Environmental change and sockeye salmon life histories across space and time

by

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B.Sc. (Hon.), University of British Columbia, 2016

Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Science

in the
Department of Biological Sciences
Faculty of Science

SIMON FRASER UNIVERSITY
Summer 2019

Approval

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Degree:	**Master of Science**
Title:	**Environmental change and sockeye salmon life histories across space and time**
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Date Defended/Approved:	June 12, 2019

Ethics Statement

Abstract

Animals with complex life cycles migrate to exploit resources from different environments, but are exposed to multiple stressors and challenges. Here I investigated stressors across ontogenetic shifts in sockeye salmon. First, I examined migration and condition of juvenile sockeye salmon fry as they migrate from the Babine River, British Columbia, to upstream lake rearing habitat. High water velocities increased challenges to successful upstream migration to the lake, but lake rearing habitat was associated with larger fry (30% longer, 150% heavier). Second, I examined how multiple ocean stressors impact freshwater fecundity using a nearly 7-decade dataset from Fraser and Skeena sockeye salmon. Good ocean conditions and low biomass of salmon competitors were associated with younger, larger, more fecund sockeye. Spawning channel enhancement was associated with a small additional increase in fecundity. Collectively, my thesis highlights intricacies in the effects of multiple stressors on sockeye salmon across their complex life cycle.

Keywords: salmon; life history; habitat; ontogenetic shift; migration; fecundity

Acknowledgements

This thesis would not have been possible without the generous support, patient mentorship and passionate perseverance of so many individuals. To my senior supervisor, Dr. Jonathan Moore, thank you for your guidance, compassion, and consistent commitment to applied, and collaborative salmon science and conservation. Your mentorship throughout this process has been instrumental in my growth as both a scientist and collaborative resource steward. To my supervisor, Dr. John Reynolds, thank you for your big picture thinking, for challenging me to consider many perspectives and ensuring that I held myself to a high standard of scientific integrity.

To my mentor and friend, Donna Macintyre, thank you for modelling steadfast commitment to Indigenous-led resource stewardship. Your dedication to the salmon and salmon people of the Babine and Skeena watersheds has been inspiring. In the future, I hope to continue learning how to best support Indigenous resource sovereignty, and I hope to have your continued advice and guidance along that journey.

To all the people from Fort Babine, Tachet, Woyenne, Old Fort and Donalds Landing, who welcomed me into their communities, workplaces and lives, thank you for your time, energy, kindness and wisdom. Thank you for pulling me out of creeks in spring flood, for teaching me a thing or two about the river, the bush and the planet, and for all the stories and knowledge you've shared about how to monitor, understand and protect salmon and the places they need to survive.

To the Lake Babine Nation Fisheries staff (past and present), Andy, Mark, Emily, Peter, Gillie, Carole, Angel, Fern, Christie, Eugene, Craig, and many others, for your intellectual and physical support throughout this journey. I couldn't have done it without you. I hope to continue working with and learning from you for many years to come.

To the Salmon Watersheds Lab and the Earth to Oceans Research group, thank you for making my time at SFU feel like home. Thank you for the endless stats help (literally endless, I'll be asking y'all more questions in the future, for sure), the laughs, the coffee breaks, lunch chats. It has been a true honour to be surrounded every day by such a hardworking, intelligent, genuine, and big-hearted group of humans. A huge thank you to Kyle, for both your expertise and friendship. I couldn't have asked for a

more kind-hearted Bayesian Spirit Guide to lead me on what could have been a seriously soul-destroying journey; discovering Bayes' mountain was a blast.

To my mentors, Ken Rabnett and Michael Price, who've patiently answered countless questions about the Skeena watershed and the people and animals that call it home, thank you for encouraging me to dip my toes into the waters of salmon. You were so influential in setting me out on this journey, and have been irreplaceable informants on topics and challenges not taught in books or classrooms. Your lived experience is invaluable, and I thank you for sharing it with an open mind and warm heart.

This thesis could not have been possible without the support and funding from many groups, organizations and foundations. I am consistently struck by the massive energetic and monetary cost that comes with doing remote, collaborative research, but simultaneously in awe of what thoughtfully spent dollars can do to support and sustain communities and promote applied conservation action. Thank you to Lake Babine Nation Fisheries Department, Tides Canada, Pacific Salmon Foundation, Pacific Salmon Commission, Salal Foundation, Skeena Watershed Conservation Coalition, the Babine River Foundation, Department of Fisheries and Oceans Canada, Salmon Watersheds Lab, and Liber Ero Foundation for funding this work.

To my family and friends, thank you for your positive attitudes and multi-faceted encouragement over the past few years. I would not have made it through if it weren't for the ski days, bike rides, trail runs, cups of tea, baked goods, hugs and constant light that you brought to my life. Sorry for being a bit of a nutcase while I was cranking this out. To my parents, thank you for always pushing me to do my best, for insisting that I understand that, just because something is difficult, scary, or intimidating, that's no reason not to try, and above all, for teaching me the wonder and fragility of our planet.

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Chapter 1. Introduction

Complex life cycles can involve drastic ontogenetic changes in behavioural, morphological, or physiological characteristics of individuals (Wilbur 1980; Moran 1994). Many species require geographically distinct habitats to fulfill development requirements (Rijnsdorp *et al.* 2009). For example, the transition from aquatic to terrestrial habitats made by many pool-breeding amphibians (Salice *et al.* 2011) requires eggs and larva to develop first within freshwater pools before an individual can further grow into its mature form in the terrestrial environment. Occupation of different habitats allows individuals to exploit different environments, balancing the benefits of optimal growth opportunities while minimizing mortality risk (Werner *et al.* 1983).

Species with complex life histories may be particularly vulnerable to environmental change, due to their reliance on multiple habitats that span various geographies and types and intensities of human use (Runge *et al.* 2014). Habitat is simply the site and type of local environment an organism occupies (Lincoln *et al.* 1987) and provides both conditions and resources needed for survival (Hall *et al.* 1997). Both abiotic (i.e. temperature, flow, salinity) and biological (e.g., prey abundance) characteristics and processes of a habitat can affect growth and survivorship of individuals and therefore, population dynamics (Gimenez 2004). The requirement of multiple habitats across a complex life cycle has been suggested to put individuals and populations at elevated risk, due to exposure to isolated or cumulative threats in multiple environments (e.g., pollutants, environmental degradation, food web variability, etc.; Dunson *et al*. 1992).

The vulnerability associated with multiple habitat usage is further complicated by the need for movements between environments during life cycle transitions. Migrations further expose individuals to additional habitats with novel environmental characteristics and unique threats along migration routes. Although potentially occupied for only a short duration, movement corridors and stopover habitats are often crucial to the survival of migratory populations (Weber *et al*. 1999). Thus, additional impacts experienced in migratory habitats and the periods of transition between life stages and their associated environments warrants further investigation (Griesemer 2016). Considering migration habitat used throughout complex life cycles is necessary to identify functionally important areas and the connectivity between them (Runge *et al.* 2014).

Multiple stressors in one habitat can affect the performance or survival of an individual at subsequent life stages in other habitats. Small changes in the environment, such as temperature increase, could affect multiple ecosystem functions, causing larger, magnified impacts than would be predicted for each stressor in isolation (Anthony *et al.* 2008; Kaniewska *et al.* 2012; Albright & Mason 2013; Lurig & Kunzmann 2015). Most populations are exposed to multiple stressors (Wilcove *et al.* 1998; Halpern *et al.* 2008; Vorosmarty *et al.* 2010), an effect that may be compounded when populations use multiple habitats. Exposure to different impacts or stressors across the migratory life cycle (Webster *et al.* 2002; Hodgson *et al.* 2016) may interact, accumulate and/or be synergistic (Francis & Mantua 2003; Mote *et al.* 2003). Population-level effects of stressors are likely largest when multiple stressors impact a population both before and after a phase of density dependence (Hodgson *et al.* 2017). Thus, further understanding of the interactions between multiple stressors may further explain the vulnerability of species with complex, migratory life cycles across temporally or geographically distant habitats.

Climate change may have multiple pathways of impact on species with complex life cycles. Different pathways of impact could include climate-induced changes in: the quantity and quality of habitat, the connectivity among habitats, or the (mis)matching in space and time of key life-history events with environmental conditions (Dickey-Collas *et al*., 2009; Peck *et al.,* 2009; Petitgas *et al*., 2009; van der Veer & Bergman, 1987). Within complex life cycles, specific stages may be particularly sensitive or vulnerable to climate change (Petitgas *et al.* 2013). Thus, climate change may pose particular challenges for species with complex life cycles (Reynolds *et al.* 2017).

Pacific salmon are one example of a species with complex, migratory life cycles. Pacific salmon are anadromous, meaning they are born in freshwater rivers, streams or lakes, but then migrate to the marine environment to feed and grow (Quinn 2018). Prior to ocean outmigration, Pacific salmon juvenile may rear in freshwater habitats for a period ranging from a few months to a few years. They then undergo smoltification, a process where their bodies change in order to prepare for the saltwater environment of the ocean (Burgner 1991). Some migrations to the marine environment can stretch hundreds of kilometers, while others may be less than one. In the ocean, salmon acquire upwards of 90% of their adult body mass and can travel thousands of kilometers while foraging offshore in the Northeast Pacific (Groot & Margolis 1991). Mature salmon then return to their natal freshwater habitat, via potentially arduous upriver migrations, to lay their eggs before they perish (Cooke *et al.* 2011). Thus, Pacific salmon migrations integrate across many habitats.

This thesis focuses on sockeye salmon (*Oncorhynchus nerka*) from the Skeena and Fraser River watersheds. The Fraser River is the largest river in British Columbia, and its watershed drains a large extent of the central and southern interior of the province (220,000km$_2$) into the Strait of Georgia at the city of Vancouver. The Skeena River is second largest salmon-watershed in the province, and drains 55,000km$_2$ of northwestern B.C. into Chatham Sound, just south of the city of Prince Rupert. Both rivers support 5 species of Pacific salmon (*Oncorhynchus* spp.), including pink (*O. gorbuscha*), chum (*O. keta*), coho (*O. kisutch*), Chinook (*O. tchawytscha*) and sockeye (*O. nerka*), as well as steelhead trout (*O. mykiss*). The Fraser and Skeena also support the first and second largest sockeye salmon runs in the province, respectively, in most years. Sockeye salmon are the most valuable commercial salmon species on the west coast of Canada and are also the most desired for Indigenous food, social and ceremonial (FSC) harvest due to their high fat content (Suttles 1968; Gottesfeld & Rabnett 2008). Currently, sockeye salmon are also the most widely consumed traditional seafood item among B.C. coastal First Nations, estimated to be eaten by 85% of Indigenous people over the age of 19 (Marushka *et al*. 2019). The life-cycle and migration of Pacific salmon are a social and cultural icon in British Columbia and across the Pacific Northwest.

Indigenous resource sovereignty and stewardship was a key impetus of this thesis. I was guided at its outset by salmon conservation priorities identified by the Ned’u’ten Dakelh people, the Lake Babine Nation (LBN). LBN territory surrounds Babine Lake, in north central British Columbia, at the east edge of the Skeena watershed. Babine Lake produces over 90% of Skeena River sockeye salmon and is the upstream lake of the Babine River, which together represent the largest tributary sub-basin of the Skeena. LBN Fisheries Department is working on catchment-wide salmon monitoring and conservation to ensure that many generations to come are able to access abundant Babine salmon populations. Salmon have been the foundation for the economy of

Indigenous peoples in the Fraser and Skeena watersheds for over 10,000 years (Gottesfeld & Rabnett 2008). Indigenous salmon fishery management is grounded in thousands of years of observation and stewardship of the local environment and governed by core conservation values shared throughout communities. Upon initiation of the commercial fisheries in the late 1800s, First Nations fishery resource management had maintained “vigorous, diverse and healthy” salmon populations (Gottesfeld & Rabnett 2008). Although enhanced populations in the watershed (Pinkut River and Fulton River spawning channels) are relatively healthy and stable, the wild tributary populations seem to be in decline, with some currently returning at only a small fraction of their former abundance.

We examined two questions regarding sockeye salmon life cycles and multiple stressors acting across their complex life cycle. These questions were identified by LBN as being important research priorities. First, how might early-life migratory habitat conditions be affecting population dynamics of the Babine River lake-outlet-spawning sockeye population, once the largest wild population in the Babine catchment, but now depleted to a mere fraction of its former abundance? Second, how are life-history traits and environmental stressors changing over time, and in particular, are there population-specific patterns in fecundity that differ between wild and enhanced sockeye stocks, such as body size, age at maturity, and fecundity?

