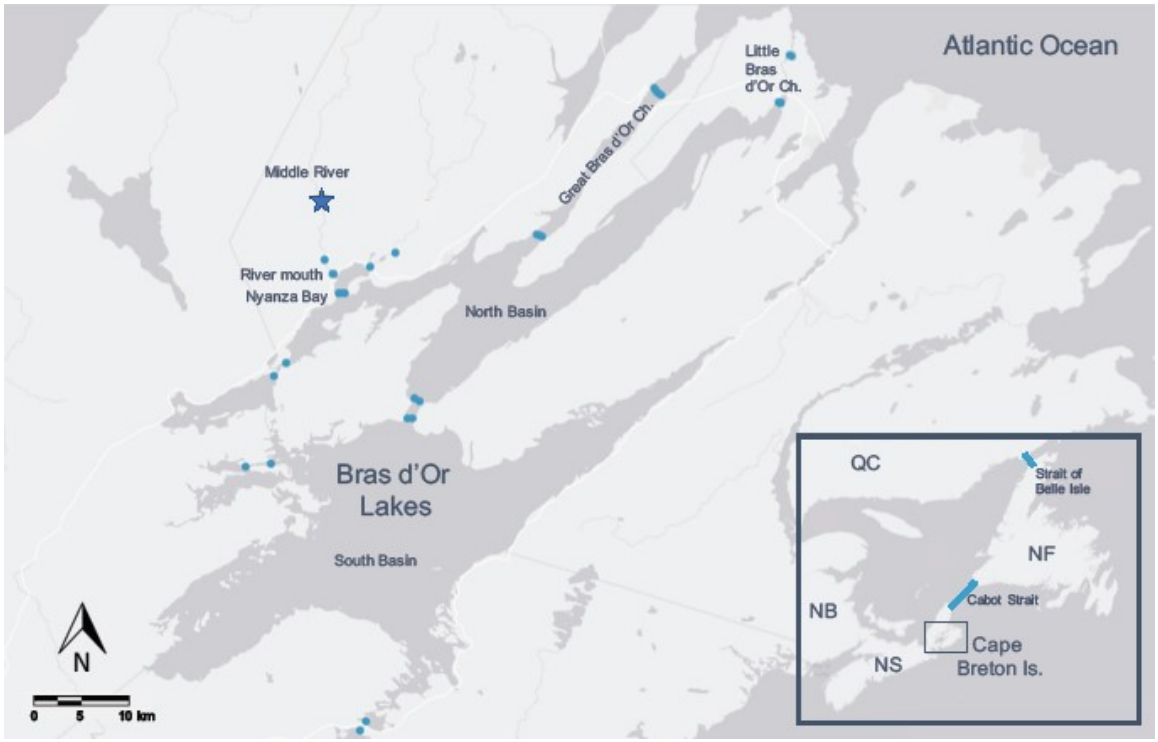

Fig. 3.1. Map of the acoustic array positioned in the Bras d'Or Lakes, Nova Scotia and in the Atlantic Ocean. Acoustic receivers are indicated by blue circles in the Bras d'Or Lakes (n = 30) or blue lines in the Ocean, and the star symbol indicates the release location of kelts (the map was produced using Esri, HERE, Garmin, NGA, USGS).

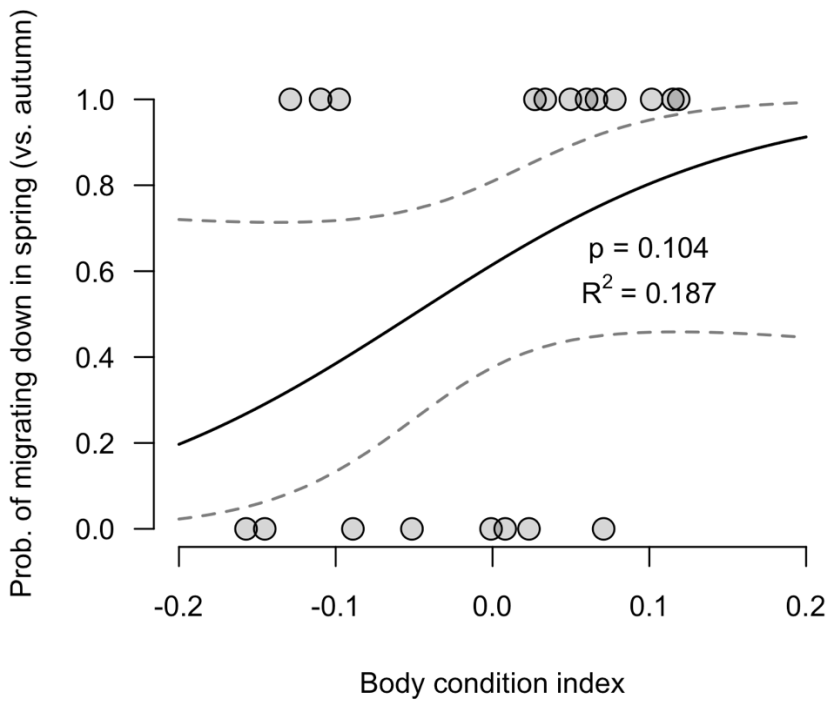

Fig. 3.2. Binomial logistic regression of the probability of spring downstream migration timing *vs.* the alternative autumn migration as a function of body condition index (as a numerical variable - for visualization purposes only as it was not the best fitting model, Table 1). The coefficient of determination (R^2) of the logistic regressions was computed using the *lrm* function of the *rms* package in *R* (Nagelkerke, 1991). Dashed lines represents the 95 % CI.

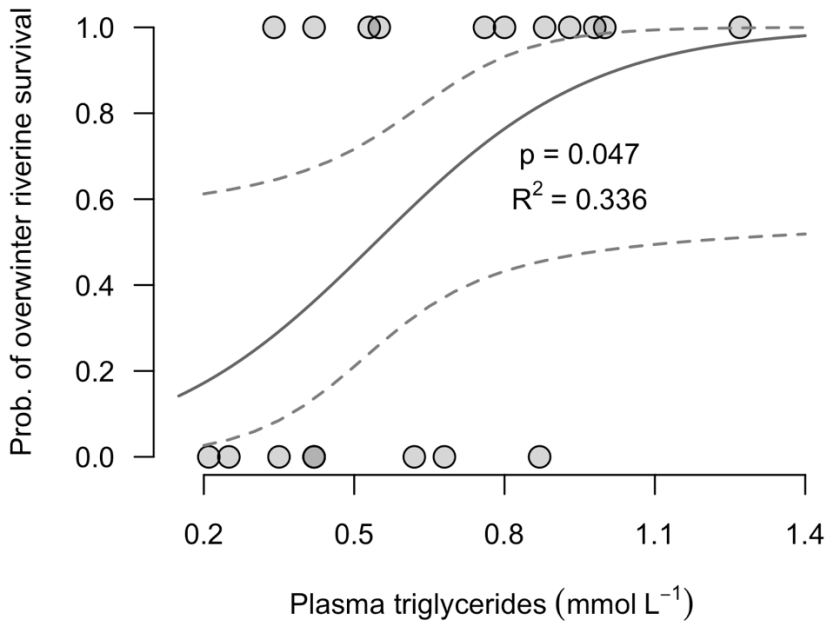

Fig. 3.3. Binomial logistic regression of the probability of riverine overwinter survival as a function of plasma triglyceride concentration (only 2SW kelts are displayed as survival was perfect for 1SW kelts and not influenced by triglyceride level, Table 2). The coefficient of determination (R^2) of the logistic regressions was computed using the *lrm* function of the *rms* package in *R* (Nagelkerke, 1991). Dashed lines represents the 95 % CI.

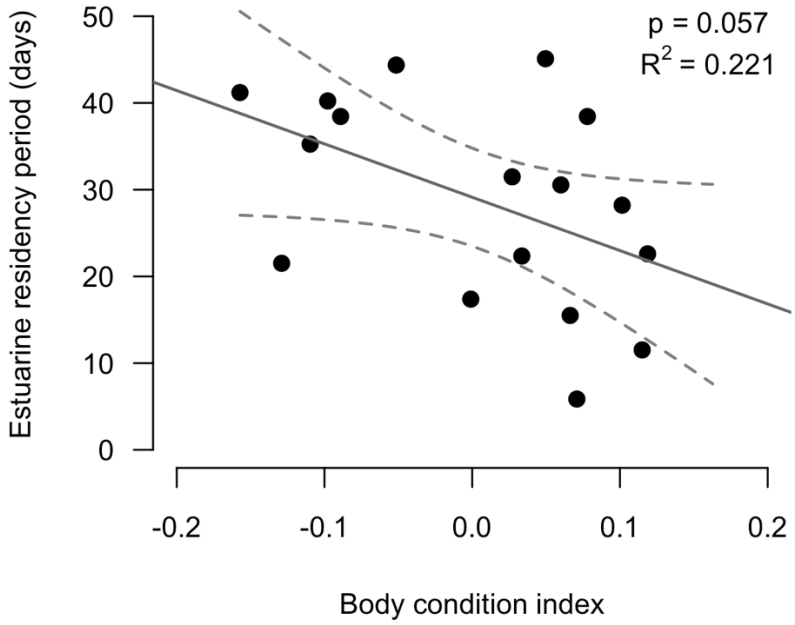

Fig. 3.4. General logistic regression of the estuarine residency periods of kelts (n = 17) as a function of body condition index (i.e. residual mass) (best fitting model, Table 2). The Pearson correlation coefficient *r* was -0.47. Dashed lines represent the 95 % CI.

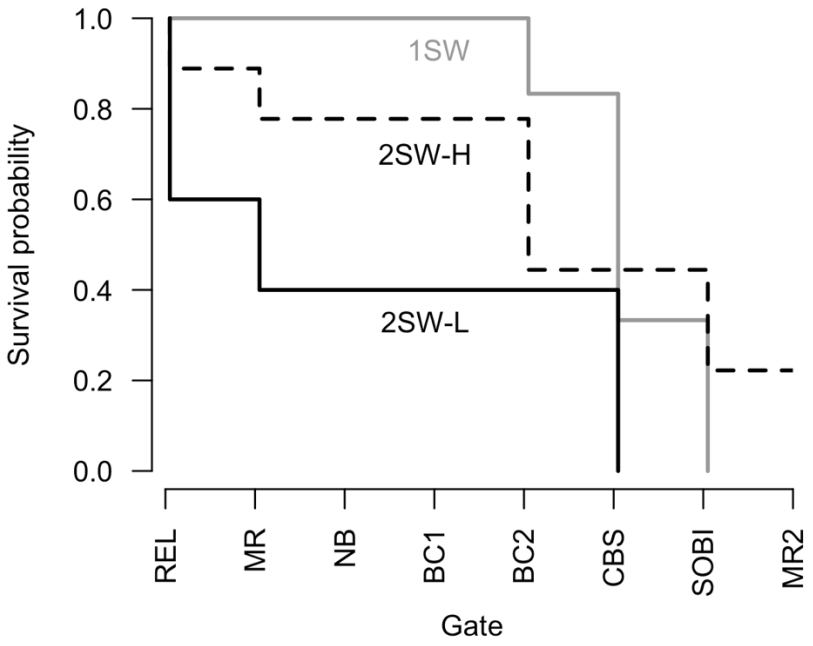

Fig. 3.5. Kaplan-Meier product-limit survival fit of the progression or survival probability of kelts along the different stages of migration (from detections on different acoustic receiver gates) for three different groups based on sea-age at maturity and plasma triglyceride concentration (according to the best fitting model, Table 3.2): all 1SW kelts (n = 6, solid pale grey line); 2SW kelts with high triglyceride level or 2SW-H (n = 9, dashed black line); and 2SW kelts with low triglyceride level or 2SW-L (n = 10, solid black line). REL is release site, MR is Middle River mouth, NB is Nyanza Bay, BC1 is the first gate of either Bras d'Or channels, BC2 is the second gate of either Bras d'Or channels, CBS is Cabot Strait, SOBI is Strait of Belle Isle, and MR2 is return to the Middle River mouth to repeat spawning (Fig. 3.1).

Chapter 4

Consequences of Captive Breeding: Fitness Implications for Wild-Origin, Hatchery-Spawned Atlantic Salmon Kelts Upon Their Return to the Wild [3]

4.1 Abstract

Broodstock collection and enhancement programs are a widely-used management practice within the Atlantic salmon's (*Salmo salar*) native range. Wild-origin adult salmon captured as part of these programs experience multiple stressors during their time in hatcheries. However, no studies have assessed the potential consequences of hatchery practices on the physiology (stress and immune states), migratory behaviour, and long-term survival of hatchery-spawned kelts that are subsequently released back to their natal river. To address these knowledge gaps, I obtained blood samples from, and acoustically tagged 30 hatchery-spawned kelts and 31 wild-spawned kelts, originating from endangered populations native to a UNESCO Biosphere Reserve in Canada during the autumns of 2014 and 2015. I then tracked individuals for up to two years through their downstream river migration, estuarine residence, ocean entry, and subsequent return as repeat-spawners. The current findings indicate that hatchery-spawned kelts showed significantly higher stress levels (elevated

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Authors' contributions: XB and BGH collected the telemetry data with contributions from SD, FGW and GTC; XB ran laboratory assays with contribution from DAP, MDF and GTC; XB analyzed the data; XB wrote the manuscript; BGH, SD, MDF, FGW, DAP and GTC contributed several ideas, comments, edits in the manuscript; XB reviewed the manuscript during the peer-review process.

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plasma cortisol and glucose), as well as potentially altered immune states (increased circulating prostaglandin E_2) in comparison to wild-spawned individuals. Behaviourally, hatchery-spawned kelts exited freshwater prematurely (~66 days earlier on average) compared to wild-spawned counterparts, which was associated with a marked increase in estuarine mortality. Furthermore, survival to repeat-spawning was 0 % (0/30) for hatchery-spawned kelts and 6.5 % (2/31) for wild-spawned. Given that female repeat-spawners are generally larger and have increased fecundity, these findings suggest that a reduction in the fitness of post-spawners and likelihood of repeat-spawning as a result of hatchery stressors could have population-level consequences. Such impacts should be considered in conservation and management planning.

4.2 Introduction

In the face of global declines of wild animal populations (Bar-On *et al.*, 2018), recovery efforts have increasingly turned to captive breeding programs as a major restoration tool for reintroducing captive-reared animals into the wild (Snyder *et al.*, 1996). The artificial rearing conditions and stress associated with captivity have been shown to negatively affect the physiology, health and/or behavior of captive-reared reptiles, birds, fishes and mammals, which has the potential to reduce their survival when freed (e.g. Fleming and Petersson, 2001; Araki *et al.*, 2008; Fraser, 2008; Dickens *et al.*, 2009; Kostow, 2009; McPhee and Carlstead, 2010; Arena *et al.*, 2014; Carrete and Tella, 2015; Kanghae *et al.*, 2016). However, in iteroparous species, little is known about the fitness implications of such practices for the future reproduction of captive-breed adults used for restoration purposes.

For the Atlantic salmon (*Salmo salar*) and other salmonid fishes, the capture of wild broodstock and subsequent progeny release to nature is a widely-used management practice in both anadromous and landlocked populations, and one of the most important investments made in species recovery efforts and conservation planning in North America and Europe (Araki *et al.*, 2008; Fraser, 2008; Kostow, 2009). While protocols vary amongst jurisdictions, broodstock collection usually involves the capture

of wild adult salmonids each year in freshwater, when fish are migrating upriver to spawning grounds. They are then transferred to hatcheries where they are held until sexual maturity and are then stripped of eggs and sperm (Kincaid and Stanley, 1989; Araki *et al.*, 2008). Fertilized eggs are incubated and hatched, and alevin are grown to the fry, parr, or smolt stage in hatchery tanks or ponds, until their eventual release into their natal river. For iteroparous species, the stripped, post-spawned adults are often returned to their natal river as well, where they may resume a wild existence, undergo ocean migrations and, if they survive, spawn again in the future. The duration of adult captivity in hatcheries can range from ~1 to >6 months, depending on the enhancement program (Kincaid and Stanley, 1989). While significant effort has been directed at improving the rearing conditions and survival prospects of juvenile salmonids in hatcheries (Kincaid and Stanley, 1989), the impacts of captive spawning on wild broodstock has received minimal attention. Despite the stress that captivity and handling can have on spawning salmonids (Barton and Iwama, 1991; Fast *et al.*, 2008), no studies have assessed the potential impacts of such programs on the physiology, seaward migratory behaviour, and long-term survival of post-spawning individuals upon their return to the wild.

In North America and Europe, Atlantic salmon populations (*Salmo salar*) have been decreasing throughout their native range, with many populations at the southern margin of their distribution now considered endangered (COSEWIC, 2010; Hindar *et al.*, 2011). As an iteroparous species, wild Atlantic salmon returning from the ocean can survive a first reproductive event to spawn again a year or two later (and in rare cases up to as many as seven times, Ducharme, 1969). After spawning in autumn, post-spawned individuals (i.e. kelts) spend varying durations in the river before migrating back to sea. Within populations, the seaward migration timing of individual kelts can vary from November (i.e. shortly after spawning) to May (Jonsson *et al.*, 1990; E Niemelä *et al.*, 2006; Halttunen *et al.*, 2013). Once at sea, kelts embark on extensive feeding migrations, which can last from a couple of months up to about a year and a half, before returning to spawn as “consecutive” or “alternate” repeat spawners, respectively

(Thorstad *et al.*, 2011). In most populations, repeat spawners generally constitute <11 % of a given spawning run, although repeat spawning incidences as high as 42.5 % have been documented (Fleming, 1998). Repeat spawners are experienced spawners of large body size, and females have generally much higher fecundities (i.e. number of eggs) than smaller first-time spawners (Reid and Chaput, 2012). These characteristics mean that experienced repeat spawners can make significant contributions to population size, viability, stability, and genetic diversity (Halttunen *et al.*, 2009; Thorstad *et al.*, 2011; Reid and Chaput, 2012; Buelow and Moffitt, 2015). Virtually nothing is known, however, about the behaviour and survival of hatchery-spawned kelts returned to rivers compared to wild-spawned counterparts, and whether repeat spawning probability might be compromised by hatchery operations.