In Chapter 2, I investigated spatial and temporal characteristics of the hydrologic landscape and of juvenile sockeye salmon fry body size and condition across the lake-outlet reach of the Babine River, B.C. with an intensive set of field studies. This population undertakes an early-life upriver migration to juvenile rearing lake habitat, when most individuals are only a couple centimeters long. First, we discovered that there were both spatial and seasonal velocity patterns in the lake-outlet reach that challenge the swimming abilities of sockeye fry, potentially acting as temporary barriers to upstream migration to the rearing lake. Second, higher water discharge in the river, associated with rain and snowmelt driven spring freshet conditions, created more high velocity areas in the reach, and may be associated with less upstream migration of sockeye fry. Last, I found that successful upstream migration to lake rearing habitat was associated with larger fry (30% longer and 150% heavier) that increased in size at almost twice the rate of fry in river habitat. These findings highlight the potential challenges faced by salmon who undergo ontogenetic habitat shifts and require connectivity between habitats used in different life stages. In addition, long-term changes in river habitat hydrology, potentially driven by climate change and landscape modification, may exacerbate the difficulty of challenging salmon migrations. Therefore, populations that have challenging ontogenetic habitat shifts, such as lake-outlet spawning sockeye, may be particularly vulnerable to anthropogenic impacts.

In Chapter 3, I examined potential effects of multiple ocean stressors on life-history traits of adult sockeye salmon. I analyzed a nearly 7-decade dataset on British Columbia sockeye salmon to trace multiple pathways of direct and indirect stressors on linked sockeye salmon life-history traits. I used a multi-level mixed effects regression model in a Bayesian framework to evaluate the strength of associations between environmental conditions and varying life-history traits. Ocean age, or the number of years a female sockeye has spent in the ocean, was associated most strongly with the biomass of Northeast Pacific chum salmon during her second year of ocean foraging. Size at maturity, was then most strongly associated with ocean age, specifically, whereby an additional ocean year (returning as a 5-year-old, rather than a 4-year-old) led to an average 5.2 cm increase in female fork length. Size at maturity was also positively related to favourable ocean conditions, namely high North Pacific Gyre Oscillation indices and low Multivariate El-Nino Southern Oscillation indices and biomass of chum salmon. Fecundity, or egg count, was, on average nearly double for the largest females (2 S.D. from mean fork length) in comparison to average sized individuals. Additionally, the effect of spawning channel enhancement led to a further 3% increase in fecundity. The results from linked models in the multi-level approach, one each predicting ocean age, body length, and fecundity, add to our understanding of the complex multiple pathways through which complex life-history traits may be influenced. This modelling approach could be built upon with additional linked life stages (e.g. marine survival) to further understand cumulative effects of multiple stressors across complex salmon life-cycles.

In my final chapter (Chapter 4), I discuss broad implications of my research. My thesis provides i) an in-depth case study of potential environmental and habitat impacts on the body condition of sockeye salmon during a migratory transition to freshwater rearing, and ii) an extension of complex life cycle analysis in the form of a multi-level model to track multiple pathways of environmental stressors on sockeye life-history traits over nearly 7 decades. I discuss what my findings may mean for the future direction of the study of complex life cycles, and management implications through the lens of Indigenous community-led salmon resource stewardship.

Chapter 2. Ontogenetic habitat shifts and vulnerability: lake outlet-spawning sockeye salmon (*Oncorhynchus nerka*) sensitivity to habitat connectivity and hydrologic change[1]

2.1. Abstract

Sockeye salmon that spawn downstream of rearing lakes demonstrate an important example of the challenges faced by organisms with complex life histories requiring habitat connectivity in aquatic habitat complexes. Here, we examine the spatial and temporal dynamics of the water velocity landscape and sockeye salmon fry movement and condition in the lake and lake outlet reach of an important sockeye salmon system, the Babine Lake of British Columbia, one of Canada's largest and most important sockeye salmon rearing lakes. We discovered three main findings. First, there were seasonal and spatial patterns of water velocities that exceed the ability of fry to swim upstream to lake rearing habitat. Second, higher water discharge was associated with more velocity barriers and potentially with less upstream movement of fry. Last, fry rearing in the lake tended to obtain larger sizes (30% longer and 150% heavier) than those in downstream river habitats, suggesting that fry that are displaced downstream of the lake outlet are not thriving. Years and seasons with high discharge may temporarily create one-way, downstream transport routes at lake outlets. Long-term changes in hydrology, perhaps driven by climate variability or land-use change, may control the degree to which lake outlets function as bidirectional travel corridors or one-way check valves for young sockeye salmon.

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[1] A version of Chapter 2 is in preparation for journal submission, with coauthors Donna Macintyre and Jonathan W. Moore

2.2. Introduction

The spatial arrangement of habitats and their connectivity is of critical importance to species with complex life cycles (Wiens 2002). Many aquatic species use different habitat types throughout their life history, ranging from within-lake ontogenetic shifts of trout (e.g. *O. clarkii, O. mykiss, Salvelinus namaycush*) to large-scale migrations of anadromous Pacific salmon (*Oncorhynchus* spp.). For aquatic organisms in freshwater ecosystems, habitat connectivity is constrained by the presence of water (Hermoso 2012) and is determined by both habitat patch quality (e.g. cover, prey) and the properties of habitat connections (e.g. distance, flow characteristics) (Wiens 2002). Thus, the spatial arrangement of aquatic habitats, such as the dendritic structure of river networks, can determine the productivity of freshwater habitat complexes (Wiens 2002; Fausch *et al*. 2002; Fagan 2002). Further, connectivity may be asymmetric; aquatic habitat connectivity can be influenced by habitat features such as waterfalls or high velocity reaches that can block upstream movement for some species or life-stages. However, barriers between habitats are not always fixed. Hydrologic variation can transform bidirectional movement corridors to one-way travel routes; for example, in high flows, organisms may be able to travel downstream, but not upstream. Thus, the spatial arrangement of aquatic habitats and potential dynamic barriers may challenge species with complex life-histories.

Sockeye salmon (*O. nerka*) that spawn downstream of rearing lakes are an important example of the challenges faced by organisms with complex life-histories requiring connectivity in aquatic habitat complexes. There is often productive spawning habitat in lake outlets due to moderated water flow and temperature (McCart 1967). Yet, sockeye salmon generally rear in lakes as juveniles for 1 to 2 years. Thus, unless there is a downstream lake, fry that emerge downstream of lake outlets have the challenge of swimming upstream to reach lake rearing habitats. In many outlet spawning populations, some proportion of the brood cohort is carried downstream upon emergence, where habitat conditions can be drastically different than those in upstream rearing lakes (Hartman *et al*. 1962; Brannon 1967; Raleigh 1971; Clarke & Smith 1972). In some cases, outlet fry that move downstream, rear in off-channel habitat or estuaries for 6 to 24 months before migrating to the ocean (Gilbert 1913; Semko 1954). Upon emergence, outlet fry have been observed to navigate this migration by orienting themselves towards the nearest river bank, swimming at an angle to the main current, schooling into large groups once they reach the river's edge, and moving upstream to their rearing lake (Andrew & Geen 1960; Clarke 1967; McCart 1967; Clarke & Smith 1972). A time lag has been observed prior to the initiation of upstream migration (Clarke 1967; McCart 1967) likely due to poor initial swimming ability and challenging water velocities (Killick 1949; Hoar 1958; Byrne1971). While sockeye salmon migrate thousands of kilometers over their migratory life-cycle, lake outlets represent specific habitats where configuration and conditions (e.g. water velocities) could determine the fate of individuals and the productivity of populations. Thus, while there is general appreciation for the potential importance of the early life history of lake-outlet-rearing sockeye salmon, there is a need for studies of large spatial scales that examine the potential area that fry from a single population may inhabit temporarily while trying to reach upstream rearing lakes.

The early life-history stages of salmon can have both direct and indirect influences on population dynamics. Juvenile salmon have high mortality while transitioning from endogenous to exogenous energy acquisition, when juveniles begin to obtain their own food in the first few weeks after emergence (Elliot 1989; Armstrong 1997; Einum & Fleming 2000). This could be due to low prey accessibility, subsequent intense intraspecific competition for food, high predation, or downstream losses (McCart 1967). Survival depends heavily on whether environmental conditions meet juvenile requirements (Underwood & Fairweather 1989; Cushing 1990). Growth in early life allows individuals to survive size-selective threats (i.e. predation) and maximize later growth potential (i.e. large gape, superior fitness) (Sogard 1997). For example, in Babine Lake, size-selective mortality is present in juvenile sockeye salmon, and faster growth rates in larger individuals maintain a hierarchy of lengths within a cohort (West and Larkin, 1987). Large size upon migration to the ocean subsequently increases marine survival (Pearcy 1992; Beamish & Mahnken 2001; Beamish *et al*. 2004; Zabel & Achord 2004; Moss *et al*. 2005; Claiborne *et al*. 2011; Thompson & Beauchamp 2014). Thus, body size during early life and the factors that impact may influence individual survival.

Here we examine the spatial and temporal dynamics of the water velocity landscape and sockeye salmon fry movement and condition across the lake-outlet reach of an important sockeye salmon system. We focus on the lake outlet of Babine Lake, British Columbia, the longest natural lake in B.C. and the most productive sockeye lake in the Skeena River watershed (Wood *et al*. 1998). We ask the following questions with corresponding predictions: first, what are the water velocity landscapes of the lake outlet reach in relation to the ability of sockeye fry to swim upstream? We predict that the lake outlet reach contains locations with high velocities that could challenge fry upstream migration, and these challenges will be greater during higher river discharge. Second, how does river discharge relate to directional movement by sockeye salmon fry? We predict that higher water discharge decreases the probability of upstream movement by sockeye salmon fry. Third, what are the seasonal patterns of fry size, abundance, and condition across the lake, lake outlet, and downstream rearing habitats? We predict that sockeye salmon fry size (i.e., length and weight) and condition will be higher in lake sites compared to sites downstream of the lake outlet, evidence that downstream rearing areas are sub-optimal rearing habitats. Further, we examine long-term variation in hydrology and discuss how this variation may influence the degree to which lake outlets function as bidirectional corridors or one-way check valves for young sockeye salmon.

2.3. Methods

2.3.1. Overview of Approach

Our study consists of the following components. First, we mapped nearshore water velocities across a 1.5 km reach on five occasions that varied in river discharge. Second, we used underwater video to examine the relationship between river discharge and fry movement. Third, we performed an extensive field study of fry abundance and condition across the lake and lake outlet reaches during the emergence and migration period. Specifically, we measured relative abundance, size, and energetics of sockeye salmon fry in the lake, outlet, and downstream rearing habitats as well as those that were being transported downstream. Sampling was done between mid-May and mid-August to fully capture fry emergence and migration, which generally begins in early June and is complete by late July. We describe these methodologies in more detail below.

2.3.2. Study System

The Babine watershed is the largest tributary basin of the Skeena River, the second largest Pacific salmon producing river system in Canada (Figure 2.1). The Babine Lake watershed produces, on average, over 90% of Skeena River sockeye salmon with at least 24 distinct sockeye populations within the larger lake stock complex (Cox-Rogers & Spilsted 2012). Formerly the largest contributing population to the Babine watershed, Babine River sockeye spawn below Nilkitkwa and Babine lakes and some juveniles have been observed swimming upstream to reach rearing areas in the lakes (Cox-Rogers & Spilsted 2012; McDonald & Hume 1984; Wood *et al*. 1998). However, many juvenile sockeye have also been observed being swept some distance downstream, where their fate is unknown (Clarke 1967; LBNF 2016; LBNF 2017). Research in the estuary of the Skeena River found that Babine Lake sockeye spend very little time in the estuary (mostly less than 2 days; Moore *et al*. 2016), suggesting that estuary rearing does not appear to be a common life-history strategy.