For the adult salmon captured as part of broodstock collection programs, stressors are frequent and numerous. These include the initial capture event and transportation to a hatchery, occasional handling and air exposure, confinement, and the eventual stripping of gametes (procedures described in Kincaid and Stanley, 1989; stressors reviewed in Patterson *et al.*, 2017). In vertebrates, the physiological stress response involves the activation of the hypothalamic-pituitary-interrenal axis (HPI), leading to the secretion of glucocorticoid hormones. Cortisol is the primary glucocorticoid in fish, and is commonly used as an indicator of physiological stress (Barton, 2002). At stress-induced levels, cortisol is an important mediator of energetic trade-offs, which can influence behaviour and survival (Crespi *et al.*, 2013; Midwood *et al.*, 2015; Crossin *et al.*, 2016b). As such, cortisol secretion leads to increases in circulating glucose levels during stress, to power behavioural responses. In the context of captive spawning in hatcheries, stressors can be sustained over an extended period, which can result in the suppression of immune responses, resulting in deleterious health effects and diseases (Wendelaar Bonga, 1997). Due to its role in the inflammatory response, circulating prostaglandin E_2 (PGE_2) levels have been shown to increase in salmonids following fungal infection (*Saprolegnia spp.*; Espelid *et al.*, 1996), thereby inhibiting the expression of several immune-related genes (Fast *et al.*, 2005, 2006;

Belmonte *et al.*, 2014). The disruption of physiological mechanisms via stress might thus lead to lethal or sub-lethal behavioural effects (e.g. altered migration timing, reduced feeding and growth, and increased overwinter lipid depletion, Midwood *et al.*, 2014, 2015; Peiman *et al.*, 2017). However, to my knowledge, the effects of hatchery practices on physiological condition, and more generally on the seaward migrations of wild broodstock after their return to natal rivers, are unknown.

To quantify the potential consequences of hatchery confinement and artificial spawning for wild adult Atlantic salmon captured as part of a broodstock enhancement program, I compared the physiology, migration behaviour, and survival of hatchery- and wild-spawned kelts from two populations of endangered salmon native to the Bras d'Or Lake UNESCO Biosphere Reserve in Nova Scotia, Canada. I used a combination of acoustic telemetry and bio-sampling techniques to test the overarching null hypothesis that the physiology, behaviour, and survivorship of hatchery and wild-spawned kelts would not differ. I did so through several comparisons: 1. physiological stress states (indicated by plasma cortisol and glucose levels); 2. index of immune states (indicated by plasma PGE_2 levels); 3. freshwater survival; 4. freshwater exit timing; 5. estuarine survival; 6. estuarine residency period; 7. estuarine exit timing (i.e. Atlantic Ocean entry timing); and 8. survival to repeat-spawning. The conservation and management implications of my results are discussed.

4.3 Methods

4.3.1 Study System and Acoustic Receiver Array

I conducted this study on two populations of Atlantic salmon native to rivers within the Bras d'Or Lake watershed in Cape Breton, Nova Scotia, Canada. The complex, brackish Bras d'Or Lake forms an inland sea ecosystem, constituting a vast estuary of ~1100 km^2 in area centered at 45°51'37"N, 60°46'44"W (Fig. 4.1). The Middle and Baddeck rivers are the two largest rivers draining into the Bras d'Or Lake, and support the largest salmon runs in the watershed. Similar to Atlantic salmon populations in other

parts of the species' range, spawning escapements have been low during the last few decades, and recent spawner numbers in both of these rivers are <350 on average (Gibson and Levy, 2014). This prompted the recommendation to list the Eastern Cape Breton populations as endangered by the Committee on the Status of Endangered Wildlife In Canada (COSEWIC, 2010).

For seaward migrating Atlantic salmon leaving these two rivers and passing through the Bras d'Or Lake, the closest access to the Atlantic Ocean is located ~64 km away, either through the Great or Little Bras d'Or Channels (Fig. 4.1). In order to document the seaward migrations of acoustically tagged Atlantic salmon kelts from spawning areas in the upper Middle and Baddeck rivers, a total of 30 VR2W acoustic receivers (Vemco Ltd, NS, Canada) were deployed throughout the Bras d'Or Lake, forming acoustic detection "gates" that fish must cross en route to the Atlantic Ocean (Fig. 4.1; see Crossin et al., 2016a for additionnal details on the array). To evaluate the detection efficiency of the key gates within the acoustic array, I examined the 4 receiver gates fish have to cross on their way to the Atlantic Ocean (i.e. river mouth, Nyanza Bay, and two gates in either the Great or Little Bras d'Or channels, Fig. 4.1), and determined that all individuals that were detected on a gate were also detected on the previous more inland/upstream gate. Thus, performance of the array was highly reliable to detect tagged fish.

4.3.2 Fish Sampling, Tagging and Holding Conditions

Fish were handled in conformity with guidelines established by the Canadian Committee on Animal Care, approved by Dalhousie University and Cape Breton University Animal Care Committees (protocol numbers: 14-105 and 1213-16, respectively), and Scientific Fishing Licence granted by Fisheries and Ocean Canada (number: 340450).

4.3.2.1 Hatchery-Spawned Kelts

Starting in mid-October 2014 and 2015, 30 pre-spawning adult Atlantic salmon (50.0 – 91.5 cm in fork length) were captured on the Middle and Baddeck rivers via beach seine as part of the Margaree Hatchery broodstock enhancement program (see Table 4.1 for sample sizes). Immediately after capture, fish were transferred by hatchery staff to oxygenated transport tanks and transported to the Margaree Fish Hatchery, 48 km away (Margaree Valley, NS; operated by the Nova Scotia Department of Fisheries and Aquaculture; Fig. 4.1). Each population was held separately in two large tanks (~5500 L) devoid of any kind environmental enrichment (e.g. rocks), which were supplied with a constant flow of ambient water from the adjacent Margaree River. Fish were exposed to natural photoperiods and remained unfed during their time at the hatchery. Salmon reached full sexual maturity about a month later, in mid-November. At that point, hatchery staff collected gametes from salmon over a period of ~2 weeks. Stripped, or post-spawned salmon were then allowed to recover for a minimum of 24 hours (average of 4 days, range: 1-17 days). Following recovery, individual salmon were removed via dip net and placed in a padded V-shaped trough prior to anesthesia to collect ~2 mL blood samples via caudal venipuncture (as described in Huston, 1990). Ambient water was pumped into the mouth and over the gills during the procedure. Blood sampling occurred at random times between 9:35 – 15:40 as hatchery operations allowed and the average time from capture to blood sampling was of 2:43 min (± 1:07 min (SD), range: 1:20 - 4:50 min). Blood samples were placed in an ice-water slurry before centrifugation (10 min at 1163 *g*). The resultant plasma was isolated and frozen at -80 °C in 0.6 ml cryovials. Immediately following blood sampling, kelts were anesthetized using tricaine methanesulphonate (MS222) at 60 mg L^{-1} and a V16-4H (69 kHz) acoustic transmitter was surgically implanted into the abdominal cavity (16-mm diameter x 68 mm, 24 g in air; Vemco Ltd, NS, Canada), according to standard surgical procedures (Cooke *et al.*, 2011). All transmitters were programed to ping at random 20-70 second intervals and had an estimated battery life of ~1257 days. Transmitter mass relative to body mass varied between 0.3-2.1 % for all kelts; well within the tolerance

limits for tag burden (Lacroix *et al.*, 2004). At the end of the tagging procedure, fork length and mass were recorded, scales were collected for ageing, and sex was determined morphologically. Fish were then transferred to a recovery tank filled with ambient water until regaining equilibrium. Hatchery-spawned kelts were then allowed to recover for at least 24 hours before being transported back to their natal river and released at their initial capture site (average of 6 days, range: 1-12 days).

4.3.2.2 Wild-Spawned Kelts

Starting at the end of November 2014 and 2015, 31 post-spawned Atlantic salmon (51.1 – 95.0 cm in fork length) were captured on the Middle River by angling (Table 4.1). Immediately after capture, individual salmon were placed in a padded cradle supplied with ambient river water and blood was sampled as described above. Blood sampling occurred at random times between 9:30 – 15:30 as catch rates allowed and the average time from hooking to blood collection was of 8:08 min (± 6:28 min, range: 2:02 - 30:49 min) for wild-spawned kelts (where >50 % of individuals were sampled in less than 5:50 min). Following blood sampling, fish underwent surgical procedures for tag implantation at the site of capture, in the same manner as described above for hatchery-spawned kelts. Wild-spawned kelts were then released at the capture site after regaining full equilibrium and swimming capacities about 1 hour later. Wild-spawned kelts were tagged and released on average 12 days later than hatchery-spawned kelts (which was later taken into account in statistical analyses).

4.3.3 Physiological Assays

Plasma samples were analyzed for cortisol, glucose and PGE_2. Plasma cortisol was assayed in duplicate using commercially available ELISA kit (#402710, Neogen Corporation, USA), according to the manufacturer's standard procedure and read at 450 nm after the addition of 50 µl of 1N HCl using a Molecular Devices Spectramax 240pc plate reader (Labconco Corporation, USA). The mean coefficient of variation between cortisol duplicate was 3.2 %. Plasma glucose was measured in duplicates using a YSI

2300 STAT Plus Glucose/Lactate Analyzer following methods described in Farrell *et al.*, 2001. Plasma PGE_2 was assayed in duplicate using commercially available forward sequential competitive enzyme immunoassay kit (#KGE004B, Parameter ™, R&D systems Inc., USA), and read at 450 nm with a BioTek Synergy HTX microplate reader (BioTek Instruments, Inc., USA), according to the manufacturer's standard procedure. Due to the complexity of this assay and large plasma volume required, 27 samples could not be measured with confidence (CV's >35 % between duplicates) and were excluded from subsequent analyses. For the reminding 34 samples, the mean coefficient of variation between PGE_2 duplicate was 16.1 %.

4.3.4 Data Analysis

4.3.4.1 Physiology and Morphology

To test the first two null hypotheses that stress (plasma cortisol and glucose) and immune state (PGE_2) indicators would not differ between hatchery- and wild-spawned kelts, non-parametric Mann–Whitney *U* tests were computed using the *wilcox.test* function of the *stats* package specifying the argument "paired=FALSE" in *R* v.3.3.1 (R Development Core Team 2017). Difference in body condition between hatchery- and wild-spawned kelts was assessed using an analysis of covariance (ANCOVA; *aov* function in R), where body mass (log_{10} transformed) was regressed against body length (log_{10}) for the comparison of slopes and intercepts (Cone, 1989). As the mass-length relationship did not differ significantly between hatchery and wild-spawned kelts ($p = 0.94$) and year ($p = 0.083$), mass residuals were used as an index of individual body condition for subsequent analyses (Kaufman *et al.*, 2007). To better visualize potential morphological differences in mass and body condition between hatchery- and wild-spawned kelts in both years of tagging, parametric Welch Two Sample t-tests were computed using the *t.test* function of the *stats* package in *R* and data were presented in boxplots. Also, potential statistical differences in mean sea age between spawning conditions (hatchery or wild-spawned) were assessed using non-parametric Mann–Whitney *U* tests. Sea age, in previous number of years spent in the ocean, was determined from scale readings.

Mann–Whitney *U* tests were preferred over Welch Two Sample t-tests when the non-normal distribution of the response variable within each group precluded the use of parametric statistics.

4.3.4.2 Freshwater Survival and Exit Timing

For kelts acoustically tagged in Middle and Baddeck rivers in late fall/early winter of 2014 and 2015, an individual was deemed to have survived in fresh water if it was recorded on a receiver at the river mouth, with subsequent detection on the Nyanza Bay line (confirming that the fish left the river, Fig. 4.1). For freshwater survivors, the date of freshwater-exit was assigned to the last detection date at a river mouth receiver indicating that the fish had moved downstream of the river mouth to enter the estuary. To test the third null hypothesis that the probability of freshwater survival would not differ between hatchery- and wild-spawned kelts, binomial logistic regression models were computed using the *glm* function with a "logit" link in R. Spawning condition (i.e. hatchery or wild-spawned), population of origin, year, sex, and first-degree interactions were considered as potential explanatory variables. The best fitting model was selected using a forward stepwise model building approach, based on AIC scores (using the *step* function in *R*).

To test the fourth null hypothesis that the freshwater-exit timing would not differ between spawning conditions, general linear models were computed using the *lm* function in *R*. In addition to spawning condition, population, year, sex, and first-degree interactions were included as predictor variables, and release date was also included as a covariate in the model to control for its potential influence on freshwater-exit timing. The best fitting model was also selected using a forward stepwise model building approach. Furthermore, to visualize differences in the freshwater-exit timing of hatchery- and wild-spawned kelts, Kaplan-Meier product-limit survival curves were computed using the *survfit* function of the *survival* package in *R*.

To assess how individual level of plasma cortisol, glucose, and PGE_2 might directly influence the freshwater survival and freshwater exit timing of hatchery-spawned kelts, I

compared the concentration of these three parameters between: i. survivors versus mortalities; and ii. for those that survived, between early (fall/winter) versus late (spring) migrants. These comparisons were computed using non-parametric Mann–Whitney *U* tests.

4.3.4.3 Estuarine Survival and Residency

For kelts that survived fresh water and entered the Bras d'Or Lake, fish were deemed to have survived in this extended estuary if they were detected subsequently on both receiver gates crossing the Little or Great Bras d'Or channels, which lead to the North Atlantic Ocean (thus indicating seaward movement; Fig. 4.1). Because estuarine survival was 100 % for wild-spawned kelts in both years of tagging, potential statistical differences between spawning conditions could not be assessed using a binomial logistic regression, as the outcome survival probability is equal to 1 for wild-spawned kelts. Alternatively, to test the fifth null hypothesis, statistical differences in estuarine survival of hatchery- versus wild-spawned kelts was assessed by computing a Welch Two Sample t-test, which compared the average survival of the tagging groups (2 hatchery- and 1 wild-spawned groups, in both 2014 and 2015; Table 4.1). For consistency, this method was also used to compare the average group freshwater survival of hatchery- versus wild-spawned kelts to make sure the results were comparable to those of a binomial logistic regression (Table 4.1).

Further, to assess how individual levels of plasma cortisol, glucose, and PGE_2 might directly influence the estuarine survival of hatchery-spawned kelts, I compared the concentration of these three parameters between survivors and fish that died in the estuary, using non-parametric Mann–Whitney *U* tests.

For the estuarine survivors, Bras d'Or (estuarine) residency period was calculated from the moment at which an individual entered the estuary (as given by the last detection at a river mouth receiver) until the moment it left the Bras d'Or Lake to enter the Atlantic Ocean (as given by the last detection at an outermost receiver gate of either one of the Bras d'Or channels, Fig. 4.1). Accordingly, the estuarine exit timing of

individuals or Ocean entry was given by the date of last detection at an outer most Bras d'Or gate. Non-parametric Mann–Whitney *U* tests were used to test the remaining sixth and seventh null hypotheses that the estuarine residency period (i.e. number of days spent) and Ocean entry timing (i.e. date) would not differ between the two spawning conditions.

4.4 Results

4.4.1 Physiology

In contrast to the first null hypothesis, both stress indicators, plasma cortisol and glucose, were significantly higher in hatchery- versus wild-spawned kelts, for both years of tagging (Fig. 4.2). The difference was especially strong for plasma cortisol, the primary stress hormone, which was ~15-fold higher in hatchery-spawned kelts (averaging of 149 ng ml^{-1} vs 10 ng ml^{-1}). This is despite the fact that it took 5:25 minutes longer on average to capture and draw blood from wild-spawned kelts and that, as a result, I might be overestimating the baseline stress levels of these fish. However, blood-sampling time was not positively correlated with plasma cortisol or glucose (*p*-values > 0.31, Pearson's r). While both stress indicators were significantly elevated in the hatchery-spawned kelts of both sexes (*p*-values < 0.003), differences with wild-spawned kelts were stronger in females (200 vs 8 ng ml^{-1} and 8.2 vs 4.6 mmol L^{-1}) than in males (92 vs 16 ng ml^{-1} and 7.0 vs 4.9 mmol L^{-1}) – for plasma cortisol and glucose, respectively. Although PGE_2 could only be measured with confidence for 34 out of 61 individuals (Fig. 4.2), a significant difference was nevertheless evident between groups when pooling years (p = 0.015, Mann–Whitney *U* test), with hatchery-spawned kelts expressing a 2.2-fold increase in circulating levels (819 pg ml^{-1}) versus wild-spawned kelts (375 pg ml^{-1}). Furthermore, males (779 vs 361 pg ml^{-1}) and females (870 vs 384 pg ml^{-1}) from both spawning conditions expressed similar average plasma PGE_2. This result counters the second null hypothesis that this index of immunological state or health would not differ between the two spawning conditions. In all of these physiological tests, population of origin for the hatchery fish was not a significant factor in either year (*p*-values > 0.064, Mann–

Whitney *U* tests), which allowed us to pool Middle and Baddeck river fish in the hatchery group for these analyses. Furthermore, no differences in sea-age (i.e. prior number of years spent at sea) or morphology (i.e. body condition, mass and length) were found between hatchery- and wild-spawned kelts, for both years of tagging (*p*-values > 0.22, Welch Two Sample t-tests; Fig. 4.2).

4.4.2 Freshwater Survival and Exit Timing

From the 61 kelts (30 hatchery- and 31 wild-spawned) that were tagged in 2014 and 2015, 39 (20 hatchery- and 19 wild-spawned) were detected leaving fresh water and entering the Bras d'Or Lake, for a combined freshwater survival of 67 % and 61 % for hatchery- and wild spawned kelts, respectively. Freshwater survival of the six different tagging groups varied between 33 % and 86 %, with the greatest variation in wild-spawned kelts (33 % in 2014 versus 68 % in 2015, Table 4.1). No statistically significant differences were found between hatchery- and wild-spawned kelts in relation to freshwater survival probability (p =0.66, binomial logistic regression). In fact, following a stepwise model building approach, the null model had a lower AIC value than alternative models. This is also consistent with the absence of a statistically significant difference between the average group freshwater survival of hatchery- (67 %) and wild-spawned (51 %) kelts (p = 0.51, Welch Two Sample t-test, Fig. 4.3). These findings support the third null hypothesis that there is no difference in the freshwater survival of hatchery- and wild-spawned kelts.

In contrast to the predictions of the fourth null hypothesis, hatchery-spawned kelts exited freshwater significantly earlier than wild-spawned counterparts. Using general linear models, the model with the lowest AIC score included spawning condition (either hatchery- or wild-spawned), sex, and population of origin as statistically significant explanatory variables in addition to controlling for release date (final model in Table 4.2). An interaction between spawning condition and sex was also retained in the best fitting model, indicating that the difference in timing between hatchery- and wild-spawned kelts from the Middle River was greater in females than in males (Table 4.2),

although the difference was statistically significant for both sexes. In Middle River, female hatchery-spawned kelts exited fresh water on average ~132 days earlier than wild-spawned counterparts ($p < 0.001$, Table 4.2), while that difference was reduced to ~70 days in males ($p = 0.040$, post-hoc test). Furthermore, in both years some hatchery-spawned kelts left the river on the very first day of release (Nov-21 and Nov-24, in 2014 and 2015 respectively), while no wild-spawned kelts left the river before Apr-9 (Fig. 4.4). No significant inter-year differences in exit timing were found for hatchery- and wild-spawned kelts from Middle River, nor for hatchery-spawned kelts from Baddeck River ($p > 0.46$, Mann–Whitney *U* tests; Table 4.1), which allowed us to pool data from both years of study. Unlike in Middle River, no hatchery-spawned kelts from Baddeck River left the river before Dec-13 (Fig. 4.4), and hatchery-spawned kelts from Baddeck River left significantly later than hatchery-spawned kelts from Middle River, a difference of ~86 days on average ($p = 0.008$, Table 4.2). Pooling hatchery-spawned kelts from both populations and sexes, hatchery-spawned kelts exited freshwater on average ~66 days earlier than wild-spawned kelts, a difference that remained statistically significant ($p = 0.009$, Mann–Whitney *U* test). Moreover, despite some wild-spawned kelt that moved down to the lower section of the Middle River to overwinter (Chapter 3 – Bordeleau *et al.*, 2019a [Under review]), none of them (0/19) exited the Middle River (to enter the estuary) before spring, while a combined 45 % (9/20) of hatchery-spawned kelts did (67 % in Middle River and 27 % in Baddeck River; Fig. 4.4).

In assessing how individual levels of plasma cortisol, glucose, and PGE_2 might directly influence the freshwater survival and exit timing of hatchery-spawned kelts, unexpectedly the only significant difference found was an elevated cortisol level in freshwater survivors (182 pg ml^{-1}) versus hatchery-spawned kelts that presumably died in rivers (83 pg ml^{-1}, $p = 0.009$, Mann–Whitney *U* test). However, this pattern seemed to be driven by hatchery-spawned females with significantly higher cortisol levels than males (200 pg ml^{-1} versus 92 pg ml^{-1}, $p = 0.002$), and who also showed higher freshwater survival probability (81 %, 13/16) than males (50 %, 7/14), although the difference was not statistically significant ($p = 0.079$, binomial logistic regression). Nonetheless, these

results indicated that, at the individual level, high cortisol concentrations did not directly impair freshwater survival probability. In addition, lower recovery times (between artificial spawning and blood sampling) were not correlated with increased plasma cortisol, glucose or PGE_2 in either year (p-values > 0.39, Pearson's r). Furthermore, individual level of plasma cortisol did not differ between early and late migrating hatchery-spawned kelts (p = 0.71), nor did glucose (p = 0.058) and PGE_2 levels (p = 0.93, Mann–Whitney U tests).

4.4.3 Estuarine Survival and Residency

Of the 39 kelts (20 hatchery-spawned and 19 wild-spawned) that were detected leaving the rivers and moving into the Bras d'Or Lake system, a total of 31 kelts (12 hatchery- and 19 wild-spawned) survived to leave the system and reach the Atlantic Ocean (Table 4.1). Bras d'Or or estuarine survival of the six different tagging groups varied between 50 % and 100 % (Table 4.1), with an average group survival of 59 % versus 100 % for hatchery- and wild spawned kelts, respectively (54 % vs 100 % for females alone). In contrast to the fifth null hypothesis, hatchery-spawned kelts showed significantly lower estuarine survival in comparison to wild-spawned kelts (p = 0.001; Fig. 4.3).

Assessing the factors influencing estuarine survival, freshwater-exit timing was the only significant predictor of estuarine survival (p = 0.002, binomial logistic regression; Fig. 4.5), with an increase of 0.02 in the log odds of survival for every additional day spent in river before migrating out to the estuary. While all wild-spawned kelts (n = 19) exited the river to enter the Bras d'Or in the spring and subsequently survived to reach the Atlantic Ocean, estuarine survival was much lower for hatchery-spawned kelts (Fig. 4.3). Looking specifically at the physiological, morphological, and phenological factors, as well as sex that influenced the estuarine survival probability of hatchery-spawned kelts, the model with the lowest AIC score only included freshwater-exit timing (following forward stepwise model building). In fact, spring-migrating hatchery-spawned kelts showed significantly higher estuarine survival (82 %, n = 11)

than earlier migrating counterparts (33 %, n = 9; p = 0.037, binomial logistic regression). Furthermore, in hatchery-spawned kelts, individual levels of plasma cortisol, glucose, and PGE_2 did not differ significantly between estuarine survivors and mortalities ($p > 0.2$, Mann–Whitney *U* tests).

The residency period of kelts in the Bras d'Or estuary varied between 5 and 191 days. Although more variable in hatchery-spawned kelts (54 $\pm$ 59 days), their average estuarine residency period did not differ significantly from wild-spawned counterparts (31 $\pm$ 16 days; p = 0.64, Mann–Whitney *U* test), consistent with the sixth null hypothesis. Interestingly, the three early-migrating, hatchery-spawned kelts that survived to the Ocean showed highly contrasting estuarine residency patterns. Two of them spent the entire winter in the Bras d'Or system with residency periods of 159 and 191 days, while the third one left the system on Dec-21 (9 days residency period) and is the only individual that was detected entering the North Atlantic Ocean before spring. Furthermore, consistent with the seventh and last null hypothesis, the Bras d'Or exit timing (or Ocean entry) did not differ significantly between the two spawning conditions (p=0.70, Mann–Whitney *U* test). Apart from the only individual that left the system in December, fish exited in a narrow period between May-30 and Jun-21.

4.4.4 Survival to Repeat-Spawning

Of the 61 Atlantic salmon kelts that were initially tagged over the two years of study, 0 % (0/30) of hatchery-spawned kelts survived to come back to the river as repeat-spawner, while 6.5 % (2/31) of wild-spawned kelts did. Both kelts that survived were wild-spawned, 2SW females that were tagged in late November 2015, which then came back to the Middle River on Sep-7 and Sep-10, 2017, as alternate repeat spawners. Strictly looking at females, 0 % (0/16) of hatchery-spawned kelts survived to repeat spawning, while 9.1 % (2/22) of wild-spawned counterparts did. These two kelts spent 489 and 504 days in the marine environment between spawning events.

4.5 Discussion

Overall, my findings indicate that hatchery-spawned Atlantic salmon kelts differed from their wild-spawned counterparts physiologically, behaviorally, and in relation to survival. Physiologically, hatchery-spawned kelts showed significantly elevated stress levels (high plasma cortisol and glucose) as well as potentially altered immune state (through significantly elevated plasma PGE_2 levels) compared to wild-spawned kelts (Fig. 4.2). While no differences in freshwater survival were found between the two spawning conditions, hatchery-spawned kelts showed significantly earlier freshwater-exit timing, a difference of ~66 days. This likely resulted in significantly lower estuarine survival probability for hatchery-spawned kelts, with estuarine survival being the lowest in early-migrating, hatchery-spawned kelts. Furthermore, none (0/30) of the hatchery-spawned kelts survived to spawn again, while 6.5 % (2/31) of wild-spawned counterparts did, coming back as alternate repeat-spawners (0 % vs 9.1 % for females alone). While these are low numbers, it supports the idea that the difference in estuarine survival might be carried through the rest of the marine migration. Collectively, these findings suggest an effect of hatchery operations on individual fitness with potential influence on the likelihood of repeat spawning. This in turn could have consequences for population level processes, which I discuss below.

Physiological condition differed markedly between hatchery- and wild-spawned kelts, suggesting that the stress associated with confinement and handling in the hatchery was at least an indirect driver of their premature freshwater-exit timing and reduced survivorship. Although elevated plasma cortisol, glucose, and PGE_2 levels were not associated with premature freshwater exit timing nor decreased survival, this might have been due to the time lag between initial blood sampling dates, return to the rivers, and subsequent migration dates. For the purpose of this study (i.e. documenting the physiological stress resulting from hatchery operations), hatchery-spawned kelts were sampled at the hatchery, prior to their transportation back to their river of origin. Therefore, the stress state and immune health indicator measured did not necessarily correspond to the final levels, upon hatchery-spawned kelts return into the wild. I can

speculate, however, that the elevated stress response in hatchery fish had some disruptive effect on some other physiological system (or systems) related to the perception of seasonal migratory cues, resulting in altered migratory behaviour. But whatever the mechanism, I show that hatchery exposure resulted in a mismatch between migration timing and survival, which had implications for individual fitness. Despite the absence of direct links between physiology and subsequent migratory decision in this study, stress and corticosteroids can have a broad range of impacts on the immune system by acting directly on immune cells or thorough secondary agents (Espelid *et al.*, 1996). It is also possible that all hatchery-spawned kelts had an increased susceptibility to infections through a threshold cortisol effect. For example, in adult brown trout (*Salmo trutta*), chronic elevation of plasma cortisol above 30 ng ml^{-1} was sufficient to increase fish susceptibility to infectious diseases (Pickering and Duston, 1983). Furthermore, plasma cortisol has been shown to reduce the number of lymphocytes to abnormally low level in brown trout (Pickering, 1984). In Atlantic salmon, cortisol injections (which raised circulating concentration to levels similar to those observed in the current study) had an immunosuppressive effect through the alteration of lymphocyte functioning (Espelid *et al.*, 1996). Similarly, Atlantic salmon subjected to a prolonged stressor (i.e. infection of the parasitic copepod *Lepeophtheirus salmonis*) showed significantly elevated plasma cortisol levels along with increased PGE_2 levels relative to uninfected fish. This led to inhibition of immune-related genes interleukin-1ß (IL-1 ß) and major histocompatibility (MH) class II (Fast *et al.*, 2006). In addition, *Saprolegnia parasitica*, a parasitic mycelium commonly observed on salmonids in aquaculture and in nature, can produce PGE_2 to suppress the expression of genes related to cellular immunity (Belmonte *et al.*, 2014). Although I did not quantify the external fungal infection (e.g. *Saprolegnia spp.*) in these fish, I noted qualitatively that the hatchery-spawned kelts had higher incidences of fungus on their fins, flanks, and nose relative to the wild-spawned fish. This is likely due to fish handling and abrasion occurring in hatchery tanks, which might have contributed to the increased PGE_2 levels in those fish. In juvenile anadromous brown trout in the wild, fish with artificially

elevated cortisol levels showed amplified weight loss, increased overwinter freshwater mortality, and earlier freshwater-exit timing with a majority of fish entering the estuary during winter (Midwood *et al.*, 2015; Peiman *et al.*, 2017). In a similar study, juvenile anadromous brown trout with cortisol injections expressed reduced growth and lower survival during the spring downstream migration (Midwood *et al.*, 2014). Although these studies were conducted on a different species at a different life-history stage, their findings complement my current findings that hatchery-spawned kelts, with elevated stress levels and potentially altered immunity, showed premature freshwater-exit timing. While PGE_2 is a common biomarker of inflammation in mammals (de Grauw *et al.*, 2009; Morris *et al.*, 2013; Solcà *et al.*, 2016; van de Water *et al.*, 2016), and increases in circulating levels of PGE_2 were previously associated with altered immune-competence in salmonids (Knight and Rowley, 1995; Espelid *et al.*, 1996; Fast *et al.*, 2005, 2006; Gómez-Abellán and Sepulcre, 2016), I recognize that plasma PGE_2 needs further characterization and validation as its role as a biomarker for inflammatory/immunological status in teleosts. In general, there is a paucity of biomarkers for non-destructively assessing salmonid/teleost health, and PGE_2 among other protein-based assessments could provide a much clearer picture in the future.

Among iteroparous salmonids, the energetic cost of spawning is reported to be highest in Atlantic salmon, with both sexes investing upwards of 60-70 % of their total somatic energy reserves (Jonsson *et al.*, 1997). In combination with sparse post-spawning feeding opportunities in fresh water throughout the winter months, the total degree of somatic depletion through reproduction is a key determinant of individual survival (Belding, 1934). Variation in survival probability is mediated by variation in post-spawning condition, which may influence decisions about the timing of seaward migration. Halttunen *et al.* (2013) showed that Atlantic salmon kelts with low body condition factors initiated their seaward migrations early in the winter months, as opposed to kelts with better condition factors that migrated later in the spring. However, I did not observe this relationship; although hatchery-spawned kelts exited fresh water significantly earlier than wild-spawned kelts (~66 days on average), this

difference in phenology was independent of individual body condition (i.e. residual mass). However, whereas Halttunen *et al.* (2013) examined variation in post-spawning body condition and its implication on the seaward migratory timing of naturally-spawned kelts, I examined differences between artificially-spawned versus naturally-spawned kelts. As such, given the observed increase in plasma cortisol and glucose for hatchery-spawned kelts, I cannot rule out that aspects of their energy reserves perhaps not reflected in body condition index might have been depleted as a result of elevated stress levels and increased basal metabolism.

Ice covered freshwater habitats are believed to offer safe overwinter refuges for salmonids when available (Komadina-Douthwright *et al.*, 1997), raising concerns that early migrating individuals (i.e. those deciding to leave the river before spring) might experience reduced estuarine and marine survival due to increased predation, low food availability, and/or sub-optimal environmental conditions in winter (Halttunen *et al.*, 2013; Peiman *et al.*, 2017b). I have shown that early winter migrants, which were entirely composed of hatchery-spawned individuals, had a significantly lower probability of estuarine survival (~2.5-fold lower) relative to later spring migrants. This might potentially reflect an additive effect of entering the estuarine environment at a time when conditions are sub-optimal, plus secondary effects of elevated stress levels and potentially weakened immunity. Interestingly, hatchery-spawned kelts that did migrate later in the spring had similar survival as their wild-spawned counterparts, and had similar overall patterns of behaviour for estuarine residency period and ocean-entry timing. This might indicate that some individuals have the potential to recover from hatchery exposure and avoid the deleterious consequences of early migration. However, none of those hatchery-spawned kelts survived to spawn again.

4.5.1 Management Implications

The physiological, behavioural, and survival consequences for wild adult Atlantic salmon captured as part of broodstock collection program were significant, and might be of particular concern to hatchery operations in other jurisdictions more broadly. In the

present context, considering the small numbers of spawners collected each year from the Middle and Baddeck rivers for broodstock collection purposes (7-8 fish collected from populations estimated at 312 and 215 spawners respectively between 2007-2011, Levy and Gibson, 2014), as well as the low frequency estimate of repeat spawning in Middle and Baddeck rivers (3.4 % and 4.8 % respectively, Gibson and Levy, 2014), the potential population-level impact of an increase in kelt mortality is likely minimal. This is important considering that these populations were proposed to be listed as endangered (COSEWIC 2010). However, the importance of repeat spawners to Atlantic salmon population dynamics is slowly being recognized. For example, female repeat spawners, and especially alternate repeat spawners, have increased reproductive potential due to their larger size and associated higher fecundity. Comparing maiden spawners with alternate repeat spawners that matured at the same sea-age (1SW or 2SW), alternate repeat spawners have fecundities ~2.8-fold (~7200 vs 2539 eggs) and ~1.7-fold greater (~11000 vs 6320 eggs) for salmon that matured at 1SW and 2SW, respectively (Reid and Chaput, 2012). Previous estimates suggested that repeat spawning frequencies from 3 % to 30 % can contribute to 8 % up to >40 % of the total annual egg deposition in Atlantic salmon populations (Randall, 1989; Moore *et al.*, 1995; Halttunen, 2011; Hubley and Gibson, 2011). Therefore, efforts to increase juvenile freshwater survival (e.g. egg to fry survival) via hatchery rearing practices should consider the potential trade-off in the reduced survival of hatchery-spawn kelts and the lost future recruitment potential from this reduction of iteroparity. While further research is required, the frequency and composition of repeat spawners (e.g. sex ratio, numbers and proportion of consecutive versus alternate females) are likely to be good proxies for assessing the potential importance of kelts to population level processes. And while these components vary greatly across the species' global distribution and among years (Fleming, 1998; Chaput *et al.*, 2006), potential population level effects of a reduction in kelt survival should be considered.