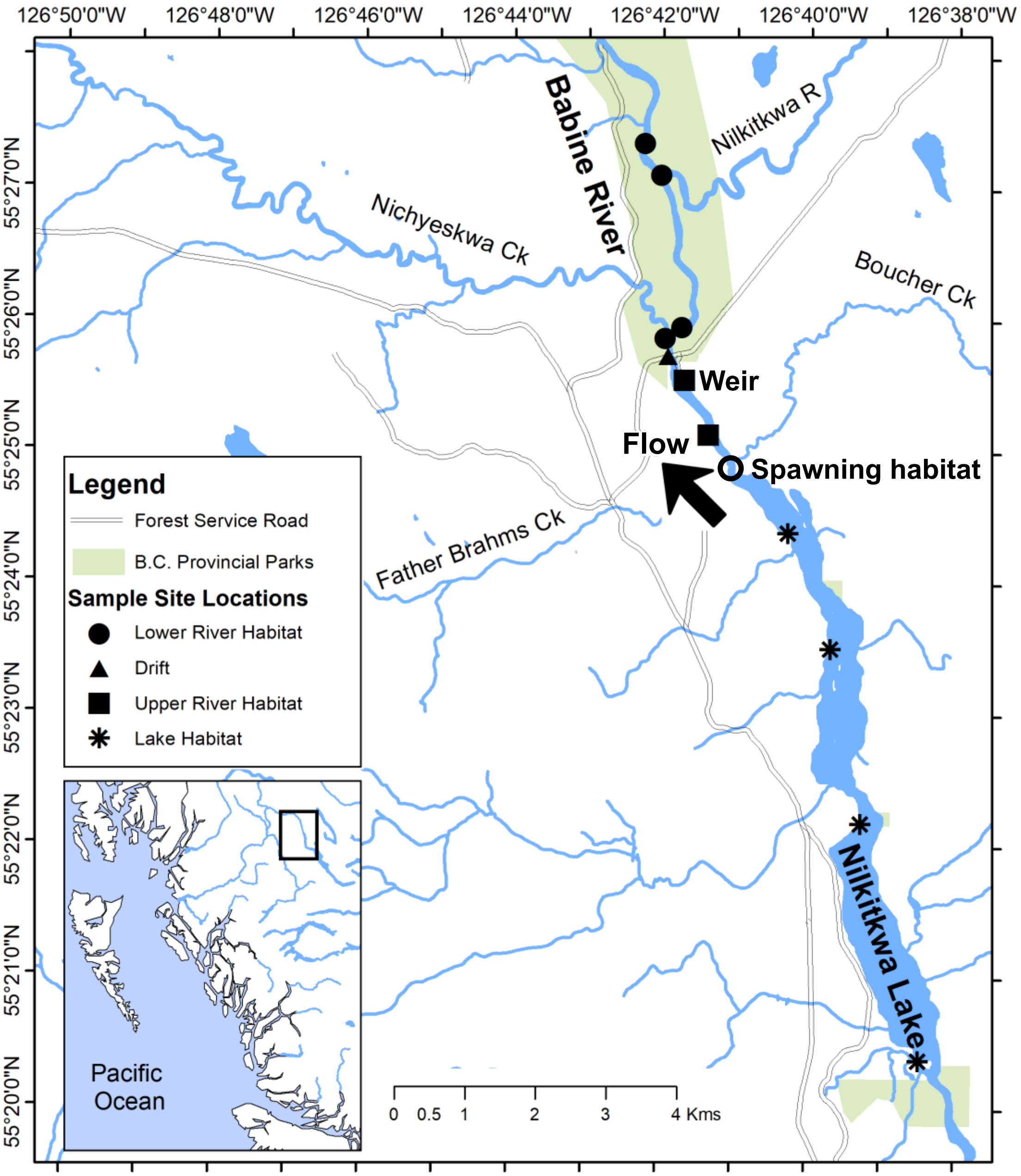

Figure 2.1 Locations of sampling sites in Nilkitkwa Lake and the Lower Babine River, British Columbia, Canada.
Babine Lake is drained by the Upper Babine River, which flows into Nilkitkwa Lake.

The lake-outlet spawning Babine River sockeye salmon population has declined dramatically over the last several decades, contributing to conservation concerns for the wild Babine Conservation Unit (Cox-Rogers & Spilsted 2012). Returns of Lower Babine River sockeye, the focal population in this study, have fallen by approximately 85%, from over 80,000 during the 1950s and 1960s, to around 12,000 in the last four decades, with two counts of less than 2000 spawners in the last decade (Fisheries & Oceans Canada 2018). All study activities were carried out in the Lower Babine River, downstream of Nilkitkwa Lake, but this section will be, henceforth, segregated into upper river habitat (above the adult enumeration weir) and lower river habitat (below the adult enumeration weir; Figure 2.1).

2.3.3. Velocity Conditions

Babine River water level and discharge have been recorded near continuously at the Water Survey of Canada station about 50 m below the Babine River enumeration weir since 1972. To create a large-scale map of the velocity environment in the Lower Babine River, measurements were taken over 1.5 km downstream of known sockeye spawning grounds in the Lower Babine River. This was done between May and August in 2017 and 2018, to capture the full extent of velocity conditions that emerging and migrating fry may encounter. Spring and summer water levels in 2017 and 2018 were low to average, and thus may represent conditions slightly more amenable to juvenile upstream migration than in average or high discharge years. Point velocity measurements were recorded at 25 m intervals, at 0.5 m, 1 m and 2 m from the river's edge. To obtain the average water speed, velocity was measured at 60% depth from the water's surface when total water depth was less than 1 m, or was averaged between 80% and 20% depth from surface when water depth was greater than 1 m (BCMOE 2009). This standardized method approximates average water velocity from river substrate to water surface. We used this method to approximate broad-scale velocity conditions over a large habitat area, but acknowledge that velocity refugia within the three dimensional riverscape may exist (e.g., eddies, interstitial space). To determine thresholds, published estimates of sockeye salmon fry sustained (0.47 m•s$_{-1}$) and burst swimming speed (0.60 m•s-1; Clarke 1967) were used to categorize areas with velocity near or beyond sockeye fry swimming capabilities.

2.3.4. Fry Movement

Data on fry movement in the Babine River were collected across a range of water discharges. These data were collected with Lake Babine Nation Fisheries between 2015 and 2017 using underwater cameras at points of key interest (e.g., the adult enumeration weir). Fry movement along the west and east banks was captured using a GoPro4 camera, positioned immediately upstream of the adult salmon enumeration weir. The camera was fastened to a wooden frame on the west bank, facing the bank, perpendicular to flow, and positioned about 1.5 m from the bank. Footage from the east bank camera revealed very little sockeye fry usage, and thus this data was not analyzed.

A viewing grid (1 m by 2 m aluminum panel with a 5 cm by 5 cm grid) affixed to the bank was used to observe and track approximate speed and size of fish observed. Video footage was captured in 1-hour segments throughout daylight hours and for the duration of the upstream migration (approximately May 20th – June 30th, 2016). These samples allowed for observation of fry behaviour along the banks, where fry must travel when trying to return upstream. Successful upstream travelling individuals were classified as those facing upstream and travelling upstream. Unsuccessful individuals included (1) fry oriented downstream and travelling downstream, (2) fry oriented upstream but moving downstream, and (3) fry oriented upstream, moving upstream but unsuccessful in travelling to the upstream side of the video frame (i.e., swept backwards, downstream and out of frame).

2.3.5. Relative Abundance

Abundance of sockeye fry in lake and river habitat sites was assessed using beach seines. Seining was conducted at 4 sites in Nilkitkwa Lake and 6 sites in the Lower Babine River in the spring of 2017 to observe fry condition and size. At each site, temperature was also recorded and found to vary by about 1°C or less between sampling sites. The seine net dimensions were 1.2 m in height and 2.4 m in length with a mesh size of 0.32 cm. Seine passes were done parallel to shore, with one end following the water's edge. We used total catch per seine, divided by total distance seined, divided by the length of the seine net, to calculate catch per unit effort (CPUE) in units of fry•m^{-2}. To collect information on drifting individuals, downstream trapping was used to collect abundance, size, and condition data on individuals displaced downstream during the spring of 2016 and 2017. Drifting individuals were captured using 30.5 cm diameter square-shaped nets suspended from the adult enumeration weir, fishing the top foot of the water column, following Clarke (1967). CPUE of drift individuals was calculated from total individuals caught, divided by number of 15 min sets fished, multiplied by 10.76

(conversion to m$_{2}$), to give units of fry•m$_{-2}$•15 min set$_{-1}$. Across the monitoring period, 7115 sockeye fry were sampled to estimate abundance.

2.3.6. Size and Condition

Fork length (±1 mm) and weight (±0.01 g) data for fry from the Lower Babine River and Nilkitkwa Lake was gathered during seine and drift sampling. We calculated Fulton's Condition Factor (CF) with the following:

$$CF = 10^{N} \times \frac{weight}{length^{3}}$$

where an N between 3 and 5 is generally used for salmonids and juvenile fish. when weight is measured in grams and length is measured in millimeters, giving CF values near to 1 (Ricker 1975). Over the sampling period, up to 25 individuals were measured per sampling site, when possible (n = 1876).

Energy density, or the energy (i.e., calories) per gram of body tissue, was assessed using a bomb calorimeter. Some sockeye fry samples did not have enough body tissue mass for the calorimeter to operate within manufacturer guidelines, so energy density was measured of a dried and homogenized pellet made up of all body tissues from two complete fry for all samples. Six fry were drawn at random from a body size sample sets, and were then grouped into three pairs (two smallest, two medium, two largest) based on wet body mass. Energy density was assessed for six individuals from every sampling site within each habitat type, for sampling weeks four, six and eight. A total of 218 fry were analysed, in pairs (n = 109).

2.3.7. Statistical Analyses

All statistical analyses were conducted using the statistical software R, version 3.4.4. (R Development Core Team 2016). We used a generalized linear model to determine the logistic regression curve for upstream travel success at the Babine River enumeration weir as a factor of river discharge. We used a linear mixed model approach to examine how location (lake or river habitat) affected body size and condition of sockeye salmon fry recently emerged from incubation gravels. We used the *nlme* package to implement linear and nonlinear mixed-effect models (Pinheiro *et al*. 2009).

Abundance, size, and condition metrics were modelled as response variables, including relative abundance (CPUE), fork length (FL), weight, CF, and energy density. When necessary, we log-transformed variables to satisfy the assumptions of normality and homogeneity of residual errors. Habitat type (i.e. lake, drift, upper river, and lower river), river discharge, and sampling week (i.e., time) were modelled as fixed covariates. Week and river discharge were highly correlated ($r = 0.8$), so we competed these two covariates instead of including them together in any model. Interaction terms between habitat type and week and habitat type and discharge were tested in all model sets. Size and energy density responses (FL, weight, CF, and energy density) were modeled at the individual fish level, while relative abundance was modeled at the site level. Site was set as a random effect to account for variation among capture sites within habitat types.

Model selection was carried out using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson 2002) using the *model.sel()* function in the *nlme* package (Pinheiro *et al*. 2009). For each response variable, we reported the top model and all candidate models within a threshold of ΔAICc = 2 (Burnham & Anderson 1998; Zuur. 2009).

2.4. Results

2.4.1. Discharge

Throughout the lake outlet reach, for 1.5 km below spawning grounds, numerous locations were observed to have water velocities beyond the swimming ability of sockeye fry (Figure 2.2). Previous observations of this population suggested that sockeye fry have sustained and burst swimming abilities of approximately 0.47 $m \cdot s^{-1}$ and 0.6 $m \cdot s^{-1}$, respectively (Clarke 1967). Sustained swim speed is that which a fish can maintain for more than 20 s, and burst swim speed is typically the max speed an individual can sustain for less than 20 s (Beamish 1978; Kolok 1999). In general, the number of potential velocity challenges increased with increasing river discharge (Table 2.1). For example, in areas where complete sampling of fry was possible (over all discharge levels observed), proportional area beyond sustained swimming speed of sockeye fry more than doubled from 8% to 21% when discharge increased from 62 $m^3 \cdot s^{-1}$ to 188 $m^3 \cdot s^{-1}$. It should also be noted that the estimated proportion of sampled area beyond sustained swim speed at the largest two discharge levels is likely conservative, as the data could not be gathered in river sections where the water velocity was fastest, due to safety concerns. Thus, when river discharge is higher, it would be more challenging for fry to swim upstream.

Table 2.1 Counts (#) and proportions (Prop) of river sections with measured velocity below (<0.47 m•s^{-1}), at (0.47 - 0.60 m•s^{-1}) or above (>0.60 m•s^{-1}) swimming capability of age 0+ sockeye fry (*Oncorhynchus nerka*) at varying levels of discharge in the Babine River, B.C.