In threatened populations of anadromous rainbow trout or steelhead (*Oncorhynchus mykiss*), another iteroparous salmonid species that shares similar

incidence of repeat-spawning as Atlantic salmon (Fleming, 1998), increasing iteroparity has been identified as a goal to aid in stock recovery through management actions such as the development of appropriate dam downstream passages, kelt transportation and reconditioning (Keefer *et al.*, 2008; summarized in Penney and Moffitt, 2014). However, the current findings suggest that nutritional requirements should not be the only consideration to improve the survival of broodstock kelts returned to the wild, but that the stress imposed through captivity and handling might also have cascading effects on the physiology, behaviour, and survival. Therefore, management practices that mitigate the many stressors that wild salmon experience when captured for broodstock programs should be considered (e.g. minimizing confinement period, reducing air exposure time during stripping and handling frequency, allowing moderate flow in hatchery environment to favors exercise, Patterson *et al.*, 2004). Reducing such stressors could be beneficial for adult salmonids, and also for the survival of eggs and juveniles that might also be negatively affected by high stress levels through maternal effects (Patterson *et al.*, 2004; Sopinka *et al.*, 2016). In terrestrial and aquatic species more broadly, mitigating the stressors imposed on reproductive animals through captive breeding programs may be key in improving the survivorship of both post-reproductive adults and juveniles reintroduced into the wild. Research and management efforts should be directed at the evaluation and integration of stress mitigation measures, moving towards improving animal welfare and the effectiveness of captive breeding programs.

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Table 4.1. Number of Atlantic salmon tagged (number of females are indicated and the rest are males), average freshwater-exit timing (± SD, in days), as well as freshwater survival and estuarine survival of the three groups, for both years of tagging.

Group	Sample size		Freshwater survival		Freshwater exit timing		Estuarine survival	
	2014/15	2015/16	2014/15	2015/16	2014/15	2015/16	2014/15	2015/16
Wild – Middle	6 (3 F)	25 (19 F)	33% (2/6)	68% (17/25)	May-1 (± 33 d.)	May-11 (± 10 d.)	100% (2/2)	100% (17/17)
Hatchery – Middle	7 (2 F)	8 (4 F)	57% (4/7)	63% (5/8)	Feb-10 (± 74 d.)	Jan-16 (± 73 d.)	50% (2/4)	60% (3/5)
Hatchery – Baddeck	8 (6 F)	7 (4F)	63% (5/8)	86% (6/7)	Mar-21 (± 85 d.)	Apr-11 (± 60 d.)	60% (3/5)	67% (4/6)

Table 4.2. Output of the best fitting linear regression model of freshwater-exit timing (in days after release) as a function of spawning condition and population of origin, while controlling for individual differences in release date. The baseline outcome (or intercept), represents female hatchery-spawned kelts from the Middle River.

Explanatory variable	Coefficient	SE	t-statistic	*p*-value
Intercept	35.0	21.0	1.7	0.10
Spawning condition (Wild)	131.6	26.3	5.0	<0.001
Sex (Male)	59.4	24.4	2.4	0.021
Spawn. Cond. (Wild) : Sex (Male)	-62.0	35.2	-1.8	<0.001
Release date	0.288	1.0	0.3	0.77

Multiple $R^2 = 0.50$

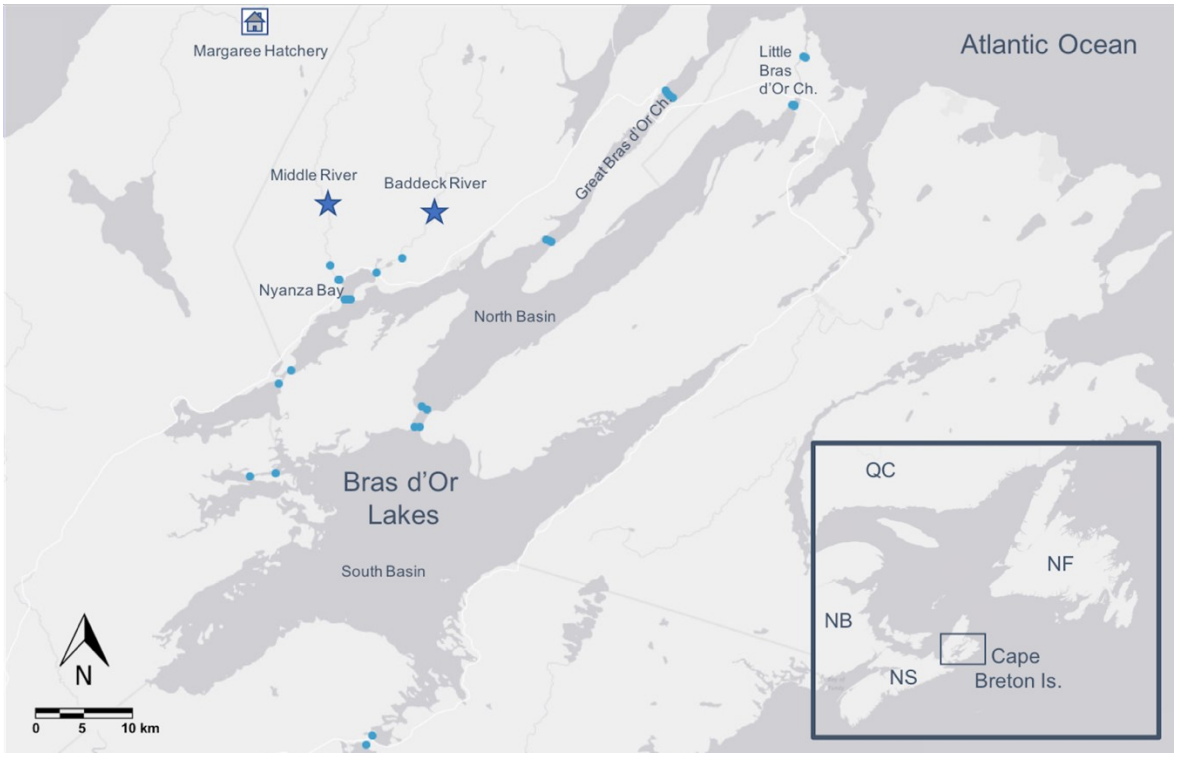

Fig. 4.1. Map of the acoustic array positioned in the Bras d'Or Lakes, Nova Scotia. Acoustic receivers (n = 30) are indicated by blue circles, and star symbols indicate the release location of wild-origin, hatchery-spawned kelts in both rivers. Wild-spawned kelts of Middle River were captured, tagged, and released between the release site of hatchery-spawned kelts and the river mouth (the map was produced using Esri, HERE, Garmin, NGA, USGS).

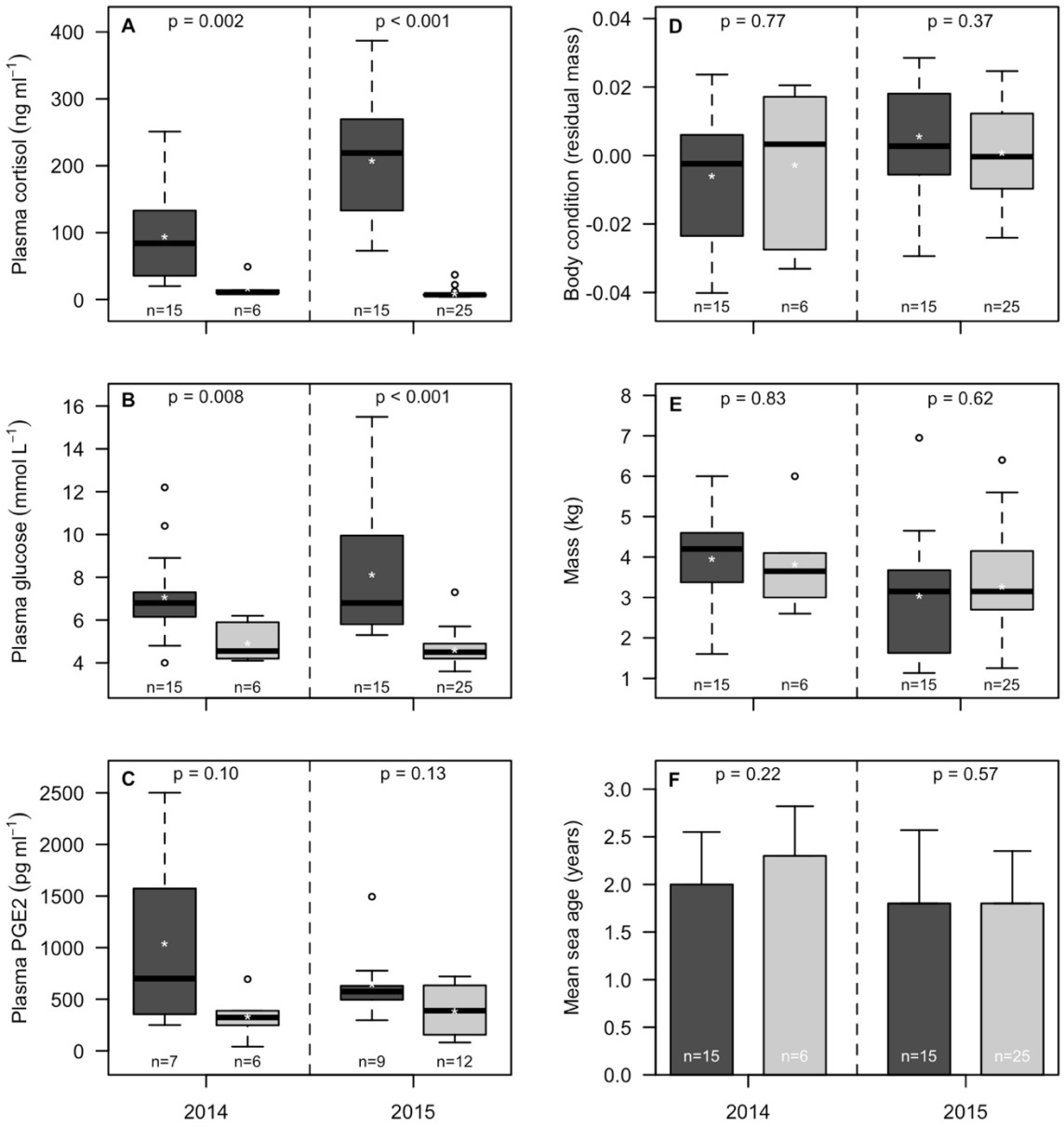

Fig. 4.2. Physiological, morphological and sea age comparisons between hatchery- (dark grey) and wild-spawned Atlantic salmon kelts (pale grey) from both years of tagging. The boxplots (panels A-E) show median (black lines) and mean values (white dots), as well as the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). The barplot (panel F) shows mean values with standard deviations. Details on the statistical tests can be found in the method section.

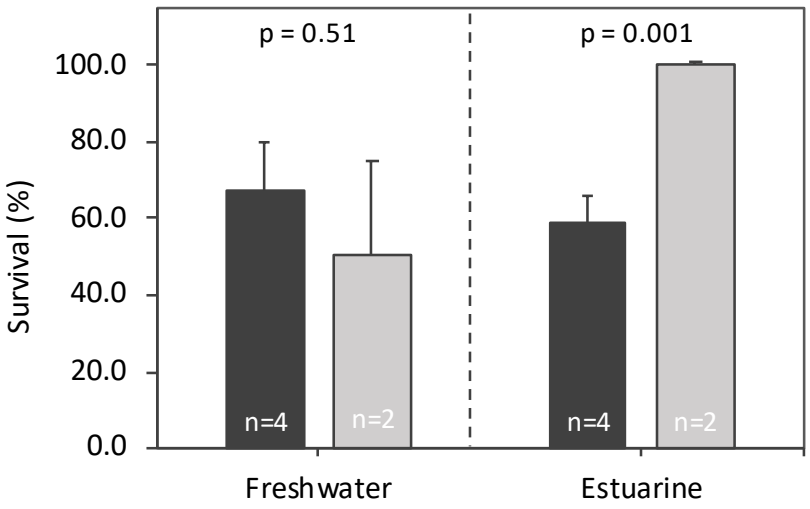

Fig. 4.3. Comparisons of the mean freshwater and estuarine survival of hatchery- (dark grey) and wild-spawned kelts (pale grey), with bars representing standard deviations. Statistical differences were computed using Welch Two Sample t-tests comparing the average survival of the six tagging groups: 4 hatchery-spawned groups (Middle 2014, Middle 2015, Baddeck 2014, Baddeck 2015) versus 2 wild-spawned groups (Middle 2014, Middle 2015; Table 4.1).

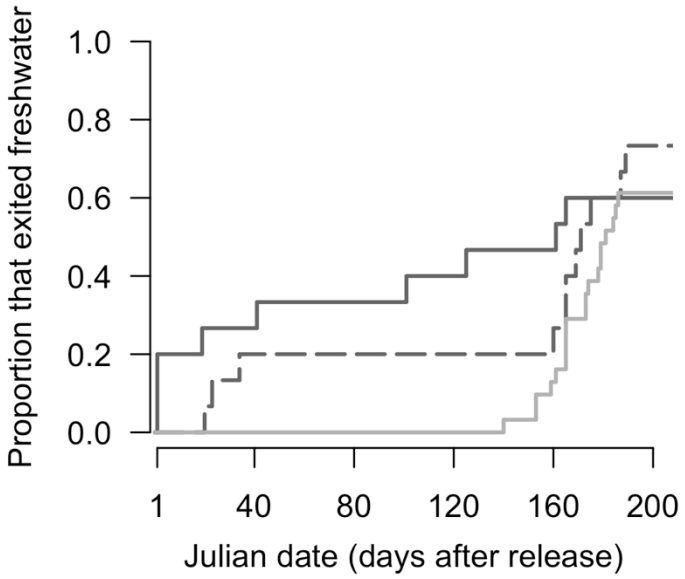

Fig. 4.4. Kaplan-Meier product-limit survival fit of freshwater-exit timing for the different tagging groups: wild-spawned kelts from Middle River (solid pale grey line); hatchery-spawned kelts from Middle River (solid dark grey line); and hatchery-spawned kelts from Baddeck River (dashed dark grey line). Day 1 represents Nov-21 in 2014-15, and Nov-24 in 2015-16. Mar-21, which marks the limit between early (fall/winter) and late (spring) migrating kelts, occurred on day 121 after release in 2014-15, and on day 119 in 2015-16.

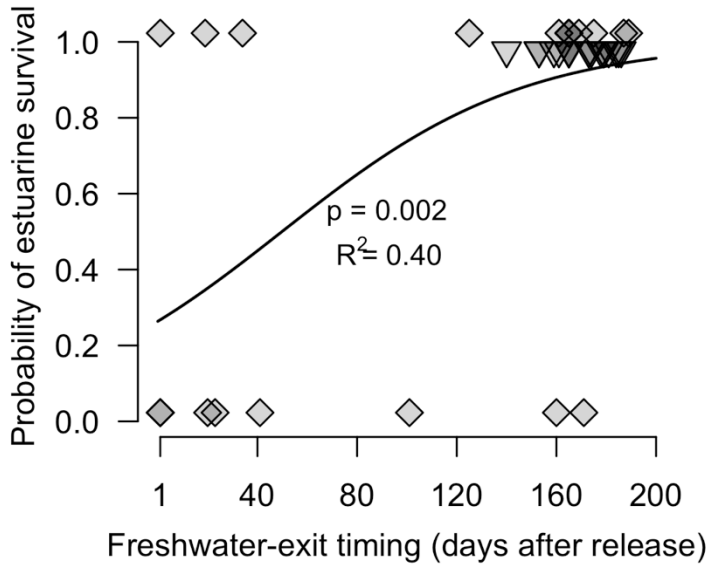

Fig. 4.5. Binomial logistic regression of the probability of estuarine survival as a function of freshwater-exit timing for hatchery- (diamonds, n = 20) and wild-spawned (triangles, n = 19) kelts combined. Day 1 represents Nov-21 in 2014-15, and Nov-24 in 2015-16. Mar-21, which marks the limit between early (fall/winter) and late (spring) migrating kelts, occurred on day 121 after release in 2014-15, and on day 119 in 2015-16. The coefficient of determination (R^2) of the logistic regression was computed using the *lrm* function of the *rms* package in *R* (Nagelkerke 1991).

Chapter 5

Nutritional Correlates of Spatio-Temporal Variations in the Marine Habitat Use of Brown Trout, Salmo Trutta, Veteran Migrants [4]

5.1 Abstract

The brown trout (*Salmo trutta*) is an iteroparous, anadromous salmonid that exhibits a complex continuum of feeding migration tactics, ranging from freshwater residency, to potamodromy, to estuarine migration, as well as short-to-long distance coastal migrations. While anadromous migrants are believed to play an important role in the species' population dynamics, little is known about the factors driving differences in the extent of individual marine habitat use. In this study, 32 brown trout veteran migrants were acoustically tagged prior to their seaward migration and sampled for indices of their nutritional state. The current findings suggest that: i. body condition factor differed amongst fish adopting different migratory tactics, with outer fjord migrants being in poorer condition; and ii. Within migratory groups, plasma triglyceride concentration was negatively correlated with the duration of marine residency. Results support the idea of condition-dependent migration in veteran migrants, with individual variation in nutritional state influencing the spatio-temporal aspects of marine habitat

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use. Furthermore, overall marine minimum survival during the summer feeding migration was 86 %, the highest reported estimate for this life-stage.

5.2 Introduction

From an evolutionary point of view, migration can be regarded as an individual adaptation to the changing requirements of life-histories and resource availabilities (Dingle, 2006). As an individually expressed trait, migration can also be viewed as a syndrome, shaped by natural selection, wherein correlated behavioural, physiological, morphological and other traits combine to maximize fitness within particular life-history contexts (Dingle 2006, e.g. Peiman *et al.* 2017). As such, partial migration has been described in a variety of taxa, in which variable proportions of a population are either migratory or non-migratory (Chapman *et al.*, 2011). While differences in migratory strategies can have both environmental and genetic links, the degree to which these contribute to an expressed migratory strategy can vary widely (Pulido, 2011). In anadromous brown trout (*Salmo trutta*) for example, little genetic variation seems to exist among migrant and resident individuals living sympatrically (Hindar *et al.*, 1991). According to the conditional strategy concept, different tactics regulated by the same genotype can be maintained within populations. This can occur when the migratory decisions and fitness gained from alternative tactics depend primarily on individual phenotype, e.g. age, size, sex, energetic state, etc. (Repka and Gross, 1995).

The brown trout is a facultative anadromous, iteroparous salmonid species native to the cold waters of Eurasia and North Africa. The species is socially and economically important, and because of its high adaptability and phenotypic plasticity, it has been successfully introduced to every continent except Antarctica (MacCrimmon and Marshall, 1968). Within a population, the species shows complex variation in its feeding migratory tactics, a continuum ranging from freshwater residency, to potamodromy, and estuarine migration (Cucherousset *et al.*, 2005; Boel *et al.*, 2014), as well as beyond, to short- and long-distance coastal migration (del Villar-Guerra *et al.*, 2014; Eldøy *et al.*, 2015; Flaten *et al.*, 2016). This migratory continuum has been

observed in both first-time migrants (i.e. parr and smolts; Boel *et al.*, 2014; del Villar-Guerra *et al.*, 2014; Flaten *et al.*, 2016), as well as veteran migrants (i.e. either mature or immature individuals that have previously completed a first summer feeding migration; Eldøy *et al.* 2015). While the drivers of the different migratory tactics remain obscure, especially for the marine migrations of veteran migrants (Drenner *et al.*, 2012; Thorstad *et al.*, 2016), previous studies of first-time migrants suggest that the choice of migratory tactic is a plastic response to individual physiological state, metabolic rate, and food availability (Wysujack *et al.*, 2009). In experimental feeding studies, brown trout exposed to low food availability had lower pre-migratory body condition factors, which has been shown to influence the decision of first-time migrants to adopt anadromy, whereas higher-condition fish tended towards non-anadromy (Olsson *et al.*, 2006; Wysujack *et al.*, 2009; Davidsen *et al.*, 2014). Wysujack *et al.* (2009) similarly concluded that energetic state (i.e. body lipid content) close to the time of actual migration was likely responsible for the choice of migratory tactic. A recent telemetry study of the marine migrations of brown trout veteran migrants concluded that migratory decisions were likely influenced by body condition (Eldøy *et al.*, 2015). However, the link between individual pre-migratory nutritional state and the spatio-temporal extent of subsequent marine habitat use by brown trout has not been well-defined (Aldvén and Davidsen, 2017).

Following marine feeding migrations, mostly occurring in summer, anadromous brown trout usually return to freshwater to spawn and/or over-winter. During the winter, feeding opportunities in freshwater can be sparse, and so brown trout depend on somatic lipid stores for survival, especially in post-spawned individuals (summarized in Jonsson and Jonsson 2011). Lipids stored in adipose and muscle tissues are catabolized and released into circulation as triglycerides. Triglycerides are delivered to target tissues, where hydrolysis (lipolysis) produces glycerol and free fatty acids, the major source of metabolic energy production in fish (Sargent *et al.*, 2002). During starvation, plasma triglyceride concentration diminishes in an effort to sustain basal metabolic processes (Kakizawa *et al.*, 1995). As such, plasma triglyceride concentration

can be used as an indicator of nutritional status in many taxa including wild brown trout (Boel *et al.*, 2014; Gauthey *et al.*, 2015), and is therefore a good candidate parameter for testing hypotheses about condition-dependent models of migratory behaviour in wild animals. However, virtually nothing is known about how natural variation in pre-migratory levels of plasma triglycerides might affect the migratory decisions of brown trout veteran migrants.

By providing enhanced growth opportunities, the marine environment is believed to support higher abundances and more productive brown trout populations (Thorstad *et al.*, 2016). Marine foraging, especially in areas where nutrient rich feeding opportunities are numerous (e.g. pelagic fish species, Davidsen *et al.* 2017), allows anadromous individuals to attain larger sizes than their freshwater resident counterparts, which for females translates to a higher fecundity-at-age (Jonsson and Jonsson, 1993). Coupled with the higher prevalence of anadromy in females (as increased size represents a more direct fitness gain for females), it is likely that anadromous brown trout make important contributions to the species' population dynamics (Thorstad *et al.*, 2016), although this has yet to be fully investigated. With the recent increase in marine mortality and decreased growth of anadromous brown trout due to anthropogenic impacts on marine habitats (Thorstad *et al.*, 2015), researchers have speculated that a reduction in the benefits of anadromy might favour selection for freshwater residency (Hendry *et al.*, 2004; Thorstad *et al.*, 2016). Better knowledge about the whereabouts of brown trout veteran migrants at sea and the endogenous factors affecting the extent of the marine migrations (e.g. distance and duration) will contribute to a fuller understanding of the drivers of marine habitat use of this important life-history stage. Such information is currently lacking but needed for improving current management and conservation actions.

To address these knowledge gaps, I combined acoustic telemetry and physiological sampling techniques within a fjord system in Northern Norway to quantify variation in migratory tactics and in the extent of marine habitat use of brown trout veteran migrants (e.g. duration of marine residency and distance travelled), as well as

the influence of pre-migratory nutritional state (i.e. body condition factor and plasma triglyceride concentration). Utilizing this approach, I addressed the over-arching hypothesis that nutritional state underlies inter-individual differences in migratory behaviour. I tested the following predictions: i. individuals in poorer nutritional state (i.e. low body condition factor, low plasma triglyceride concentration) have a stronger tendency towards marine migration, and this tendency would be emphasized in females; ii. Within marine migrants, fish in poorer nutritional state migrate further out; iii. Fish in poorer nutritional state require more time in the marine environment to recondition; and iv. Marine survival (i.e. to completion of the summer feeding migration) is lower for fish migrating to the outer reaches of the fjord.

5.3 Materials and Methods

5.3.1 Study Area and Acoustic Receiver Array

The study was conducted in the inter-connected, marine, Tosenfjord and Bindalsfjord (65.13°N, 12.13°E) in Nordland country, Norway (Fig. 5.1). Brown trout were captured from two different watercourses (i.e. freshwater systems): Åbjøra and Urvold. Both watercourses, situated ~14 km apart, drain into the Tosenfjord (~97 km^2, maximum depth of ~550 m) which then leads to the Bindalsfjord (~91 km^2, maximum depth of ~700 m) and finally to the Atlantic Ocean, located at ~33 km from Åbjøra and Urvold estuaries (defined as the interface between river mouth and fjord). During the study period, from April 8 – September 5, 2015 the surface salinity level (~1 m depth) of the Åbjøra estuary (i.e. Floet, station 69 in Fig. 5.1) and the outer-fjord (station 1) varied respectively from 0.0 – 28.6 ppt (mean = 9.4 ppt) and 4.8 – 33.5 ppt (mean = 20.0 ppt). Surface water temperature (~1 m depth) for those two sections of the fjord varied from 3.0 – 17.6 °C and 4.5 – 17.0 °C, respectively. The eastern section of Tosenfjord is similar to other inner-fjord areas in terms of depth, temperature, and surface salinity level that varies between ~0 – 34 ppt depending on areas, freshwater inputs, and tidal cycles.

In Åbjøra, the tagging site was located 2.7 km upstream of the river mouth (around station 65, Fig. 5.1). This area is situated in the tidal zone of the river with a surface salinity level that varied from 7.4 – 22.3 ppt (mean = 10.1 ppt) and water temperature from 2.7 – 16.7 ^{o}C during the study period, depending on tidal cycle and freshwater discharge. Spawning in the Åbjøra watercourse occurs in River Åbjøra and its tributaries (> 2 km upstream of the tagging area), while the lower part of the system includes deep pools and slow currents, and is consequently considered suitable overwintering habitat. In Urvold, the tagging site was situated in a freshwater lake, near the outlet (around station 61, Fig. 5.1). Lake Urvold has a surface area of ~0.6 km^2 and is ~80 m deep, which provides good overwintering habitat for brown trout. The lake then drains into the fjord through a 0.2 km riverine stretch. Unlike Åbjøra, the transition from freshwater to the fjord is much more direct in Urvold due to the steepness of the short river section. In this watercourse, the main spawning site is located upstream of the lake.

5.3.2 Capture, Blood Sampling and Tagging

A total of 32 brown trout veteran migrants were captured, sampled (i.e. for blood, measurements and scales), and tagged with an internal acoustic transmitter between April 9 – 12, 2015 prior to their seaward feeding migration; 20 individuals from the tidal zone in river Åbjøra and 12 from lake Urvold (Table 5.1). At capture, veteran migrants were distinguished from smolts and parr based on size, which was later confirmed by scale readings. Fish were captured using a combination of angling (n = 26) and gill netting (n = 6; 35-42 mm mesh size), and efforts were made to reduce stress and the risk of injury by minimizing fight times and monitoring the gill net continuously (e.g. the net was pulled-in as soon as vibrations were felt). The average time-to-blood-sampling, as calculated from the first encounter with fishing gear, was similar for both methods; 7:51 $\pm$ 5:15 min for angling and 10:32 $\pm$ 5:20 min for gill netting (*p*-value = 0.29; Welch Two Sample t-test). Shortly after landing and prior to anaesthesia, ~2 ml blood samples were collected via caudal venipuncture from all fish (as described in

Huston, 1990). Samples were then placed in an ice-water slurry until processing. Following blood sampling, fish were kept for no more than 2 hours in a net cage situated in the river to allow recovery from capture and sampling before the tagging procedure. Prior to tagging, brown trout were anesthetized using 2-phenoxyethanol at a concentration of 0.5 ml L^{-1} water (SIGMA Chemical Co., USA). Depending on fish size, a 69 kHz MP-9 (for fish between 310-390 mm in total length) or a 69 kHz MP-13 acoustic transmitter (for fish between 400 to 720 mm in total length) was inserted in the abdominal cavity (nominal delay of 30 – 90 seconds, Thelma Biotel AS, Norway), according to standard operating procedures (as described in Cooke *et al.*, 2011). MP-9 tags (5.2 g in air; estimated battery life of ~15 months) were 1.0 – 1.8 % of fish total body mass, and MP-13 (11.8 g in air; estimated battery life of ~24 months) were 0.4 – 2.3 % of fish total body mass. Immediately after surgical transmitter implant, fish were weighed and measured (i.e. total length), ~5-10 scales were sampled and stored for later aging, and a small adipose fin clip was collected for genetic sexual determination. Following tagging, the brown trout were released back at their respective capture site, and subsequently detected on an acoustic receiver array composed of 54 VR2W-69 kHz receivers (Vemco Ltd., Canada) deployed throughout the lakes, rivers, and marine fjords (Fig. 5.1). The array was established prior to the start of tagging and was in place until fall 2017 (although I am focusing on 2015 detections in the current study). The experimental procedures followed national ethical requirements and were approved by the Norwegian National Animal Research Authority (permit number: 7277).

5.3.3 Blood Processing and Triglycerides Assay

Within three hours of blood sampling, samples were centrifuged at 1163 *g* for 10 minutes and the resultant plasma was collected and flash-frozen in dry ice before being transferred to a -80 ^{o}C freezer. Plasma triglyceride levels were assayed in duplicate using a commercially available colorimetric kit (Cayman Chemical Company, USA) and read at 530 nm with a BioTek Synergy HTX microplate reader (BioTek Instruments, Inc., USA),

according to the manufacturer's standard procedure. The mean coefficient of variation between duplicates was 3.9 %.

5.3.4 DNA Sex Determination

DNA was extracted from ethanol preserved fin clips with the QuickExtract kit (Epigen), according to manufacturer's protocol with the exception for the extraction volume, which was reduced to 150 µl. Sex was determined by PCR amplification of a 200 pb fragment situated in the first intron of the male specific SDY gene, using the Salmo-sdY-F and Salmo sdY-R primers (Quéméré *et al.*, 2014). The PCR was performed in 10 µl reactions using the Qiagen Multiplex PCR kit. The following PCR profile was used: 95°C for 15 min, 11 cycles of touchdown PCR, 94°C for 30 seconds, 63–52°C for 30 seconds, 72°C for 1 minute, followed by 25 cycles of 94°C for 30 seconds, 52°C for 30 seconds, 72°C for 1 minute, with a final extension at 72°C for 10 minutes. Sex was scored by running the PCR products on 1 % Agarose gels. Sex could be determined with confidence for all but one fish, so this individual had to be excluded from final models including sex as an explanatory variable.

5.3.5 Data Analysis

Individual migratory behaviours can be classified into distinct tactics. First, brown trout are either riverine/lacustrine resident or marine migrant. Then, marine migrants could be further divided into groups depending on where and how far they migrated. To test the over-arching hypothesis that nutritional state underlies inter-individual differences in migratory behaviour, statistical tests were performed to assess how individuals' characteristics influenced the different spatial and temporal aspects of migration, as well as survival (specific predictions are presented in the sections below). All individuals' morphological (i.e. length, mass, body condition factor) and physiological (i.e. plasma triglyceride concentration) characteristics, as well as sex and population of origin were considered as explanatory variables. However, due to limited sample sizes, final statistical models were limited to the inclusion of a maximum of two explanatory

variables. Selection of the best model for each aspect of individuals' migratory behaviour was determined using a forward stepwise approach (based on AIC values and comparison with a null model; Anderson et al. 2001). Body condition factor (i.e. Fulton's K) was calculated from the formula: $K = 100 \times \text{Mass [g]} \times \text{Total length [cm]}^{-3}$, following the observation that the regression coefficient of the mass-length relationship was 2.99 for tagged individuals, thus confirming the assumption of isometric growth. For each statistical model, I first verified that underlying assumptions were met. Out of 32 acoustically tagged individuals, four were excluded from further analyses due to abnormal patterns of detections: one transmitter was continuously detected on a single station (no. 63 in Fig. 5.1) for about five months before disappearing, two transmitters were not detected anywhere in the array after Apr-22, and one transmitter seems to have experienced technical failure as soon after release not a single detection was registered.

Potential false detections were first flagged using the *falseDetectionFilter* function of the *glatos* package in *R*, requiring a minimum of two detections from a given transmitter in a time span of 30 minutes at given receiver. Then, flagged detections that were legitimate were kept (i.e. subsequent detections on other receivers located nearby) and others were deleted. To evaluate the detection efficiencies of various portions of the acoustic array, I examined 11 receiver gates, where spacing between receivers was 400 m and the distance from shore to the nearest receivers was 200 m. I calculated the percentage of events in which an individual was detected on a gate when crossing from one side to the other (as revealed from detections on other receivers). For example, in Fig. 5.1, if a fish was first detected on station 43 and then on station 16, I controlled if that fish was properly detected on the gate formed by stations 40, 41 and 42, as it had to cross that gate. Overall, out of a total of 203 gate-crossing events that occurred during the entire study period, individuals were detected on the gate 92 % of the time. The detection efficiency (and location) of individual gates were as follow: 100 % in Åbjøra estuary (stations 67 – 68, Fig. 5.1); 100 % on Osane opening gate (stations 31 – 32); 91 % on Terråk gate (stations 33 – 35); 100 % on Sørfjord gate (stations 28 – 30);

100 % on Bindalsfjord west gate (stations 11 – 13); 95 % on Bindalsfjord east gate (stations 16 – 17); 86 % on Tosenfjord outer gate (stations 40 – 42); 81 % in Urvold estuary (stations 43 – 44); 100 % on Tosenfjord central gate (stations 45 – 47); 100 % on Tosenfjord east gate (stations 18 – 20); and 100 % on Tosbotn gate (stations 26, 52, 53).

5.3.5.1 Riverine-Lacustrine Residency Versus Marine Migration

In Åbjøra, the tidal zone of the river offers a brackish environment in which some individuals may decide to stay in to feed. While these fish are not true freshwater resident, they were regrouped as riverine "resident" to be distinguish from marine migrants that ventured into the fjord system. In Urvold, however, the transition from freshwater to the brackish waters of the fjord is much more direct and fish can either decide to reside within the freshwater lake or to move into the fjord, and were unlikely to reside in the short river section. For this reason, models were developed separately for each population. To test the prediction that individuals in poorer nutritional state (i.e. low body condition factor and depleted plasma triglyceride level) have a stronger tendency towards marine migration, binomial logistic regression models using the logit link were performed (*glm* function in *R*; two outcomes: staying in the river/lake, or migrating to the fjord/marine environment).

5.3.5.2 Marine Migratory Tactics

Once individuals were detected entering the fjord, fish from both populations were faced with similar habitat choices. Based on migratory distances and the areas of the fjord that were utilized, three different marine migratory tactics were identified (Fig. 5.1); i. short-distance migration (furthest detection <2 km from the river mouth; Fig. 5.2); ii. long-distance/inner-fjord migration (furthest detection from ~13 to 28 km of the river mouth, without any detection on the outer receiver line, Fig. 5.2); and iii. long-distance/outer-fjord migration (furthest detection >21 km from the river mouth and detected on the outer receiver line; Fig. 5.2). To test the prediction that, within marine migrants, fish in poorer nutritional state (i.e. low body condition factor and depleted

plasma triglyceride level) migrate further out in the marine environment, multinomial logistic regression models were performed (*multinom* package in *R*), suitable for nominal categorical response variable with three outcomes, here: short-distance, long-distance/inner-fjord, or long-distance/outer-fjord migration (Kwak and Clayton-Matthews, 2002; Zuur *et al.*, 2007a). The *p*-values of the regression coefficients were computed using Wald z-tests. Furthermore, to facilitate the interpretation of the model's coefficients, changes in the predicted probabilities of adopting a given migratory tactic as a function of explanatory variables were calculated for each tactic using the *predict* function in *R* (Kwak and Clayton-Matthews, 2002).