Discharge	188 m^{3}•s^{-1}		148 m^{3}•s^{-1}		127 m^{3}•s^{-1}		89 m^{3}•s^{-1}		62 m^{3}•s^{-1}	
Velocity (m•s^{-1})	**#**	**Prop**	**#**	**Prop**	**#**	**Prop**	**#**	**Prop**	**#**	**Prop**
Total[a]	234		276		360		360		360	
<0.47	185	0.79	190	0.81	182	0.78	213	0.91	216	0.92
0.47-0.60	23	0.10	28	0.12	32	0.14	11	0.05	9	0.04
>0.60	26	0.11	16	0.07	20	0.09	10	0.04	9	0.04

[a] Total count of surveyed river sections at given discharge level, summary data included for sites that were monitored at all discharge levels.

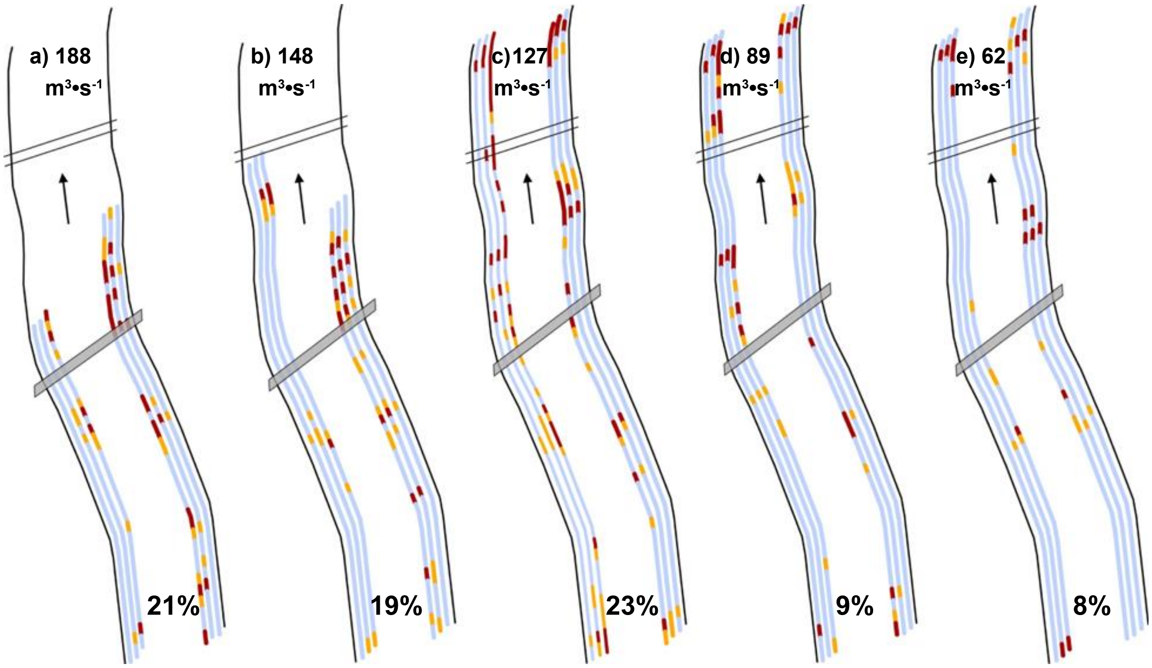

Figure 2.2 Temporal change in local velocities in the Babine River for 1.5 km below known sockeye salmon (*Oncorhynchus nerka*) spawning grounds.

Local velocities are recorded as single point estimates each 25 m in longitudinal river distance at 0.5 m, 1 m and 2 m from shore, on each bank. River discharges are (a) 188, (b) 148, (c) 127, (d) 89 and (e) 62 m$_3$•s$_{-1}$. Light blue represents velocity below sustained swimming capability (0.47 m•s$_{-1}$), orange represents velocity greater than sustained swimming speed but below burst swimming capability (0.60 m•s$_{-1}$) and red represents velocity beyond burst swimming capability. Percent area beyond literature sustained swimming capability of sockeye fry shown at bottom across only those sites which were accessible at all sampling levels. Data was collected between May and August of 2017 and 2018. Arrows indicate the direction of flow. Solid grey bars indicate the location of the adult enumeration weir, and parallel black lines indicate the road bridge

Locations of velocity challenges were relatively consistent, and grew in extent with increasing discharge, with some anomalies likely due to heterogeneous bed structure and dynamic bank location with changing river discharge (e.g., inundation of riparian vegetation). Areas with particularly high velocities that would impede upstream fry movement existed below both the adult enumeration weir and the road bridge, where the shoreline has been armoured. Upstream of the weir, water velocities were generally low enough that sockeye salmon fry would be predicted to be able to swim upstream, especially within 1 m of the bank.

2.4.2. Downstream Displacement

Only 33% of all sockeye fry (n = 134) observed moving along the bank in underwater video were able to successfully travel upstream during the spring of 2016. Although some of these observations may have been repeat attempts by individuals, fry tended to be less likely to successfully travel upstream at higher river discharge. This effect was not found to be statistically significant (z-value = -1.56, p-value = 0.12; Figure 2.3). This could be due, in part, to lack of observations at low discharge, as migration occurred at high river levels during spring freshet.

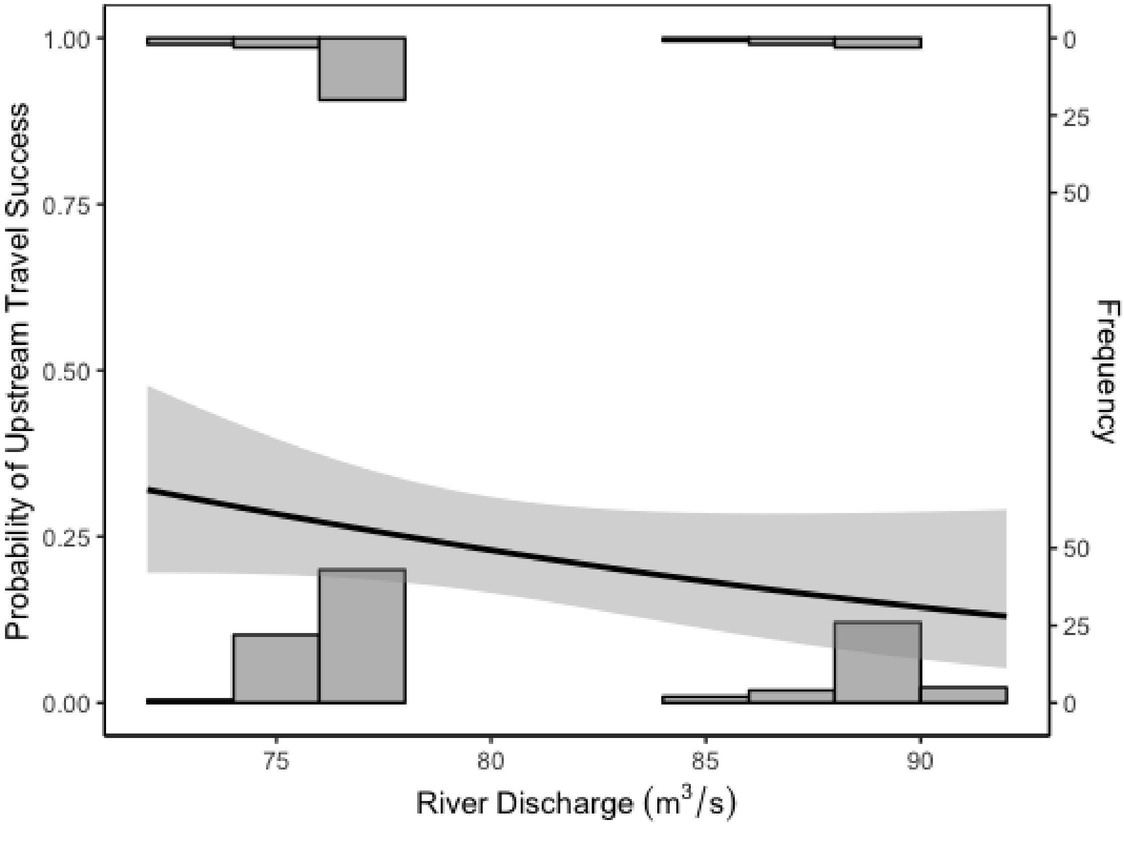

Figure 2.3 Logistic regression for upstream travel success of Lower Babine River age 0+ sockeye salmon (*Oncorhynchus nerka*) fry.
Travel behaviour was observed adjacent to Babine River west bank at the Babine River enumeration weir

2.4.3. Abundance

Spatial and temporal variation in sockeye fry abundance were influenced by habitat conditions and river discharge (Table 2.2). The relative abundance of sockeye fry across all habitat types generally increased in the month of May, and then declined for the remainder of the study, into the first week of August (Figure 2.4). The earliest peak in abundance was observed in upper river habitats (nearest to spawning grounds) around May 24th. Drift, lake, and lower river abundance was greatest three weeks later, around June 14th. A second, much smaller increase in abundance was observed in lake abundance around July 12th. The highest abundance of drift individuals, at almost 850 fry•m^{-2}•hr^{-1}, likely indicated maximum fry emergence, which decreased to zero by the end of the study period, when emergence was likely complete. Relative abundance varied within and between samplings, at some sites decreasing from over 300 fry•m^{-2} at peak migration to zero by the end of the study. Upper river habitat sites had the greatest variability in average abundance, ranging from 5 to 300 fry•m^{-2}, while lake and lower river sites generally averaged between 2 and 100 fry•m^{-2}.

Table 2.2 Akaike's Information Criterion ranking of top models (Δ AICc < 2) describing the effects of habitat type, discharge (Q) and time (Week) on abundance (natural logarithm), FL (Length), total body mass (Weight), Fulton's Condition Factor (CF), and energy density (Energy) of 0+ sockeye fry (Oncorhynchus nerka) in the lake and lake outlet reach.

Response	Covariates	k[a]	Δ AICc[b]	ω[c]
ln(Abundance)	Habitat + Q	3	0.00	0.417
ln(Abundance)	Q	2	0.25	0.368
Length	Habitat + Week + Habitat * Week	4	0.00	1.000
ln(Weight)	Habitat + Week + Habitat * Week	4	0.00	1.000
CF	Habitat + Week + Habitat * Week	4	0.00	1.000
Energy	Habitat + Q + Habitat * Q	4	0.00	0.399
Energy	Habitat + Week + Habitat * Week	4	1.21	0.218
Energy	Habitat + Week	3	1.63	0.176

[a] k = number of parameters; [b] Δ AICc = difference in corrected AIC between model and top model; [c] ω = Akaike weight

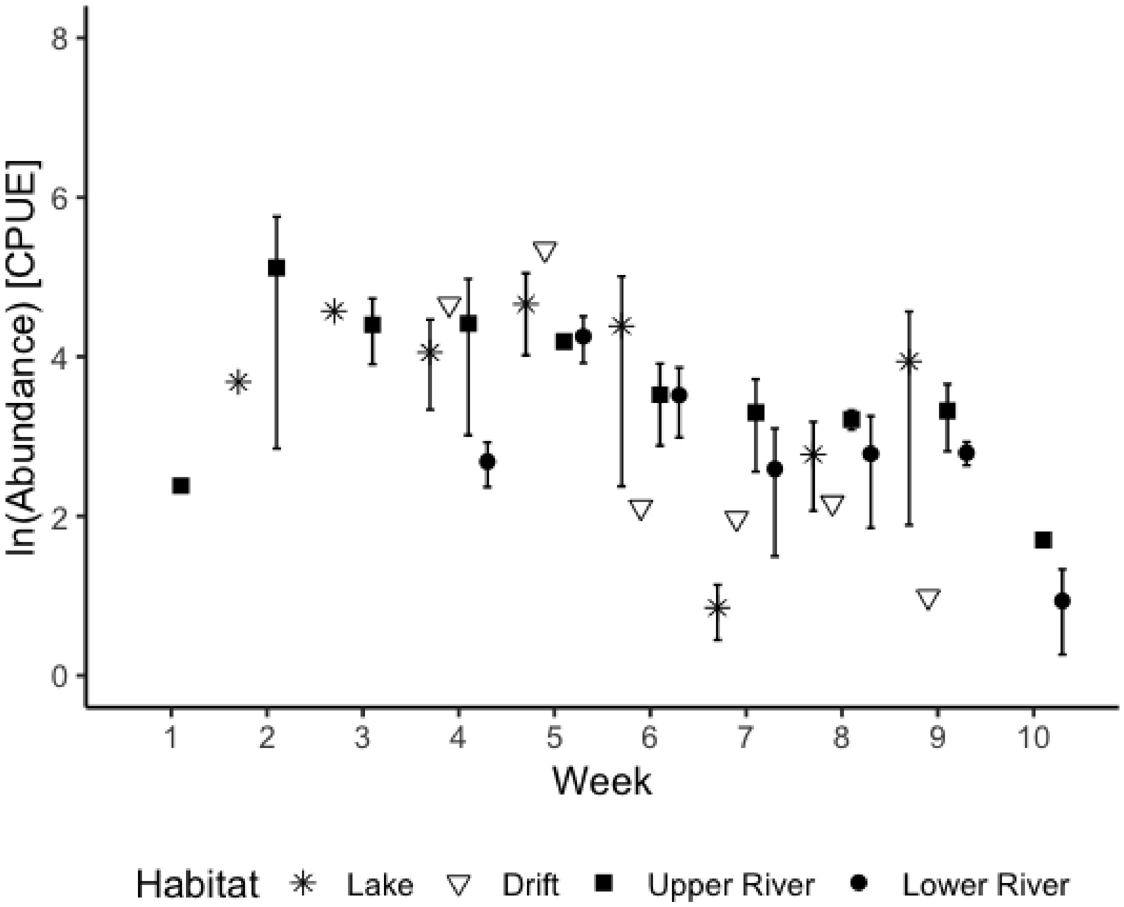

Figure 2.4 Temporal changes in abundance of age 0+ sockeye fry (Oncorhynchus nerka), expressed as catch per unit effort (CPUE), in fry per square meter sampled between May and July 2017 in the Babine River and Nilkitkwa Lake, British Columbia, Canada.

Lake, Upper River, and Lower River habitats were sampled using beach seine nets and represent fry per square meter of lake or river surface area sampled. Drifting individuals were sampled using drift nets and data represent fry• m^{-2}•15 min set^{-1}. Bars denote ± 1 standard error.

The top model common slope term for all habitat types showed a positive relationship between discharge and relative abundance (coefficient = 0.03 ln(CPUE) •m^{-3}•s^{-1}; 95% C.I. 0.02 - 0.04; Table 2.3). In general, this aligns with the gradual decrease in abundance observed throughout the middle and latter half of the sampling period, during which time discharge values were decreasing, as spring freshet declined. By the end of the sampling season, relative abundances of fry had decreased to very low levels.

Table 2.3 **Model parameter estimates from AICc-selected top models (referenced with model number). Standard errors (SE) and statistical significance (P-value) for fixed effects of habitat type (Habitat), week, and discharge (Q) on FL (Length), total wet body weight (Weight), CF, and energy density (Energy) of 0+ sockeye fry (Oncorhynchus nerka) in the lake and lake outlet reach. Intercept values are given in the units of the response variable. Slope value units are given in units of the response variable per week, except as otherwise specified.**

Response variable	Parameter	Intercept			Slope		
		Value	SE	p-value	Value	SE	p-value
ln(Abundance) [CPUE] (Model 3)[a]	Lake	-1.514	0.954	0.117	0.03	0.007	<0.001
	Lower River	-1.717	1.330	0.607			
	Upper River	-0.704	1.373	0.095			
ln(Abundance) [CPUE] (Model 7)[a]		-1.462	0.919	0.116	0.03	0.007	<0.001
Length [mm]	Drift	23.113	1.713	<0.001	1.34	0.225	<0.001
	Lake	22.342	1.844	0.688	2.45	0.236	<0.001
	Lower River	25.885	1.868	0.181	1.24	0.243	0.674
	Upper River	25.845	1.896	0.193	1.59	0.237	0.302
ln(Weight) [g]	Drift	-2.394	0.149	<0.001	0.16	0.020	<0.001
	Lake	-2.275	0.159	0.480	0.23	0.022	0.005
	Lower River	-1.905	0.162	0.019	0.12	0.022	0.043
	Upper River	-2.071	0.163	0.087	0.16	0.022	0.742
CF [g•mm^{-3}]	Drift	0.587	0.064	<0.001	0.04	0.009	<0.001
	Lake	0.664	0.068	0.292	0.03	0.009	0.110
	Lower River	0.834	0.069	0.009	0.01	0.010	<0.001
	Upper River	0.685	0.069	0.198	0.02	0.009	0.003
Energy [cal] (Model 1)[b]	Drift	6915.88	426.092	<0.001	-8.01	2.914	0.007
	Lake	5487.68	510.348	0.028	0.31	3.486	0.019
	Lower River	4838.11	535.545	0.006	3.96	3.652	0.002
	Upper River	5054.69	598.574	0.017	3.36	4.102	0.003
Energy [cal] (Model 2)	Drift	5543.04	192.061	<0.001	36.63	29.412	0.216
	Lake	5595.86	233.391	0.827	-10.60	36.021	0.193
	Lower River	5725.32	234.328	0.462	-52.25	36.300	0.016
	Upper River	5846.92	268.431	0.295	-51.45	41.594	0.037
Energy [cal] (Model 4)	Drift	5900.90	104.87	<0.001	-23.01	12.393	0.066
	Lake	5670.34	191.13	0.032			
	Lower River	5551.51	191.34	0.004			
	Upper River	5676.28	201.90	0.054			

[a] Slope coefficient units CPUE•m^{-3}•s^{-1}; [b] Slope coefficient units calories•m^{-3}•s^{-1}

2.4.4. Fork Length (FL)

The body size of sockeye fry varied temporally and spatially between habitats throughout the lake-outlet reach (Figure 2.5). FL was greatest in the lake habitat at all sampling periods, except during Week 5 when upper river fry were approximately 2 mm longer than lake fry. During the last sampling period, on average, lake fry were 10.55, 6.77, and 10.60 mm longer than drift, upper river, and lower river fry respectively; thus, an average of lake fry were 30% longer than lower river fry. AICc model selection indicated that habitat, week, and an interaction between them were the best predictors of fry FL (Table 2.2). Time (week) had a positive effect on FL in all habitat types, but the fastest FL increase occurred in lake habitat, with a top model slope term of 2.45 mm•week^{-1}(95% C.I. 1.54 - 3.35). This was almost double the rate of length increase observed in the lower river habitat (1.24 mm•week^{-1}; 95% C.I. 0.32 - 2.16).

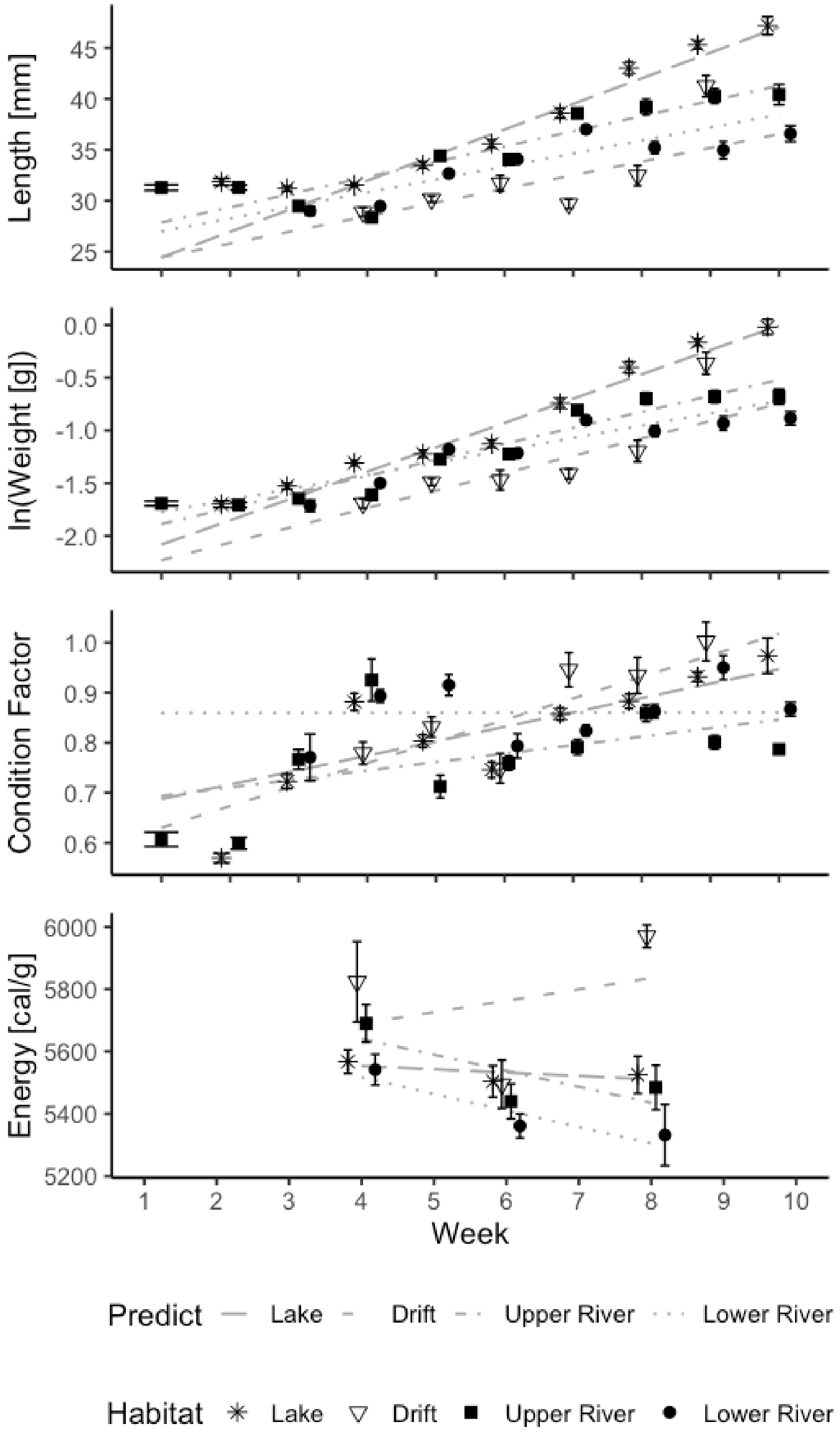

Figure 2.5 Temporal changes in (a) FL, (b) total body weight, (c) CF and (d) energy density of age 0+ sockeye fry (*Oncorhynchus nerka*).

Sampling carried out between May and July 2017 in the Babine River and Nilkitkwa Lake, British Columbia, Canada. The top AICc-selected models are presented and bars denote ± 1 standard error.

2.4.5. Weight

Sockeye fry total wet body weight was influenced by both habitat type and week and the interaction between them (Table 2.2). Weight was greatest in lake habitat throughout the entire sampling period (Figure 2.5). This difference was greatest during the last three weeks of sampling. During the final sampling period, lake fry weighed 510.5 mg and 644.3mg more than upper river and lower river fry, respectively, or more than 90% and 150% heavier than upper river and lower river fry.

Weight was positively affected by time (week) in all habitat types, but the most rapid increase in weight occurred in lake habitat, with a slope coefficient of 118 mg•week$_{-1}$ (95% C.I. 77 - 161). This was more than double the rate of weight increase observed in both upper and lower river habitat, which were only 57 and 42 mg•week$_{-1}$, respectively (95% C.I. 15 - 99 and 0 - 85, respectively).

2.4.6. Fulton’s Condition Factor (CF)

Spatial and temporal variation in CF was explained by both habitat type and week and the interaction between these terms (Table 2.2). CF of fry across different habitat types was more variable than the other size metrics over the sampling period (Figure 2.5). During the second latter of the study, drift individuals often had the highest CF, followed by lake habitat fry.

Time (week) had a positive effect on CF in all habitat types except in lower river habitat (Table 2.2). Drift fry had the highest rate of increase at 0.043 g•mm$_{-3}$•week$_{-}$1 (95% C.I. 0.025 - 0.061). Lake and upper river individuals increased in CF by 0.028 g•mm$_{-3}$•week$_{-1}$ (95% C.I. -0.009 - 0.064) and 0.015 g•mm$_{-3}$•week$_{-1}$ (95% C.I. -0.021 - 0.052). CF of lower river fry increased the slowest, with an almost stagnant rate, at only 0.005 g•mm$_{-3}$•week$_{-1}$(95% C.I. -0.032 - 0.042).

2.4.7. Energy

At the final sampling, drift individuals had the highest energy density at 5907 calories•g$_{-1}$ body weight (Figure 2.5). This is, on average, 9% and 12% greater than upper and lower river individuals, respectively.