5.3.5.3 Marine Residency Period

The marine residency period could be calculated for a total 14 individuals (5 fish from Åbjøra and 9 from Urvold) that were detected entering the fjord in the spring and returning to the rivers later in the summer. For those fish, the marine residency period started at the time of first detection at a river mouth/estuarine receiver (stations 67-68 in Åbjøra, and 43-44 in Urvold, Fig. 5.1) and ended at the time of last detection at a river mouth/estuarine receiver (conditional to later detection on upstream receiver, station 63 in Åbjøra, and 61 in Urvold). To test the prediction that fish with low body condition factor and depleted plasma triglyceride level would remain in the marine environment for longer periods of time, general linear regression models were performed (*lm* function in *R*).

5.3.5.4 Marine Survival

The marine minimum survival was estimated from the initial number of fish that were detected entering the fjord system and the proportion of them that came back to the rivers, completing their summer marine migration (as indicated by detection at a river mouth/estuarine receiver conditional to later detection on upstream receivers). In addition to those fish, marine migrants that were detected returning to Åbjøra or Urvold estuary (stations 67-69 in Åbjøra, and 43-44 in Urvold, Fig. 5.1) in late summer and fall

were also deemed to have survived their marine summer feeding migration, despite not re-entering freshwater systems. These fish were assumed to be over-wintering in estuaries, as they were detected there through the fall and early winter. Marine migrants that presumably died or disappeared from the acoustic array through the summer might be the result of tag lost, technical failure of the tag, exhaustion of tag battery life, residency in uncovered areas, or animal mortality. To test the prediction that survival to completion of the summer feeding migration is lower for long-distance/outer-fjord migrants in comparison with other marine migratory tactics, binomial logistic regression models using the logit link were performed (*glm* function in *R*).

5.4 Results

5.4.1 Riverine-Lacustrine Residency Versus Marine Migration

Out of the 20 brown trout tagged in Åbjøra, four individuals had to be removed from the analysis as their migratory decision could not be identified with confidence (as described previously). From those remaining (n = 16), 7 individuals (44 %) opted to reside in the tidal zone in the river for the summer, moving in and out of Floet but never entering the fjord (Table 5.1). In contrast, 9 individuals (56 %) moved out of the river between Apr-10 and May-29 (median of May-2) migrating into the fjord. The prediction that individuals in poorer nutritional state (i.e. low body condition factor and depleted plasma triglyceride level) would have a stronger tendency towards marine migration was not supported by the results, as the null model had a lower AIC value than alternative models. In addition, no statistically significant morphological differences (i.e. length and mass) were found between riverine resident and marine migrants (*p*-values > 0.31; Welch Two Sample t-tests). However, as expected, females tended to migrate into the fjord in higher proportion than males, as 8 out of 11 females (73 %) left the river compared to only 1 out of 5 males (20 %) ($p = 0.070$ for sex; binomial logistic regression), although marginally non-significant - which, considering the effect size, is likely due to small sample size. In contrast to Åbjøra, all 12 brown trout tagged in freshwater, near

the outlet of Lake Urvold, migrated into the fjord to feed in the marine environment irrespective of sex, morphology and physiology. Those individuals migrated into the fjord between Apr-25 and May-15 (median of May-10). As all fish from this population migrated, I could not test the hypothesis that individuals in poorer nutritional state would have a stronger tendency towards anadromy.

5.4.2 Marine Migratory Tactics

For marine migrants (pooled sample of 9 fish from Åbjøra and 12 from Urvold), 3 individuals (14 %; 2 females and 1 male) were classified as short-distance migrants, 7 individuals (33 %; 2 females and 5 males) were classified as long-distance/inner-fjord migrants, and 11 individuals (52 %; 6 females, 4 males, one unknown sex) were classified as long-distance/outer-fjord migrants (as summarized in Table 5.1). In assessing which factors might influence marine migratory decisions, the best fitting multinomial logistic model included body condition factor and sex as explanatory variables (Table 5.2). The other explanatory variables considered, i.e. population, plasma triglycerides, length and mass, were not retained in the model during the stepwise process. Because population of origin was not retained as an influential explanatory variable, and in combination with the observation that a mix of fish from both populations were present in all three migratory tactics (Table 5.1), I pooled fish from both populations in a single model. While the effect of sex on migratory decisions might be confounded to some extent by population of origin, low sample sizes constrained my ability to resolve this interaction. In support of the second prediction, for long-distance migrants, the probability of outer-fjord migration decreased significantly with increasing body condition factor (-20.7 in the log odds of migrating to the outer-fjord following a one unit increase in body condition, $p = 0.027$, Table 5.2). Thus, fish migrating to the outer part of the fjord were generally in the poorest condition prior to migration. Comparing sexes, for long-distance migrants, the log odds of migrating to the outer section of the fjord versus staying in the inner part increased by 3.15 for females, in which 75 % (6/8) migrated to the outer section versus 44 % (4/9) in males (although marginally non-significant at $p = 0.058$, Table 5.2). To

facilitate interpretation, the predicted probabilities of adopting a given marine migratory tactic as a function of body condition factor and sex were calculated using the regression coefficients (Fig. 5.3). Body condition factor and sex mostly affected the probabilities of adopting the long-distance/outer-fjord versus long-distance/inner-fjord tactic, with no significant influence on the decision to undertake a short-distance marine migration (Table 5.2). However, I interpret the latter result with caution due to the low number of short-distance marine migrants. Moreover, following the observation that no significant morphological and physiological differences (i.e. in length, mass, body condition factor, and plasma triglyceride level) existed between long-distance/inner-fjord and short-distance migrants (*p*-values > 0.68; Welch Two Sample t-tests), the two tactics were pooled to take a closer look at what might be driving the decision to migrate to the outer section of the fjord (reducing the tests to only two marine migratory outcomes: outer-fjord versus inner-fjord migrants). In this analysis, female outer-fjord migrants had significantly lower body condition factor prior to migration compared to inner-fjord migrants (0.79 ± 0.05 vs 0.92 ± 0.05, $p = 0.006$, Welch Two Sample t-test, Fig. 5.4). A similar, but non-significant difference in body condition was observed in males. Pooling both sexes, outer-fjord migrants had significantly lower body condition (0.75 ± 0.09) than inner-fjord migrants (0.87 ± 0.10, $p = 0.005$, non-parametric Mann–Whitney *U* test). While male outer-fjord migrants were significantly smaller than inner-fjord migrants (433 ± 59 mm versus 576 ± 100 mm, $p = 0.022$, Welch Two Sample t-test), females showed the opposite tendency with outer-fjord migrants being generally larger (range: 400-640 mm) than inner-fjord migrants (range: 310-445 mm, although the difference in mean length was not significant, Fig. 5.4). Supporting the assumption that plasma triglyceride concentration is informative of individuals' post-winter/pre-migratory nutritional state, body condition factor and plasma triglycerides were correlated at r = 0.45 (p = 0.009). Interestingly, females displayed a negative correlation between length and pre-migratory body condition factor (r = -0.57, $p = 0.02$), and similarly between length and plasma triglyceride concentration (r= -0.48, $p = 0.06$), so that larger females were generally found in poorer pre-migratory condition. These

negative relationships between length and indices of nutritional state were not observed in males.

5.4.3 Marine Residency Period

Of the individuals that were detected entering the fjord in the spring (n = 21), a total of 14 individuals (5 from Åbjøra and 9 from Urvold) came back to the river/lake later in the spring or during the summer (May-23 to July-16; median of Jul-4). Individuals' marine residency period varied between 32 and 83 days (average of 59 days). Looking at the factors that might explain inter-individual variance in the marine residency period, the best fitting linear regression model included plasma triglyceride concentration and marine migratory tactic (Table 5.3; multiple $R^2 = 0.60$). All other potential explanatory variables (i.e. population of origin, sex, body condition factor, length, mass, and simple interactions) were not retained in the model during the stepwise process. This, combined with the fact that no significant differences existed in the marine residency period between fish from the two study populations ($p > 0.20$; Welch Two Sample t-test), allowed us to pool fish from the two populations. Out of the 14 individuals that came back to freshwater, 7 were long-distance/outer-fjord migrants, 6 were long-distance/inner-fjord migrants, and only one was a short-distance migrant. In order to meet the assumptions of general linear regression models (i.e. independence, normality of residuals, homoscedasticity, and balanced influence of individual observations), the short-distance migratory tactic (n = 1) had to be removed from the final model as it had high leverage (hat value 3.5-fold greater than the average, *hatvalue* function in *R*) which led to a deviation from normality (Zuur *et al.*, 2007b). In support of the third prediction, within migratory groups, the duration of marine residency was negatively correlated with pre-migration plasma triglyceride concentration (Table 5.3), such that depleted individuals generally spent more time in the marine environment (~24 more days for a decrease of 1 mmol L^{-1} in triglyceride level). In addition, long-distance/inner-fjord migrants spent on average 69.2 $\pm$ 11 days in the marine environment, ~15 days more than long-distance/outer-fjord migrants (54.6 $\pm$ 16 days), a

significant difference controlling for the effect of plasma triglyceride level (Table 5.3; Fig. 5.5). The only short-distance migrant for which marine residency could be calculated spent only 35 days there (Table 5.1).

5.4.4 Marine Survival

Out of a total of 21 veteran migrants that were detected entering the fjord in the spring, seven were not detected coming back to freshwater. Of those, four individuals (i.e. three females and one male) were presumed to have survived but opted for over-wintering in the marine environment as they were detected in estuaries in the fall and winter (summarized in Table 5.1), apparently deciding to skip spawning. Those three females were generally smaller (range: 310-420 mm) than the five females that had migrated back to freshwater (range: 405-640 mm), and were possibly still immature (Klemetsen *et al.*, 2003). For the remaining three individuals that neither returned to freshwater nor over-wintered in estuaries, two disappeared from the array (as they were last detected in late May/early June in the outer section of the fjord, and were never heard from again despite the array remaining in place until fall 2017) and one was continuously detected on a single receiver for >6 months starting in mid-June. Minimum marine survival through the summer feeding migration was thus estimated at 86 %, as at least 18 out of 21 individuals that migrated out into the fjord survived to return to freshwater, or were detected in estuaries in the fall and winter. In partial support of the fourth prediction, all three fish that presumably died or disappeared in the marine environment were long-distance migrants, with significantly lower body condition factor (0.75 ± 0.02) than the average marine migrant (0.82 ± 0.12, $p= 0.048$; Welch Two Sample t-test), implying a 73 % minimum survival for this marine migratory tactic (n = 11) versus 100 % survival for the other two tactics (n = 10). However, no morphological or physiological individual characteristics, nor sex, population or marine migratory tactics statistically influenced the probability of marine survival, as the null model had lower AIC value than alternative binomial models.

5.5 Discussion

Our findings support the over-arching hypothesis that pre-migratory nutritional state, as indicated by body condition factor and plasma triglyceride concentration, is correlated with spatio-temporal variations in the marine habitat use of brown trout veteran migrants. They also bring some support to the general belief that females are more inclined to migrate to the marine environment.

I found that, after a winter in freshwater, female trout from the Åbjøra watershed showed a higher tendency than males to leave the river and migrate into the fjord in spring. This higher tendency of females towards anadromy is commonly observed in facultative anadromous salmonid populations, and is believed to be driven by the strong relationship between body size and fecundity, with the productivity of the marine environment sustaining faster growth (reviewed in Jonsson and Jonsson, 1993). Previous work on the migratory behaviour of brown trout post-smolts suggest a condition-dependent migration, with low body condition factor generally promoting anadromy (Davidsen *et al.*, 2014; Olsson *et al.*, 2006; Wysujack *et al.*, 2009), but not always (Boel *et al.*, 2014; del Villar-Guerra *et al.*, 2014). Despite the first prediction that poorer nutritional state would promote marine migration, no significant differences in body condition factor and plasma triglyceride concentration were observed between riverine/lacustrine residents and marine migrants.

However, among brown trout that initiated marine migrations, body condition factor differed between migratory tactics. As predicted, brown trout in the poorest relative body condition were those most likely to migrate to the outer section of the fjord, where nutrient rich foraging opportunities are presumably more abundant (e.g. increased dependence upon pelagic fishes, Davidsen *et al.*, 2017), and a greater proportion of female (77 %), than male long-distance migrants (44 %), opted for this tactic then the alternative inner-fjord tactic. While fish of various sizes migrated to the outer reaches of the fjord, female long-distance/outer-fjord migrants were generally larger than female inner-fjord migrants. Interestingly, females displayed negative

correlations between length and pre-migratory body condition factor as well as triglyceride concentration, so that larger females were generally found in poorer pre-migratory condition and were more likely to migrate to the outer-fjord. This negative relationship between body condition factor and length was not observed in males. By comparing immature brown trout, with first-time and repeat-spawners of both sexes, Berg *et al.* (1998) showed that lipid and protein depletion through the spawning season increased with size in female, but not males. Accordingly, while the energy content of immature individuals increased, the specific energy content of spawning females decreased with length due to increased reproductive investments (Berg *et al.*, 1998). While it was shown that anadromous female brown tout invest more into reproduction than resident counterparts (Elliott, 1988; Jonsson and Jonsson, 1997), which affects post-spawning nutritional state, my findings suggest that the costs of reproduction might influence future migratory decision by affecting the extent of individual marine habitat use the following year. Larger, depleted females might be migrating further to sea in an attempt to recondition themselves more effectively and offset the costs of reproduction. However, while the variation in weight and plasma metabolites through spawning is reflective of energy investment to reproduction (Gauthey *et al.*, 2015), post-spawning nutritional state alone, as measured in the current study, is not necessarily directly representative of reproductive investment. As such, the link between reproductive investment, post-spawning condition, and subsequent migratory decision is an area requiring further investigation.

In contrast to those initiating outer-fjord migrations, brown trout remaining within the inner-fjord tended to be in better overall condition. Interestingly, these inner-fjord migrants spent significantly more time in the marine environment than outer-fjord migrants (Table 5.3; Fig. 5.5). Anadromous trout (brown trout and Arctic charr), both first-time and veteran migrants, generally experience a rapid initial growth phase in the marine environment, which is probably a result of energetic reconditioning after winter-depletion in freshwater (e.g. compensatory growth; Berg and Berg, 1987, 1989, Rikardsen *et al.*, 2004). Fish then migrate back to safer freshwater habitats once marine

growth potential diminishes later in the season in Northern Norway (Berg and Berg, 1987, 1989; Rikardsen *et al.*, 2004). If migration to the outer-fjord was expressly for the purpose of energetic reconditioning for those incurring the greatest costs of reproduction, then it might seem counter-intuitive that they should spend less time there foraging compared to trout in the inner-fjord. This might, however, simply indicate that trout in the outer-fjord need less time to recondition because they are in an area where energy-rich pelagic fish prey are presumably more abundant (see also Eldøy *et al.*, 2015, Davidsen *et al.*, 2017), although there could also be risks associated with migration to the outer-fjord that might limit their time there, such as predation (Lyse *et al.*, 1998) and sea lice parasitism (Thorstad *et al.*, 2015). Within migratory groups that travelled to similar areas of the fjords, marine residency time was negatively correlated with plasma triglyceride levels so that fish with depleted circulating lipid levels spent more time in the marine environment, perhaps reflecting higher nutritional requirements (Table 5.3; Fig. 5.5). The duration of the marine residency period is thus probably influenced by individual lipid depletion (or nutritional requirements), and by the relative productivity of the marine habitat to which the fish migrate. As revealed from the significant positive correlation with body condition, plasma triglyceride concentration is believed to reflect post-winter, pre-migratory nutritional condition in these fish that were captured in early spring. Collectively, the current findings suggest a condition-dependent migratory tactic in brown trout veteran migrants, in which an individual's pre-migratory nutritional state influences its spatio-temporal use of the marine environment.

In the current study, the survival of marine migrants was estimated at 86 % (18 of 21). This is slightly higher than previously reported marine survival estimates of 29-85 %, for this life-stage (Jensen, 1968; Jonsson and Jonsson, 2009; Jensen *et al.*, 2014, only including post-spawners in Aarestrup *et al.*, 2015). Interestingly, mortality only occurred among those fish that migrated to the outer fjord. Although sample sizes are small, this might reflect the idea that long-distance migration to more pelagic habitats might be a riskier tactic undertaken by fish in poorer pre-migratory nutritional condition. This tendency for fish in poorer post-spawning/pre-migratory nutritional condition to opt for

a riskier migratory tactic has also been observed in Atlantic salmon, in the form of differential migratory timing. Halttunen *et al.* (2013) showed that salmon from the Alta River with lower body condition factors following spawning initiated their sea-ward migration earlier, and likely encountered unfavorable environmental condition at sea.

Anadromous migrants, and especially females, are believed to play an important role in brown trout population dynamics due to their increased growth potential in the marine environment and higher reproductive investments (Thorstad *et al.*, 2016). However, large inter-individual variation exists in the spatial and temporal extent of the marine habitat use of anadromous migrants. My results showed that the pre-migratory nutritional state of veteran migrants differed among marine migratory tactics and was associated with the duration of marine residency period. Future research efforts investigating the benefits and costs of different marine migratory tactics in veteran migrants (in terms of survival, growth and fecundity) would contribute to a better understanding of the evolution of the brown trout migratory continuum. Assessing how much intra-individual variability exists in the migratory decisions of individuals tracked through multiple consecutive marine feeding migrations, as it relates to differences in environmental conditions, would also provide novel and highly useful information in the face of rapidly changing environmental conditions.