We found that habitat, week, discharge, and the interaction between habitat and week, and habitat and discharge were all closely related to energy density of sockeye fry (Table 2.2). In all top models, as time increased and discharge generally decreased, the energy density of upper and lower river individuals decreased. This relationship was strongest (steeper slope values) in lower river habitat. Interestingly, these were the only declining trends found in all metrics sampled, but we acknowledge that this is based on only three sampling time points. In the lake, energy density of sockeye fry was maintained throughout the sampling period (weak, slightly negative slope over time). For drift individuals, as time increased and discharge decreased, energy density increased. Thus, sockeye fry in river habitat were found to be losing body energy, per unit weight, most quickly in comparison to lake and drift sockeye individuals.

2.5. Discussion

Here we described the habitat variability of a lake outlet reach across space and time, and the linked variation in body size and condition of sockeye salmon fry. There were both seasonal and spatial patterns of water velocities across the lake-outlet reach that exceeded the ability of fry to swim upstream to lake rearing habitat. At high river discharge, more velocity barriers were measured and this may have been associated with less upstream movement of fry towards the lake. We found, however, that lake rearing habitat was associated with larger sized sockeye fry, specifically 30% longer and 150% heavier, compared to fry displaced to downstream river habitats. Overall, our results suggest that fry in lake habitats experience superior growth conditions, but displacement to downriver habitats and elevated river discharge may prevent some sockeye fry from accessing these optimal growth conditions.

The hydrological landscape of a lake outlet reach was spatially and temporally dynamic, and may exert control on fry movement (Figure 2.2, Figure 2.3).This study took place during the spring, when sockeye fry emerge from the gravel and when snowmelt leads to high water discharge. As river discharge increased, the number and size of areas of high velocity that exceed swimming capabilities of fry, also increased. There was also some evidence that higher flows were associated with more downstream movement of fry, both from underwater video analyses as well as correlative evidence from fry abundance in the drift. Collectively, these data suggest that temporary barriers exist downstream of the lake outlet, that depend on discharge. The outlet may be bidirectionally connected at lower discharge but may function as a one-way check valve at high freshet flows. Thus, the physical geography of lake outlets may be extremely sensitive to land-use alterations that change patterns of flows across space. For example, observations have suggested that fry use flooded riparian vegetation to hold or begin moving upstream towards lake rearing habitat (McCart 1967; LBNF 2015; LBNF 2016). Anthropogenic channelization or straightening, and bank armouring (e.g., addition of riprap boulders or cement blocks) decreases energy dissipation capacity of the shoreline and likely increases nearshore flows, and blocks access to flooded riparian refugia (Strayer & Findlay 2010), which could further challenge fry upstream migration to lake rearing habitat. For example, the infrastructure associated with the adult enumeration weir and the Forest Service Road bridge across Babine River, namely the removal of riparian vegetation and extensive bank armouring, may serve as one such barrier. These locations could be targeted for habitat restoration to facilitate upstream migration.

Relative abundance and condition of sockeye salmon fry revealed differences among habitat types over the season. The earliest peak in relative abundance was observed in upper river habitats (nearest to spawning grounds) near the end of May with drift, lake, and lower river abundances observed at maximum about weeks later. This suggests that, following emergence, it may take a couple weeks for fry to move upstream to lake rearing habitat, and in the process some individuals may be swept further downstream. Importantly, fry abundances did not persist into the summer in the downstream river habitats—thus, fry are not rearing long term in these habitats. The fate of these individuals is unknown, as they may perish by predation, move further downstream to rear, or migrate upstream to rearing habitat in the lake. Further research, using internal or external identifiable tags (e.g. elastomer dye) is needed to investigate the ultimate fate of individuals in downstream habitat following emergence.

The environmental conditions determining which individuals are transported downstream after emergence remain unclear. Anecdotal observations suggest that early-returning adults in this population choose redd sites nearest the lake and along the river margins, nearest the bank, where water is shallower and slower flowing. Similar preference has been found in other systems, where early arriving females choose nest sites in shallower locations, and later arriving individuals make redds in deeper pools (Adkison *et al*. 2014). This might mean that those returning later to the Babine River, who build redds in the middle of the channel and further downstream, subject their offspring to higher velocity environments upon emergence, and potentially a higher probability of downstream transport. It is also possible the smaller-sized fry are more vulnerable to downstream transport. Indeed, we found that drift individuals were among the smallest sockeye fry observed. This suggests that those transported downstream may be the slower-growing or more recently-emerged individuals.

The lake-outlet reach exhibited spatially and temporally varying habitat conditions for sockeye fry growth. In general, we observed consistent increases in size over the sampling period but, individuals in lake habitats grew 30% longer and 150% heavier than those in lower river habitats. Individuals sampled in the lake also increased in both length and weight at around twice the rate of individuals in the river. These data are evidence for fry growing more rapidly in lake habitat compared with river rearing habitat. River habitat may, however, provide growth opportunities in other sockeye systems. In the Karluk River, Alaska, later river migrants were found to be about 70% longer than earlier migrants to the upstream lake, although no comparison was made to fry that had been rearing in the lake environment during the migration period (McCart 1967). This suggests that juvenile salmon may wait for reduced flows to migrate upstream, or that, in some cases, increased size later in the season may be a function of time, rather than habitat. In contrast, in the Chilko River, British Columbia, upstream migrating fry were nearly the same weight as recently emerged fry, suggesting that even if fry had held in the this river for some time, little growth had occurred (Brannon 1972). Together with our findings, it is evident that sockeye fry face different ecological tradeoffs along spatially and temporally varying lake-outlet reaches. These habitat-specific tradeoffs are likely characterized by habitat quality in the lake and downstream river, hydrologic patterns, and the strength of competitive interactions and density dependence throughout the migration and early rearing life stages. In the Babine River, our data provide evidence that river habitat is suboptimal, suggesting a higher potential survival reward if sockeye fry are able to successfully migrate to the upstream lake.

We acknowledge that fry attributes were measured at the population-level as individuals were not tracked through time, and thus changes in distributions will be driven by both individual processes (e.g., growth) as well as both immigration and emigration. While it is possible that fry displaced downstream could rear in downstream habitats, we sampled all the major off-channel habitats prior to a 17 km canyon section of the Babine River, where no suitable rearing habitat exists. Sampling in river habitats was carried out until few (e.g., 1-5) to zero fry were found at any site within the upper and lower river sections. Previous work downstream in the Skeena River estuary also found that Babine Lake sockeye salmon pass through the estuary quickly, suggesting minimal estuary rearing (Moore *et al*., 2016). Collectively, these lines of evidence suggest that downstream habitats do not sustain sockeye fry populations into the summer nor are comparable growth habitats. Thus, displaced fry likely have poor growth and survival.

One surprising result was that drifting sockeye salmon fry tended to have higher energy density than fry in lake or river habitats. Post hoc analyses revealed no significant relationship between fry length, wet mass nor dry mass and energy density of individuals (R_2 values from simple linear regression equal to 0.009, <0.001, and 0.018). It is possible that the drifters were those that had emerged most recently and thus had not fully incorporated their energy-rich yolk. Indeed, previous work has found that fry with larger yolks have higher mass-specific energy (Skoglund *et al*. 2011) and that the total energy of developing juveniles decreases over time, as the cost of growth is estimated at 35-45% of the energy content of new tissue formed (Skoglund *et al*. 2011; Brown and Srivastava 1991; Heinimaa & Heinimaa 2004; Jobling 1985; Jorgensen 1988). Thus, we suggest that the observed pattern of high energy density among drifting fry may be attributed to residual yolk associated with recent emergence, rather than energy accumulated post-emergence.

One of the key remaining questions is whether this variable hydrologic exposure and downstream movement of fry are relevant at the population level. Previous extrapolations from fry drift data in this study system suggested that massive numbers of fry are transported downstream of the weir with estimates ranging from 18% (7.5 million fry from the 1965 brood; Clarke & Smith 1972) to 67% (2.5 million fry from the 2015 brood; LBNF 2016) of total fry production in the lower Babine River (Table 2.4). While uncertain, these estimates represent a potentially substantial loss for this population, particularly relevant given the conservation concern for Babine River sockeye (Cox-Rogers & Spilsted 2012). The Lower Babine River population has decreased by approximately 85% since the 1950s, with two counts of less than 2000 spawners in the last ten years (DFO 2018). The functionality of the lake outlet and hydrological processes related to the timing of emergence and quality of rearing habitat may be contributing to basin-wide decreases and listed status of this at-risk population.

Table 2.4 Hydrologic conditions and estimated number of age 0+ sockeye fry (*Oncorhynchus nerka*) transported downstream in springs of 1966 and 2016.

Brood year	Peak discharge date	Total spawners	Potential fry production (thousands)	Peak downstream displacement date	Total fry displaced downstream	Proportion of brood displaced downstream
1965	Jun-17	176 000	40 656[a]	Jun-07	7 500 000	0.18
2015	May-17	15 644	3 614[a]– 3 989[b]	May-25	2 456 142	0.62[b]-0.68[a]

[a] Assuming 55% female, 2800 egg, 15% egg to fry survival (Clarke & Smith 1972); [b] Assuming 57% female, 2800 egg (LBNF 2016), 16% egg to fry survival (West & Mason 1987)

Given the potential linkage between hydrology and habitat connectivity, it is worth considering how hydrology may be shifting in this system over time. Hydrograph records from the Babine River reveal changing discharge patterns in the watershed, likely due to climate variability and land use change (Figure 2.6). Peak discharge date is shifting earlier since monitoring began in the early 1970s (Figure A.1). This earlier shift is towards the timing of present-day fry emergence. It is unknown whether the timing of fry emergence is changing due to changes in spawning phenology (Figure A.2) or incubation temperatures. In addition, large magnitude spring freshet events have increased in frequency; specifically, peak annual discharge events above $200 m^{3} \bullet s^{-1}$ occurred only twice during the first half of the monitoring record but have occurred 7 times in the latter half. Thus, ongoing hydrologic change may increase challenges to sockeye salmon fry in the lake-outlet reach of Babine River. These shifts in hydrology are likely driven by a combination of climate change and land-use activities. Mean annual temperatures and precipitation in the Babine watershed have increased by 0.8°C and 5.2%, respectively, over the past century (Foord 2016). Projections for the Babine watershed for 2055 (the Nadina sub-region within the Skeena Resource Region) estimate a further 3.2°C increase in mean annual temperature, a 5.1% increase in mean annual precipitation, along with an 8.2% increase in spring precipitation (Foord 2016). Concurrently, industrial activities such as associated with timber harvest and transportation infrastructure, have been expanding in the watershed, which has been shown to decrease river discharge but also increase peak flow in snowmelt-dominated watersheds (Neary 2017). In the Babine watershed, the percentage impacted area from anthropogenic land-use including transportation infrastructure, forestry, mining, and energy development is 22.8%, exceeding the high-risk threshold put forth by the Pacific Salmon Foundation's Sockeye Habitat Assessment Project (Pfalz 2017). Thus, hydrologic variability, as controlled by climate and land use change, may pose risks to the functionality of lake outlets, and specifically lake-outlet spawning sockeye populations.

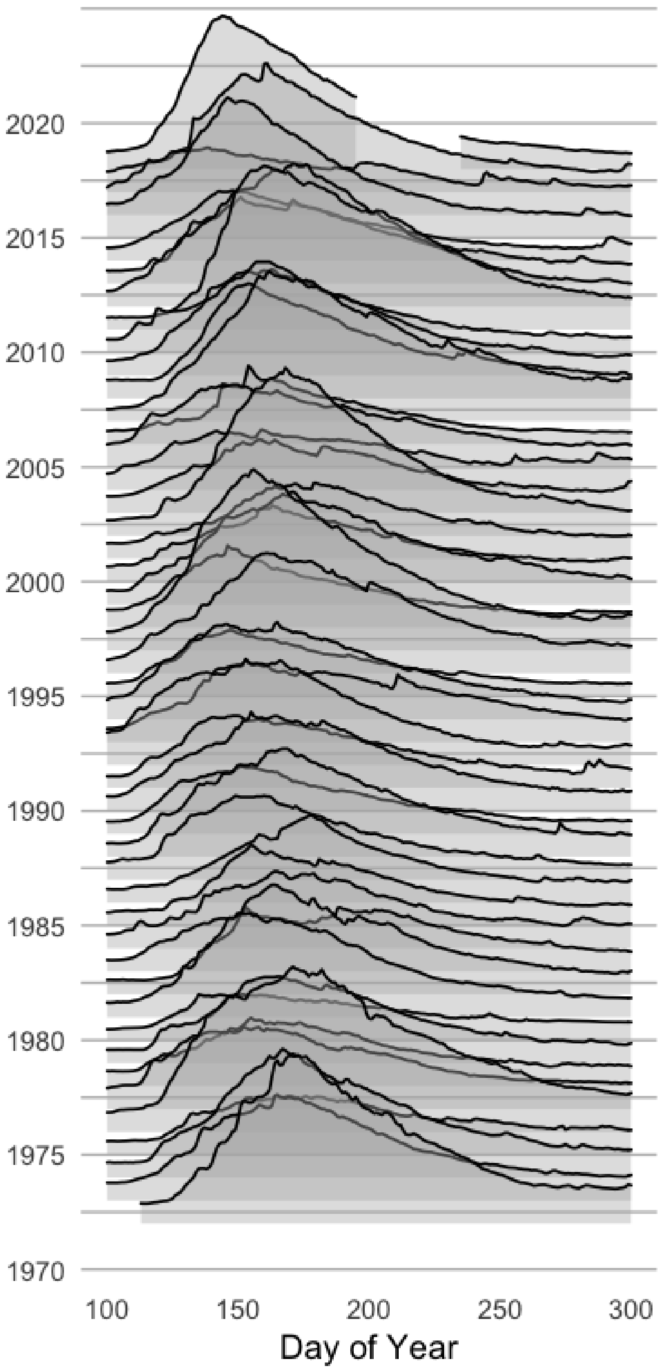

Figure 2.6 Historical daily average discharge in the Lower Babine River at the outlet of Nilkitkwa Lake, British Columbia, Canada, from 1972-2018. Data collected at the Water survey of Canada station located approximately 50 m downstream of the adult enumeration weir. Observed period of fry emergence and migration generally between May 15th and August 1st (135-213 DOY). Gap in 2018 data due to inoperability of monitoring station during wildfires.

Species with complex life cycles rely on different habitat types at different life stages. Ontogenetic habitat shifts enable species to thrive in complex habitat mosaics. While our study focused on a single lake-outlet system and the implications of its configuration and conditions, it raises the broader challenge of understanding arrangement and connectivity in habitat complexes. We highlight that habitats may shift from bidirectional corridor to one-way check-valve; these systems may be particularly sensitive to anthropogenic perturbations and climatic change. Indeed, within complex landscapes and life cycles, the conditions and configuration of a specific location could have population-level effects. For example, key stopover habitats used by long-distance migratory birds have been shown to act as nutritional, energetic and disease-risk bottlenecks, with influence on body condition and population dynamics (e.g. survival and reproduction; Buehler & Piersma 2008). At the intersection of landscape ecology and fish biology, understanding the dynamics of such key habitats is increasingly important in an era of global change.

Chapter 3. Direct and indirect drivers of shifting sockeye salmon (*Oncorhynchus nerka*) fecundity in British Columbia, Canada, over 7 decades[1]

3.1. Abstract

Large-scale shifts in the productivity of exploited fish populations can be a product of both their abundance and demographic traits. Understanding the relationships between factors contributing to productivity is further complicated by the fact that multiple stressors may influence multiple linked life-history traits, such as size and reproductive success. Pacific salmon are undergoing large-scale shifts in productivity and there has been much examination of variability in some life history traits (e.g., size and age at maturity). There is need, however, for analyses that simultaneously examine how changes in multiple stressors contribute to changes in multiple linked life-history traits that control the fecundity of Pacific salmon. We used a multi-level mixed effects model in a Bayesian framework to evaluate pathways through which environmental conditions could be associated with variation in life-history traits and ultimately impact fecundity of sockeye salmon across nearly 7 decades, 33 populations, 386 site-years, and over 17 000 individuals. We found that increased competition increased age at maturity. High chum salmon biomass in the North Pacific led to an 8% increase in the proportion of ocean-age-3 sockeye, in comparison low chum biomass years. These older individuals (ocean-age-3 sockeye) were, on average, 5.2 cm longer. Favourable ocean conditions increased mean length by a further 3.1 cm, in comparison to poor ocean conditions. Increased size was associated with increased fecundity. Large sockeye averaged 3977 eggs while small fish had a mean of 2104 eggs, and fish from spawning channel populations had 57-118 more eggs on average. Collectively, the linked sub-models incorporating multiple direct and indirect stressors explain variation in sockeye salmon fecundities. Additional sub-models for other life-stages (e.g., egg-smolt survival; marine survival) could be integrated in a nested Bayesian framework to consider the cumulative effects of multiple stressors across the sockeye salmon life-cycle.

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[1] A version of Chapter 3 is in preparation for journal submission, with coauthors Eduardo G. Martins, Kyle L. Wilson, Michael Power, David Patterson, Michael Bradford, Tracey Cone, and Jonathan W. Moore

3.2. Introduction

Large-scale shifts in the productivity of exploited fish populations can be a product of both their abundance and demographic traits. For example, fishing removes individuals from populations, which directly influences abundance (Lewin *et al*. 2006; Jorgensen *et al*. 2007; Kuparinen & Merila 2007), but the scale of impact on productivity may depend on additional demographic factors such as population age structure and age and size at maturity (Andersen *et al*. 2019). If harvest is size-selective, it may remove the largest and most fecund females (Coltman *et al*. 2003; Carlson *et al*. 2007; Kendall & Quinn 2012). The relationships between factors contributing to productivity are further complicated by the fact that multiple stressors may influence multiple linked life history traits. For example, reproductive output in fish is often controlled by body size (Beacham & Murray 1992), which may be controlled by various environmental factors (Ruggerone *et al*. 2015). Thus, there is a need to consider how shifting demography is influenced by multiple pathways of impact across exploited fishes with complex life cycles. Understanding how multiple stressors influence linked life-history traits is of particular importance given increasing evidence that exploited fish populations, such as in Pacific salmon, Pacific herring, and Atlantic cod (Vert-pre *et al*. 2013), exhibit major shifts in productivity with important implications for fishery economies and sustainability (Polovina 2005).

Pacific salmon is one group of exploited fishes undergoing large-scale shifts in productivity (Malick *et al.* 2015; Malick *et al*. 2017; Dorner *et al.* 2018). Salmon productivity, often measured as the number of offspring who survive to reproduce, relative to the number of parents, is influenced by a suite of size- and age-dependent life-history traits related to survival, abundance, and fecundity. There is increasing evidence that a variety of oceanic stressors may influence salmon productivity, including ocean climate conditions such as the multivariate El- Niño Southern Oscillation Index (MEI) and North Pacific Gyre Oscillation (NPGO), variability in oceanic prey resources, inter- and intra-specific competition, and other factors (e.g. Ruggerone & Connors 2015; Malick *et al*. 2017; Dorner *et al.* 2018). There is also increasing evidence that many of these stressors can influence important demographic life-history traits such as number of years spent in the ocean prior to returning to spawn (i.e. ocean age; e.g. Peterman 1982; Healey *et al*. 2000; Holt & Peterman 2004; Ruggerone & Connors 2015), body sizes, and somatic growth rates (Jeffrey *et al.* 2017). Slower somatic growth can lead to prolonged marine residence and delayed return to freshwater (Morita *et al*. 2005). For example, competition from pink and chum salmon is associated with older ocean ages and smaller size-at-age (Ohlberger *et al.* 2018). In addition, size of returning sockeye salmon has been variable, but stable on average, and is associated with North Pacific chum salmon biomass, the NPGO and the MEI (Jeffrey *et al*. 2017). While there have been many studies that have examined multiple response variables (e.g., size and age of returning fish), there is an opportunity and need for integrated analyses that simultaneously examine how changes in multiple ocean stressors contribute to changes in the multiple linked life-history traits that control the fecundity of Pacific salmon.

The fecundity (number of eggs) of Pacific salmon sets the limit of an individuals' reproductive output and can vary within and across species (Quinn 2018). For example, female sockeye salmon (*O. nerka*) may produce between 1500 to 6500 eggs. Pacific salmon invest in relatively few, large eggs (a few 1000s) relative to other species of freshwater fishes of similar body sizes (Quinn 2018). Given that an individual only has a certain amount of energy to invest in eggs, there is a trade-off between egg number and egg size (Bilton & Jenkinson 1966; Bilton & Smith 1973; Beacham 1982; Healey and Heard 1984; Beacham & Murray 1990; Quinn *et al*. 2004; Beacham 2010). Life-history theory suggests that there is natural selection towards optimal egg size in a given environment, and that fecundity is then determined by the total energy budget available for reproductive effort (Smith & Fretwell 1974; Sargent *et al*. 1987). In general, larger females produce more eggs. However, associations between fecundity and other factors, such as latitude of origin and length of spawning migration have been identified, but the magnitude and direction of relationships have been variable across spatial and temporal extent (e.g. Fleming & Gross 1990; Beacham & Murray 1992). To our knowledge, there have not been large-scale analyses of variation in salmon fecundity over time.

Salmon enhancement activities could also shift patterns of fecundity (Fleming & Gross 1990; Beacham & Murray 1993; Heath *et al*. 2003; Beacham 2011). In salmon hatcheries, selection pressures for egg size and number are shifted, leading to potential for rapid evolution. This rapid evolution could be a result of manipulated gravel size (lifting upper limit on egg size; Van den Berghe & Gross 1989), oxygenation during incubation (Beacham & Murray 1993; challenged by Einum *et al*. 2002), or intraspecific competition (weakening the lower limit on optimal egg size due to higher survival of smaller or weaker individuals; Heath *et al*. 2003). Hatchery populations can evolve rapidly to have smaller egg size and larger egg numbers (Health *et al*. 2003). While hatcheries may shift salmon egg size and number, another prevalent enhancement activity, spawning channels, could also shift salmon fecundity over time. Spawning channels are engineered optimal stream spawning habitat, where fish are allowed to spawn naturally, but environmental conditions are artificially maintained around optimal levels (i.e. density of spawning fish, water flow, gravel size, distribution and aeration). Based on this, spawning channel habitats may relax size-dependent natural selection pressure, leading to higher survival rates of smaller individuals and the evolution of smaller egg sizes and higher fecundities (Heath *et al.* 2003).

Here we examined effects of multiple oceanic drivers across life-history traits linked to fecundity of sockeye salmon over the last seven decades in western Canada. Sockeye salmon have exhibited major decreases in productivity over the last four decades in Canada, leading to reduced catches, fishery closures, and in some cases, conservation concerns (Grant *et al.* 2011; Rand *et al.* 2012; Irvine *et al*. 2013; Price *et al.* 2017; Walters *et al*. 2019). Sockeye salmon support substantial commercial, recreational and traditional fisheries, constituting the most valuable commercial catch in the Fraser watershed (Irvine *et al.* 2013) and the most widely consumed traditional food by B.C. coastal First Nations (Marushka *et al*. 2019). We used Bayesian multi-level models to simultaneously consider both direct and indirect pathways through which environmental conditions, namely biomass of Pacific salmon, ocean climatic indices, and enhanced habitats, may shape sockeye salmon ocean age, size, and ultimately, fecundity.
Methods

3.3. Methods

3.3.1. Overview

We used a multi-level mixed effects regression model (MLM) to analyse direct and indirect pathways by which environmental conditions could be associated with variation in life-history traits, and ultimately shift fecundity of mature female sockeye salmon. MLMs can fit complex statistical phenomena occurring at different levels within a dataset, including constant and varying effects (sometimes referred to as fixed and random variables; Gelman 2005; Gelman & Hill 2007), generalize effects across groups within the dataset (e.g. populations; Gelman *et al.* 2013), deal with unequal sample sizes or predictors with different levels of variation (Gelman *et al.* 2013), and handle complex dependency structures in the data (Janssen 2012; McElreath 2016). MLMs link simple regressions, where independent parameters from a sub-model can be fit simultaneously as outcomes in another sub-model (Gelman & Hill 2007; Gelman 2006).

We used known dominant drivers of various life-history traits to inform the structure of each sub-model. The first sub-model, for ocean age, was informed by the biomass of chum salmon in the North Pacific Ocean, in the second year of ocean residence. The second sub-model, for standard length, included predictor variables for ocean age, MEI, NPGO and chum biomass in the year of return to freshwater. The final sub-model, for fecundity, was informed by the standard length of each individual, and whether or not that individual was experiencing enhancement conditions (i.e. spawning channel populations). The relative effect sizes of the environmental and life history trait variables were evaluated using Bayesian framework to ultimately explore the complexity of shifting fecundity in sockeye salmon.