5.6 Acknowledgments

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extensive help during the field work. Marc Daverdin at the NTNU University Museum is thanked for assistance with making the maps.

Table 5.1. Summary of the migratory behaviour of tagged fish (n = 32).

Tag_ID	Pop.	TL (mm)	Sex	Marine migration	Migratory tactic	Marine res. (days)	Marine survival	Over-winter
A69-1303-13	Åbjøra	540	M	0	Resident	0	NA	NA
A69-1303-01	Åbjøra	390	F	0	Resident	0	NA	NA
A69-1303-14	Åbjøra	430	M	0	Resident	0	NA	NA
A69-1303-15	Åbjøra	430	F	0	Resident	0	NA	NA
A69-1303-16	Åbjøra	485	M	0	Resident	0	NA	NA
A69-1303-33	Åbjøra	490	M	0	Resident	0	NA	NA
A69-1303-35	Åbjøra	530	F	0	Resident	0	NA	NA
A69-1303-23	Åbjøra	420	F	1	Short mig.	NA	1	Estuary
A69-1303-19	Åbjøra	405	F	1	Short mig.	35	1	River/lake
A69-1303-29	Urvold	590	M	1	Short mig.	NA	1	Estuary
A69-1303-11	Åbjøra	445	F	1	Long/in mig.	83	1	River/lake
A69-1303-02	Åbjøra	310	F	1	Long/in mig.	NA	1	Estuary
A69-1303-31	Urvold	500	M	1	Long/in mig.	54	1	River/lake
A69-1303-30	Urvold	720	M	1	Long/in mig.	66	1	River/lake
A69-1303-28	Urvold	628	M	1	Long/in mig.	80	1	River/lake
A69-1303-27	Urvold	430	M	1	Long/in mig.	64	1	River/lake
A69-1303-25	Urvold	590	M	1	Long/in mig.	68	1	River/lake
A69-1303-17	Åbjøra	430	F	1	Long/out mig.	32	1	River/lake
A69-1303-20	Åbjøra	490	M	1	Long/out mig.	43	1	River/lake
A69-1303-21	Åbjøra	600	F	1	Long/out mig.	58	1	River/lake
A69-1303-22	Åbjøra	420	F	1	Long/out mig.	NA	0	Dead at sea
A69-1303-34	Åbjøra	400	F	1	Long/out mig.	NA	1	Estuary
A69-1303-05	Urvold	350	M	1	Long/out mig.	81	1	River/lake
A69-1303-32	Urvold	640	F	1	Long/out mig.	54	1	River/lake
A69-1303-22498	Urvold	480	F	1	Long/out mig.	NA	0	Dead at sea

Tag_ID	Pop.	TL (mm)	Sex	Marine migration	Migratory tactic	Marine res. (days)	Marine survival	Over-winter
A69-1303-22497	Urvold	560	NA	1	Long/out mig.	NA	0	Dead at sea
A69-1303-26	Urvold	450	M	1	Long/out mig.	50	1	River/lake
A69-1303-24	Urvold	440	M	1	Long/out mig.	64	1	River/lake
A69-1303-12	Åbjøra	490	F	NA	NA	NA	NA	NA
A69-1303-03	Åbjøra	310	F	NA	NA	NA	NA	NA
A69-1303-04	Åbjøra	320	M	NA	NA	NA	NA	NA
A69-1303-18	Åbjøra	430	F	NA	NA	NA	NA	NA

Note: The Information is filtered by migratory tactic: riverine/lacustrine residents (n = 7), short-distance migrants (n = 3), long-distance/inner-fjord migrants (n = 7), long-distance/outer-fjord migrants (n = 11), and 4 NA's.

Table 5.2. Output of the best fitting multinomial logistic regression model of the log odds of adopting a given marine migratory tactic versus an alternative tactic (3 outcomes; short-distance, long-distance/inner-fjord, and long-distance/outer-fjord migrants) as a function of body condition factor (*K*) and sex.

Migratory tactics comparison	Coefficient	SE	*p*-value
Long/Out vs Long/In			
K	-20.7	9.4	0.027
Sex (F)	3.2	1.7	0.058
Long/Out vs Short			
K	-15.6	9.7	0.108
Sex (F)	1.3	1.8	0.460
Long/In vs Short			
K	5.0	9.5	0.592
Sex (F)	-1.8	1.6	0.247

Table 5.3. Output of the best fitting general linear regression model of individuals' marine residency period (in days) as a function of plasma triglyceride concentration and marine migratory tactics, 2 outcomes: long-distance/inner-fjord, and long-distance/outer-fjord migrants (baseline outcome).

Explanatory variable	Coefficient	SE	t-statistic	*p*-value
Intercept	67.5	5.9	11.5	4.5×10^{-7}
Migratory tactic				
Long-dist./in	15.3	5.8	2.6	0.025
Triglycerides (mmol L^{-1})	-23.7	8.0	-3.0	0.015

Multiple $R^2 = 0.60$

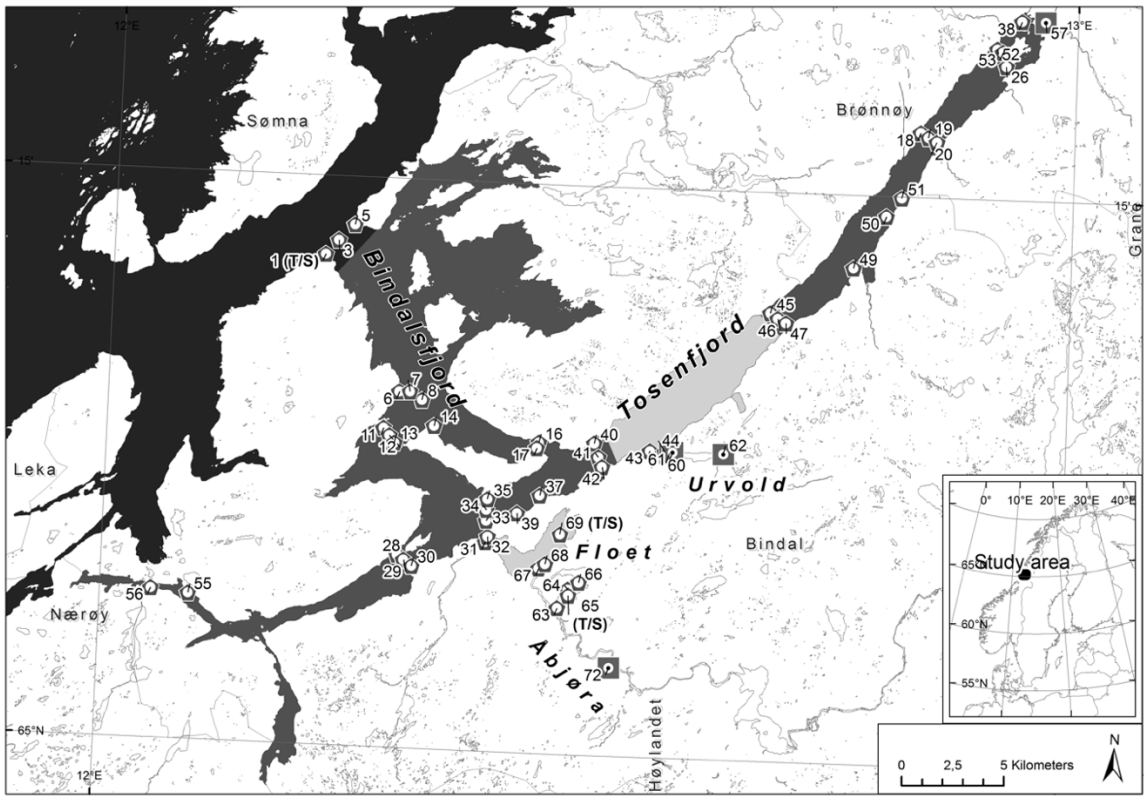

Fig. 5.1. Map of the acoustic array deployed (n = 54 receivers). Receivers deployed in freshwater are represented by squares and those deployed in brackish or saltwater are represented by pentagons. The different coloured areas of the fjords represent the different marine migratory tactics: short-distance in pale grey (two areas; for Åbjøra and Urvold fish), long-distance/inner-fjord in dark grey, and long-distance/outer-fjord in black. Temperature and salinity loggers (T/S) were deployed on stations 1, 65 and 69. The tagging site was located around station 65 in Åbjøra, and in the lake around station 61 in Urvold.

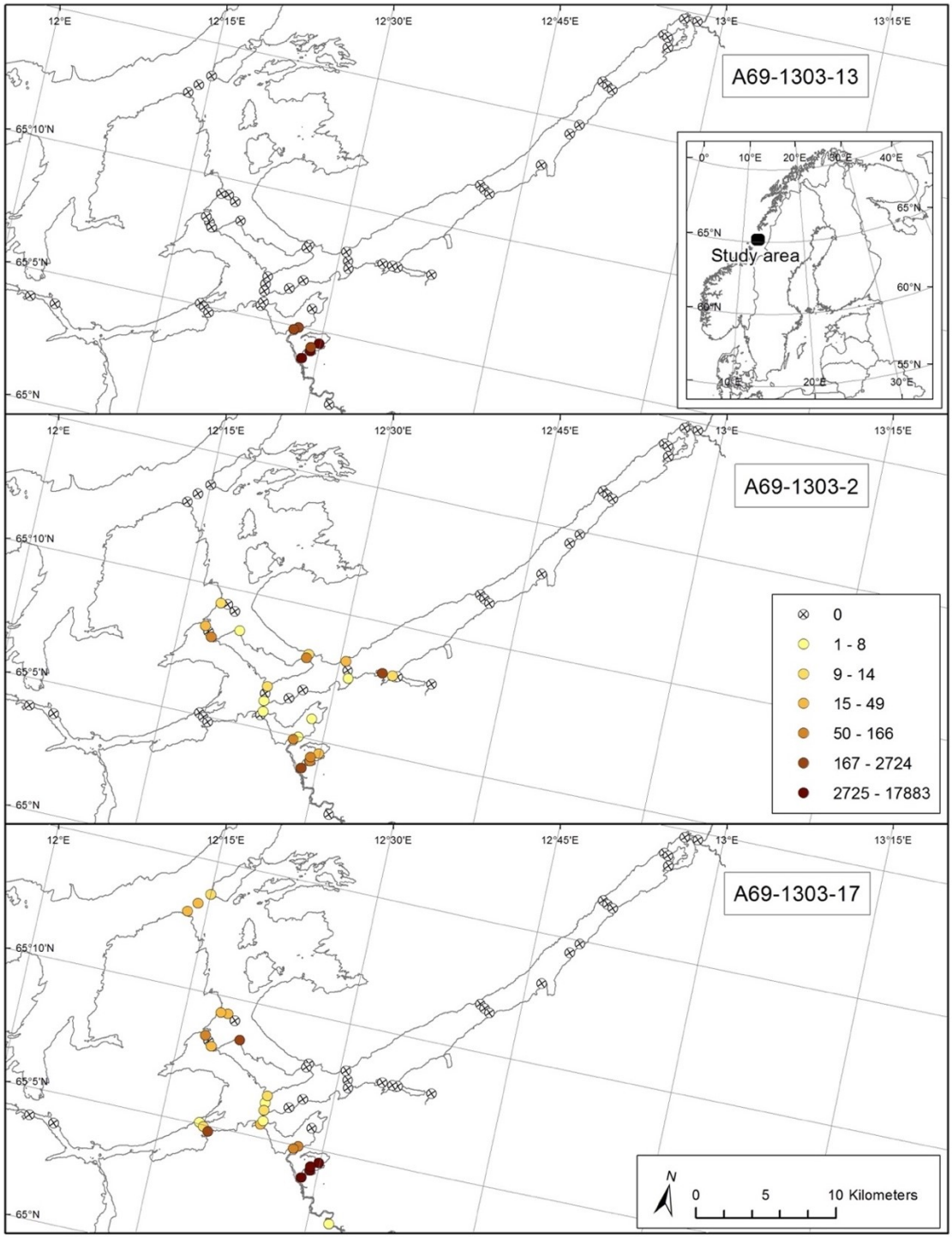

Fig. 5.2. Example of observed individuals' marine migratory tactics: top) short-distance migrant; middle) long-distance/inner-fjord migrant; and bottom) long-distance/outer-fjord migrant. The dots represent the position of each acoustic receiver: white crossed dots for receivers on which the individual was not detected; and from yellow to red for receivers on which it was detected (the colour reflecting the number of detections that were registered for that individual on each receivers).

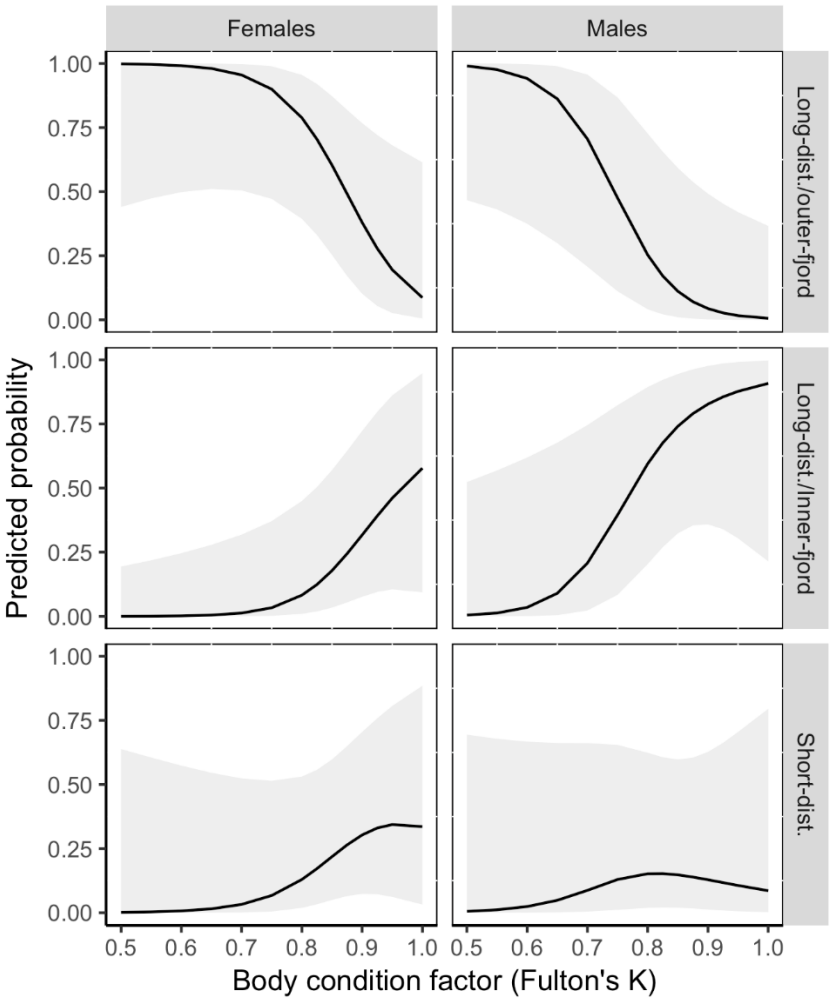

Fig. 5.3. Predicted probabilities of adopting a given marine migratory tactics as a function of body condition factor and sex, as calculated from the regression coefficients (information presented in Table 2). The shaded areas represent the 95 % confidence intervals.

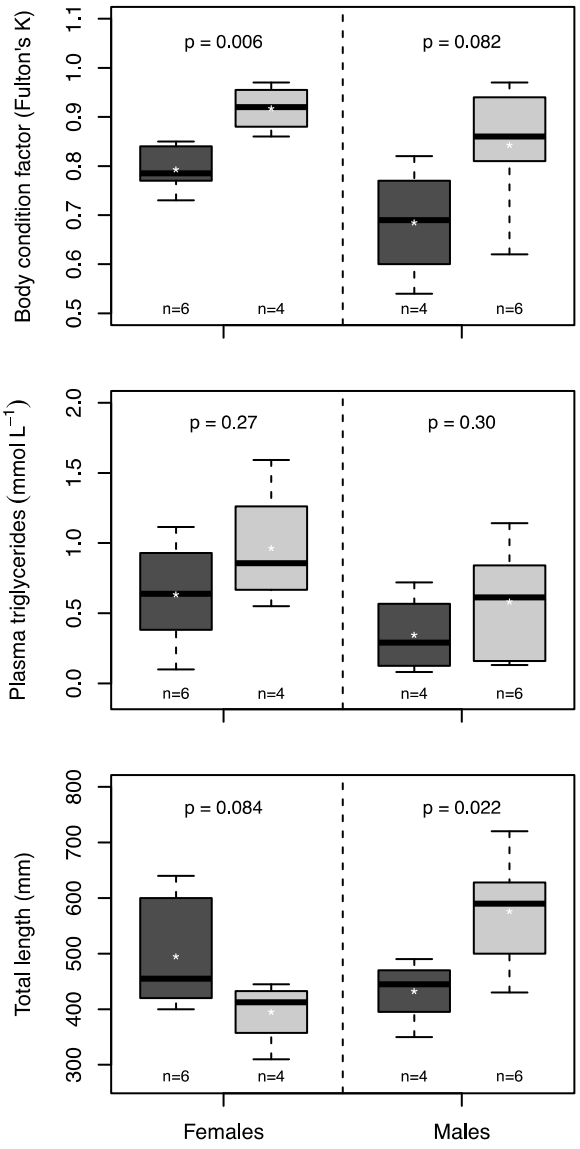

Fig. 5.4. Comparisons of body condition factor, plasma triglyceride concentration, and total length in brown trout adopting an outer-fjord (long-distance) in black versus inner-fjord marine migration tactic in grey (short- and long-distance migration tactics combined). The boxplots show median (black lines) and mean values (white dots), as well as the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Comparisons were made using Welch Two Sample t-tests.

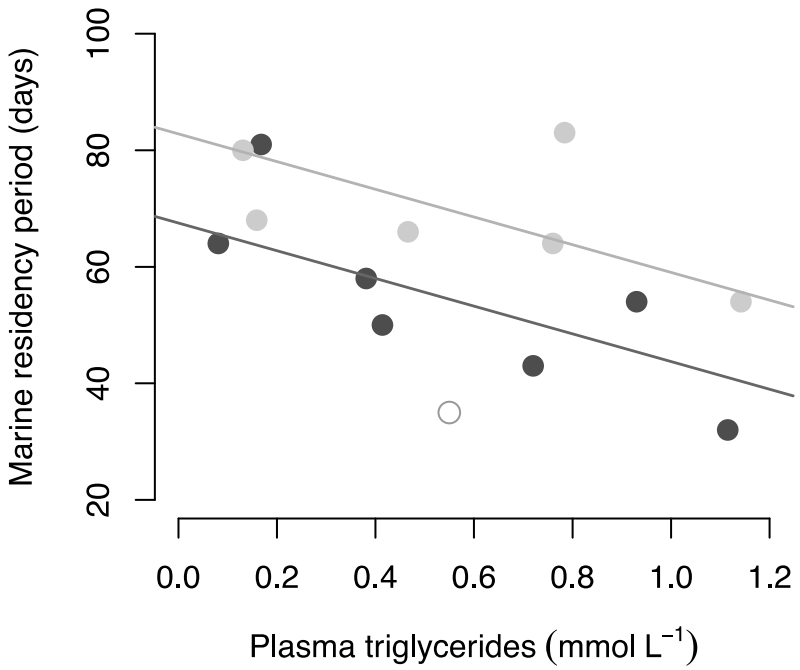

Fig. 5.5. Marine residency period as a function of pre-migration plasma triglyceride level and marine migratory tactics: long-distance/outer-fjord migrants in black; and long-distance/inner-fjord migrants in grey (regression coefficients and *p*-values can be found in Table 3). The hollow symbol represents the only short-distance migrant for which marine residency period could be calculated. However, this individual was excluded from the analysis for reasons described previously.

Chapter 6

Conclusion

In many ways, Elina Halttunen's Ph.D. thesis (2011) was a revelation into the post-spawning ecology of Atlantic salmon, and led to emerging research interests into the factors affecting the migratory behaviour and survival of kelts, ultimately limiting repeat-spawning potential. While the drivers of Atlantic salmon habitat use and mortality in the marine environment still remain mostly unknown, especially for post-spawners (Halttunen, 2011; Thorstad *et al.*, 2011; Drenner *et al.*, 2012), recent development of electronic tracking technologies (Hussey *et al.*, 2015) and infrastructure (Iverson *et al.*, 2019) allowed me and other researchers to attempt studies spanning much larger temporal and geographical scales than have been previously possible, which has yielded valuable biological insights.

Before addressing these issues, one salient question for iteroparous salmonids that needed to be addressed was: What is the role of iteroparity for population resilience? While for species exhibiting high post-spawning survival such as brown trout and Arctic charr (Fleming, 1998) the importance of repeat-spawning is clear, it is less evident in species such as Atlantic salmon that generally show a low degree of iteroparity. Furthermore, knowing that iteroparity in Atlantic salmon populations is highly variable (Fleming, 1998) and that the potential ecological benefits likely depends on the degree of iteroparity, this raises the question of what evidence is available to document spatial patterning in the degree of iteroparity across populations, and whether this changes through time. My interest in these questions led me on a multi-year quest for data on the spawning history composition of Atlantic salmon annual returns across populations of North America. Thanks to the collaboration with federal and provincial government scientists from across eastern Canada, I assembled a five-decade dataset for ten populations of the Northwest Atlantic and West Greenland mixed-stock fishery landings. From this, I estimated that the reproductive contribution

of repeat spawners (i.e. proportion of annual egg deposited) was about 2-fold higher (range: 1.4 – 2.8) than an assessment of their importance solely based on their proportions in number (i.e. proportion of repeat spawners in the annual returns of both sexes combined), due to the generally larger sizes of repeat spawners and the higher prevalence of iteroparity in females in most populations considered. Furthermore, I documented that the relative reproductive importance of repeat spawners at the population level was emphasized in years of low maiden spawner returns, contributing an average estimated 18.2 – 35.3 % of all eggs deposited annually in these years of low recruitment. Importantly, I documented broad-scale spatio-temporal shifts in iteroparity across populations of North America, with increases in mid-latitudinal and northern populations (from 3.1 % to 7.6 %) and declines in southern areas (from 4.1 % to 2.7 %) that occurred around the late 1980s – early 1990s (Fig. 2.3). While many factors are believed to have contributed to these trends, in particular the closure of the commercial fisheries which seemingly improved the survival prospects of post-spawners in common feeding areas, the declines I documented in southern populations suggest that regional factors (e.g. additional environmental and anthropogenic threats) may have been limiting iteroparity in southern areas. The contrasting regional trends I documented in Chapter 2 – Bordeleau *et al.* (2019b) highlight the potential influence of iteroparity on population-level processes, as well as the need to develop management and conservation plans to mitigate the additional challenges faced by iteroparous migratory species. As such, the extent to which iteroparity in Atlantic salmon is dictated by endogenous constraints (i.e. trade-offs between current breeding investments and survival probability to future breeding) or constrained by additional anthropogenic stressors, are key questions limiting our understanding of the potential importance of iteroparity for population viability and recovery efforts.

Extending from the findings of Chapter 2 on the importance of iteroparity for populational resilience, my subsequent thesis chapters were aimed at elucidating the role selected endogenous (Chapters 3 – Bordeleau *et al.*, 2019a [Under review]; and Chapter 5 – Bordeleau *et al.*, 2018a) and anthropogenic factors (Chapter 4 – Bordeleau

et al., 2018b) played in affecting the migratory decisions and survival of post-spawned Atlantic salmon (Chapters 3 and 4) and brown trout (Chapter 5), in freshwater, estuaries, and at sea. By combining acoustic telemetry and physiological sampling, I documented in Chapters 3 and 5 that differences in post-spawning / pre-migratory nutritional state underlie differences in the spatio-temporal aspects of the habitat use and survival of iteroparous salmonids, which ultimately affected repeat-spawning potential. By applying the same methodology across species and study systems, I consistently observed that, after spawning, the more nutritionally or energetically depleted individuals (i.e. low body condition factor and/or plasma triglyceride concentration) opted for riskier migratory tactics, such as early downstream migration in Atlantic salmon (Chapter 3) and long-distance migration to outer-fjord regions in brown trout (Chapter 5), which resulted in increased mortality risks. In combination with my observations that indices of individuals' post-spawning nutritional state were negatively correlated with: i. the estuarine residency period of seaward migrating Atlantic salmon (Chapter 3); and ii. the marine residency period of brown trout during their summer feeding season (Chapter 5), the findings from both chapters offered growing evidence for the importance of nutritional status in mediating the post-spawning migratory decisions and longer-term survival of iteroparous salmonids in both freshwater and at sea. In addition, these results compliment my findings from Chapter 4 that wild-origin, hatchery-spawned Atlantic salmon kelts that were highly stressed (i.e. high plasma cortisol and glucose concentrations) and potentially immune altered (i.e. high prostaglandins E_2 concentration), migrated out of the river prematurely (i.e. on average 66 days earlier). These fish then suffered higher estuarine mortality and none survived to spawn again in the future. While I did not observe differences in the post-spawning nutritional condition of hatchery- and wild-spawned Atlantic salmon kelts at the time of tagging, it is possible that their high stress levels contributed to increased metabolic demands and faster energy depletion during winter, which resulted in premature river exit timing and higher estuarine mortality. Collectively, I believe that findings from Chapters 3 – 5 reflect the higher energetic requirements of nutritionally depleted or highly stressed post-

spawned individuals and their apparent willingness to accept greater risk via adopting premature downstream migration and migration to areas with potentially higher predator abundances in trying to offset these and recondition for future spawning attempts. This provide examples of condition-dependent risk-taking in fish (Mcnamara and Houston, 1987; McNamara and Houston, 1994; Anholt and Werner, 2009) that has been documented in the wild for green sea turtles (*Chelonia mydas*) where individuals in poorer body condition selected for profitable, high-risk foraging habitat despite the presence of predatory tiger sharks (*Galeocerdo cuvier*) (Heithaus *et al.*, 2007). In other words, not only were more depleted post-spawned Atlantic salmon and brown trout more likely to die due to the direct effect of resource limitation and their inability to sustain basic metabolic processes and immune functions, but presumably also indirectly through riskier migratory behaviour. While these sub-lethal behavioural impacts, or deferred mortality risks, have not been detected in previous studies on the post-spawning migrations of salmonid due to temporal or spatial limitations (e.g. Halttunen *et al.*, 2013; Birnie-Gauvin *et al.*, 2019), they are key to our understanding of the drivers of mortality for this life history stage.

Considering current declines in marine survival (i.e. low probability of breeding once) and the poor post-spawning survival prospects (i.e. low probability of survival between spawning events) of Atlantic salmon, especially in southern regions of the species' North American distribution (Chapter 2), there is potential for selection pressure to favor semelparity over iteroparity (Stearns, 1976). Iteroparity is a bet-hedging strategy allowing individuals to spread the risk of reproductive failure over multiple years (Slatkin, 1974). However, the ongoing decrease in the incidence of iteroparity for salmon in southernmost regions and the potential for this decrease to become widespread is raising particular concern about the viability and recovery potential of Atlantic salmon populations, particularly under increasing environmental variability associated with climate change (Stenseth *et al.*, 2002). As such, the importance of iteroparity should be considered in recovery actions, and mitigation measures should be envisioned to reduce post-spawning mortality as it relates to

current anthropogenic threats occurring in freshwater (summarized in Keefer *et al.*, 2008; Chapters 2 and 4). Efforts should be directed at improving the design of dams to minimize downstream passage mortality for large post-spawners (Kraabøl *et al.*, 2009; Nyqvist *et al.*, 2016) and mitigating the many stressors and associated fitness consequences that wild-origin broodstock experience in current hatchery programs prior to their release back to the wild (Chapter 4). Additional management implications specific to single chapters can be found in the Discussion sections (especially for Chapters 2 and 4). As more empirical information becomes available on the reproductive output and offspring fitness of maiden compared to repeat spawners, and among consecutive and alternate repeat-spawning tactics, the consequences of iteroparity to salmon population dynamics should be examined in more detail (Reid and Chaput, 2012).

While I showed that post-spawning migratory decisions, survival, and ultimately the degree of iteroparity are at least partly mediated by endogenous constraints (Chapters 3 and 5), I also documented the consequences of additional anthropogenic stressors that are likely limiting repeat spawning potential in some regions (Chapter 2 and 4). Collectively, my thesis provides valuable biological insights into the factors currently limiting repeat spawning potential and highlights the potential for increases in iteroparity to occur when anthropogenic threats are mitigated, with quantified benefits to population resilience.

6.1 Further Perspectives

With growing evidence that both post-spawning migratory decisions and survival are mediated by aspects of individuals' nutritional state, the question then becomes: Why are certain individuals more depleted than others after spawning? Or which factors are influencing post-spawning nutritional state? While many factors can affect energy depletion rate during the lean winter months (e.g. food availability, water temperature, activity rate, and stress state), the generally high levels of energy invested into

reproduction exhibited by salmonid fishes should be a key determinant of post-spawning state. Following my observations that: i. 2SW salmon, which are known to invest more into reproduction (Jonsson et al. 1991, 1997, Fleming 1996), showed lower overwinter survival than 1SW salmon (Chapter 3); and ii. larger anadromous female brown trout, which are also known to invest more into reproduction (Jonsson and Jonsson, 1993; Thorstad *et al.*, 2016), were found in poorer nutritional condition after spawning and initiated riskier long-distance migrations to foraging areas in outer-fjord regions (Chapter 5), I speculated that differences in migratory decisions and survival might be carried-over from previous spawning investment strategies. Additional analyses which I conducted on supplementary data provided in Gauthey et al. (2015) confirmed that post-spawning levels of plasma triglycerides were reflective of the relative variation of this metabolite during the spawning season, a measure of energy investment into reproduction which was in turn positively correlated with reproductive success (Chapter 3). While I could not directly quantify reproductive investments in my thesis, findings are consistent with expectations from the life history trade-off between current reproduction and survival in which larger and more depleted individuals experienced higher post-spawning mortality as a result of higher energy investment into spawning (Fleming, 1998; Fleming and Reynolds, 2004). These offer additional support for the biological relevance of measuring post-spawning plasma triglyceride concentration as a valuable and relatively simple non-lethal indicator of nutritional condition, and indicator of a potential reproductive carryover effect on post-spawn survival. Moreover, my findings indicate additional means through which the costs of reproduction might manifest themselves in post-spawning salmonids, by prompting more depleted individuals to adopt riskier migratory tactics.

By providing enhanced growth opportunities, anadromy in brown trout can translate into larger size and increase fecundity of females (Jonsson and Jonsson, 1997; L'Abee-Lund *et al.*, 2006; Thorstad *et al.*, 2016). However, considering the recent increase in marine mortality and decreased growth of anadromous brown trout due to anthropogenic impacts on marine habitats (e.g. salmon lice *Lepeophtheirus salmonis*

parasitism: reviewed in Thorstad *et al.*, 2015), researchers have speculated that a reduction in the benefits of anadromy might favour selection for freshwater residency (Hendry *et al.*, 2004; Thorstad *et al.*, 2016), with unquantified consequences on population productivity and resilience. While a growing body of research aims to elucidate the causes and consequences of the brown trout migratory continuum, findings from Chapter 5 provide a potential mechanistic explanation for the choice of migratory tactic to originate from initial differences in spawning investment being carried-over to affect the extent of the marine habitat use of individuals in the following year, ultimately influencing their level of exposition to anthropogenic activities at sea. This led my colleagues and I to design a collaborative research project in which we are experimentally testing the relationships between the level of spawning investment and post-spawning nutritional indices in brown trout, which could then be used to guide future telemetry studies and formally test hypotheses on the link between spawning investment and subsequent migratory decisions.

Through the analysis and writing of Chapter 5, I became increasingly interested in the potential behavioural flexibility of migratory decisions in anadromous brown trout and its implications for the species' susceptibility to changing environmental conditions. After noticing that I had two consecutive years of data for a small subset of individuals, I realized the potential of the large tagging program put in place by Norwegian colleagues (led by Jan G. Davidsen, NTNU University Museum) to address this question. By pooling data from individuals tagged over many years and across multiple populations of different Norwegian fjord systems, we initiated an unprecedented study for salmonids (Eldøy *et al.*, 2019 [Under review]) in which individuals that were tracked through consecutive feeding migrations were examined for inter-annual flexibility or repeatability of marine habitat use patterns. Growing scientific evidence suggests that nutritional condition can affect inter-individual variability among the brown trout migratory continuum within a given year (Olsson *et al.*, 2006; Wysujack *et al.*, 2009; Boel *et al.*, 2014; Davidsen *et al.*, 2014; Eldøy *et al.*, 2015; in addition to Chapter 5). We therefore expected to see some level of inter-annual flexibility in the migratory decisions

of brown trout due to the likelihood for post-spawning / pre-migratory nutritional condition to vary with environmental conditions that can affect pre-breeding energy storage, reproductive investment, and overwinter depletion rate. However, the opposite was observed: brown trout showed a high degree of behavioural repeatability in marine migratory tactics (i.e. as defined in Chapter 5), despite differences in environmental conditions among years, with 88 % (n = 32) opting for the same tactic in subsequent years. While indeed some degree of environmental fluctuation among years was observed (e.g. sea surface temperature and sea lice counts in nearby open net aquaculture facilities), we cannot rule out the possibility that changes in environmental conditions were not drastic enough to trigger behavioural flexibility in marine area use. Nevertheless, these novel findings now require us to think about potential drivers of the brown trout migratory continuum that act over longer time-frames. Therefore, I suspect that some form of individual specialization is at play, beyond a plastic response to nutritional needs (as previously suggested by Wysujack *et al.*, 2008), unless there are physiological and behavioural mechanisms that would allow the post-spawning / pre-migratory nutritional condition of individuals to remain fairly constant across years. For example, these could be maintained by: i. a form of habitat selection (or prey preference) of varying levels of productivity (or nutritional value) and risks; which could, ii. affect energy storage during the feeding season and dictate the amount of resources invested into reproduction; subsequently, iii. affecting post-spawning condition; and ultimately, iv. being carried-over to affect migratory decisions in the next feeding season. As such, while higher pre-spawning energy stores can translate into higher reproductive output potential, high levels of reproductive investment can also result in poorer post-spawning nutritional state and greater nutritional needs, which can promote riskier migratory decisions required to offset these (i.e. condition-dependent risk taking: Mcnamara and Houston, 1987; Heithaus *et al.*, 2007; Anholt and Werner, 2009; and also supported by findings from Chapter 3 – 5 in which more depleted individuals opted for riskier migratory tactics). In a trade-off between foraging rewards and associated risks, adoption of riskier migratory tactics could provide richer feeding

opportunities (e.g. Heithaus *et al.*, 2007), and ultimately produce higher energy stores and higher reproductive output potential for the next spawning opportunity, for those that survived. While further research is needed to clarify the causes and consequences of the brown trout migratory continuum, in light of our novel findings that migratory behaviours are highly repeatable, these provide further thoughts on the potential physiological and behavioural mechanisms at play that could affect migratory decisions and survival over multiple years.

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