3.3.2. Data sources

Body size, age and fecundity data were collected by the federal Department of Fisheries and Oceans (DFO) Canada monitoring programs of both wild and enhanced populations throughout B.C. (Table 3.1, Figure 3.1). Fraser River data was compiled from archival records of the Sockeye and Pink Analytical Program at DFO. This data was collected by the International Pacific Salmon Commission until 1986, under the mandate of monitoring Fraser River sockeye productivity across all life stages. DFO then took over this responsibility and has continued the collection and management of the time-series data. Data was collected primarily for populations large enough to warrant mark-recapture population estimates, and where juvenile (fry or smolt) monitoring programs are carried out. In some cases, body size, age, and fecundity data were collected in smaller or more remote populations when sacrificial sampling was being carried out in conjunction with other projects. A random sample of 50 unspawned females, with skeins fully intact, was sampled from each site for each year sampling was carried out. Of these 50 fish, a complete count of all eggs was done for 1 of every 5 fish, and a gravimetric sub-sampling procedure was used for the remaining 80%. This was done by separating 25-35% of the total sample and using the sub-sample egg count, sub-sample weight and total sample weight to estimate the total egg count.

Table 3.1 Sockeye salmon (*Oncorhynchus nerka*) study populations in British Columbia, Canada in the Fraser and Skeena watersheds.

Population	Conservation Unit	Watershed	Enhancement
Middle	Takla-Trembleur-Stuart	Fraser	Wild
Fofar	Takla-Trembleur-Stuart	Fraser	Wild
Tachie	Takla-Trembleur-Stuart	Fraser	Wild
Gluske	Takla-Trembleur-Stuart	Fraser	Wild
O'Ne-ell	Takla-Trembleur-Stuart	Fraser	Wild
Driftwood	Takla-Trembleur-Stuart	Fraser	Wild
Van Decar	Takla-Trembleur-Stuart	Fraser	Wild
Dust	Takla-Trembleur-Stuart	Fraser	Wild
Sidney	Takla-Trembleur-Stuart	Fraser	Wild
Bivouac	Takla-Trembleur-Stuart	Fraser	Wild
Paula	Takla-Trembleur-Stuart	Fraser	Wild
Lower Adams	Shuswap	Fraser	Wild
Seymour	Shuswap	Fraser	Wild
Scotch	Shuswap	Fraser	Wild
Eagle	Shuswap	Fraser	Wild
Lower Shuswap	Shuswap Complex	Fraser	Wild
Horsefly	Quesnel	Fraser	Wild
Mitchell	Quesnel	Fraser	Wild
McKinley	Quesnel	Fraser	Wild
Stellako	Francois-Fraser	Fraser	Wild
Chilko	Chilko	Fraser	Wild
Upper Barriere	North Barriere	Fraser	Wild
Birkenhead	Lillooet-Harrison	Fraser	Wild
Raft	Kamloops	Fraser	Wild
Upper Pitt Channel	Pitt	Fraser	Enhanced
Harrison	Harrison Downstream	Fraser	Wild
Weaver	Harrrison Upstream	Fraser	Wild
Weaver	Harrison Upstream	Fraser	Enhanced
Gates	Anderson-Seaton	Fraser	Wild
Gates	Anderson-Seaton	Fraser	Enhanced
Nadina	Nadina-Francois	Fraser	Enhanced
Pinkut	Babine	Skeena	Enhanced
Fulton	Babine	Skeena	Enhanced

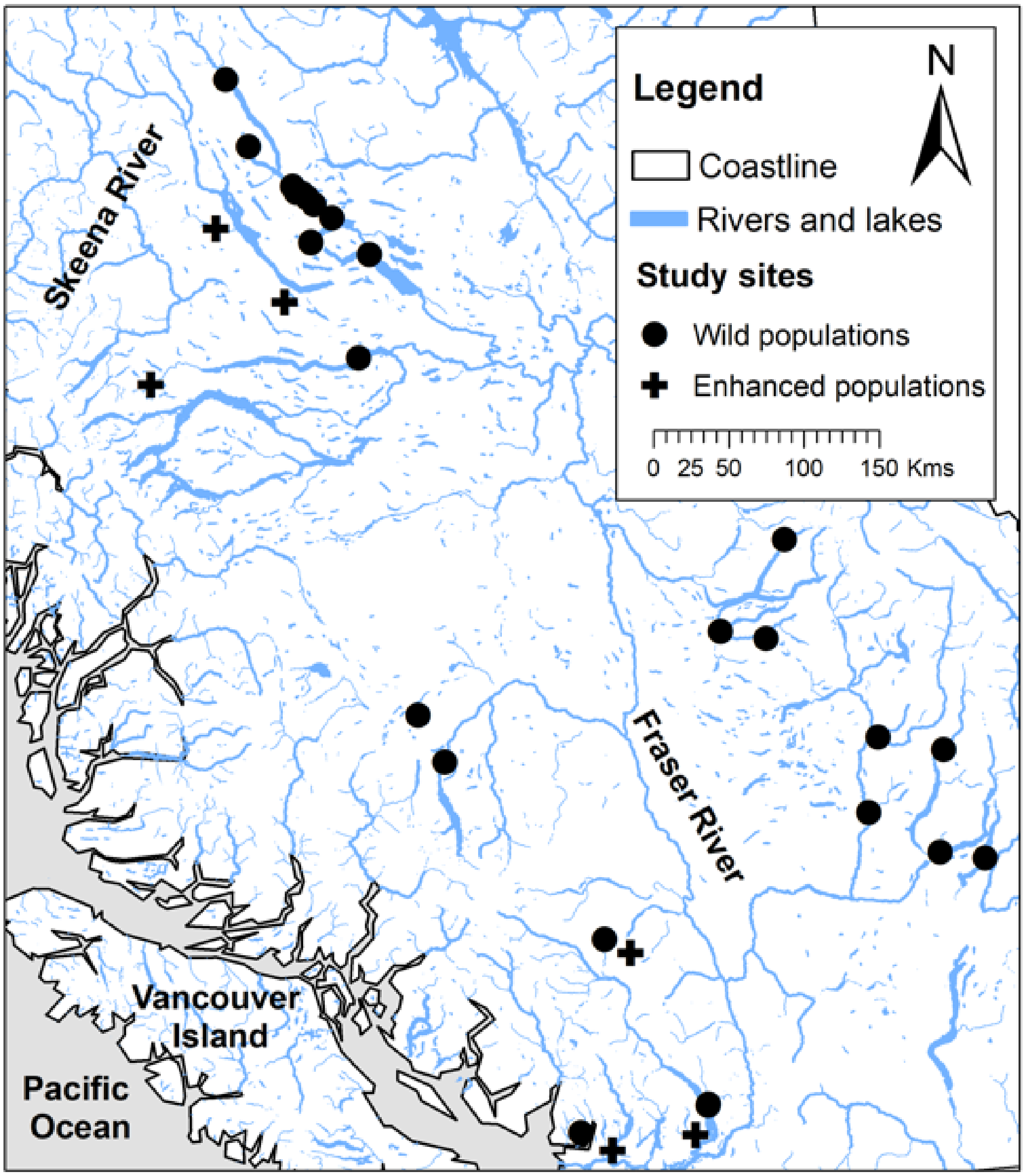

Figure 3.1 Map of sockeye salmon (*Oncorhynchus nerka*) study populations in British Columbia, Canada in the Fraser and Skeena watersheds.

Skeena River data was collated by facility managers at the DFO Pinkut Creek and Fulton River Spawning Channel facilities. At spawning channel facilities, a random sample of 50 unspawned females was also collected each year when sampling was carried out, but all fecundities were enumerated by complete egg counts. This methodology is consistent for both Fraser and Skeena spawning channel enhanced populations.

Populations (sites) were considered enhanced 4 years after the construction of enhancement channels (i.e. the first year that a 4-year-old mature female could return after hatching under spawning channel enhancement conditions) and 5 years after an enhancement facility stopped operating (i.e. the last year that a 5-year-old mature female could return from a brood year that experienced enhancement conditions).

Body size, age and fecundity data were collected from 33 distinct spawning populations (sites) over 66 years (1952-2017). Overall, we modelled 386 unique site-year combinations across the ocean age, standard length and fecundity sub-models. The number of individuals per site-year ranged from 1 to 100 (mean = 43, S.D. = 20) with a total of 17 371 individuals sampled. Biological data were collected at enhancement facilities and on or near spawning grounds of wild populations on mature pre-spawn females. Fecundity data were not included for partially spawned individuals, where fecundity count was less than 1000 eggs.

Oceanographic indices provide continuous ocean condition metrics (e.g. sea surface temperature, ocean circulation variability), which can be used to characterize conditions experienced by salmon while in the ocean. Two dominant climatic indices that have been found to have strong impacts on sockeye salmon in the North Pacific are the NPGO and the MEI (Jeffery *et al.* 2017). The MEI is calculated using six environmental variables, including sea surface temperature, surface air temperature, sea level pressure, zonal and meridional surface winds, and cloud cover (Wolter & Timlin 1998). The MEI represents ENSO strength, characterized by warmer conditions, and a decrease in both primary productivity and chlorophyll biomass (Behrenfeld *et al.* 2006). The MEI has been shown to correlate with salmon body size and is also more comprehensive than other ENSO indices (e.g. the Southern Oscillation Index, Oceanic Niño Index; Wolter & Timlin 1998). We used annual mean values of the MEI, lagged by one year, to account for the lag in propagation of the ENSO signal into oceanic regions encountered by our study populations (Litzow *et al.* 2014). MEI values were retrieved from the publicly available online database managed by the National Oceanic and Atmospheric Administration (www.esrl.noaa.gov/psd/enso/mei/).

The NPGO measures the variation in Northeast Pacific Ocean circulation. Positive values indicate strengthening of subpolar and subtropical gyres, with variability introduced by horizontal flow of seawater and upwelling driven by ocean surface winds.

The NPGO correlates positively with increased salinity, nutrients, and chlorophyll biomass (Di Lorenzo *et al.* 2008). The NPGO has been shown to be correlated with salmon abundance (Kilduff *et al.* 2015), variation in survival of juvenile salmon (Miller *et al.* 2014), and salmon body size (Jeffrey *et al.* 2017). It is available online (www.o3d.org/npgo). Salmon body size has been shown to be closely linked to winter oceanic index values as wintertime conditions have been linked to physical changes in the North Pacific Ocean (Mantua *et al.* 1997; Yeh *et al.* 2011). Thus, we followed NPGO Index convention of averaging only November to March Index values and assigning the average to the year of a fish's return including March (Litzow *et al.* 2014).

North Pacific salmon abundance and biomass values for mature salmon only were calculated by Ruggerone &Irvine (2018), using run size data (i.e., catch + escapement) estimates (Ruggerone & Irvine 2015) and individual fish masses (from http://www.npafc.org/new/scence_statistics.html). To calculate biomass of young salmon, species-specific ratios from Eggers (2009) were used by Ruggerone and Irvine (2018). In our analyses, total biomass of young and mature chum salmon (*Oncorhynchus keta*) were used, due to findings by Jeffrey *et al.* (2017) that this metric was most powerful in predicting sockeye body size, presumably due to competition in the ocean. Biomass of chum in the year of return to freshwater was used to predict body size at maturity (Jeffrey *et al.* 2017). Biomass in the second year of ocean residence was used as a predictor variable for ocean age, as density dependent effects on delayed maturation may be more influential than other oceanic condition indices (Healy *et al.* 2000; Holt & Peterman 2004; Cox & Hinch 1997). The fixed effect of chum biomass on ocean age was modeled only for fish that had scale age data, due to limitation of the JAGS software model. For all fish that did not have scale age data, only the site effect was used.

3.3.3. Multi-level model: Ocean Age Sub-Model

Our Bayesian MLM was composed of three sub-models: (1) ocean age, (2) standard length, and (3) fecundity. The number of years O a female i resided in the ocean before returning to freshwater in year t was modeled as

$$O_i \sim \mathrm{Bernoulli}(p_i)$$

where p_i is the probability that female i returning to freshwater in year t spent three years residing in the ocean, and was modeled as a generalized linear model with a logit link such that:

$$\text{logit}(p_i) = \alpha_o + \beta_{o,chum} \cdot x_{o,t,chum} + \gamma_{o,s}$$

$$\gamma_{o,s} \sim \text{Normal}(0, \sigma_o^2)$$

where α_o is the intercept, $\beta_{o,chum}$ is the slope for the effect of biomass of immature and mature North Pacific chum salmon (Jeffrey *et al.* 2017), $x_{o,t,chum}$ is the biomass of chum, estimated as the biomass caught in commercial fisheries in the second year of ocean residence (Holt & Peterman 2004; Healey *et al.* 2000; Cox & Hinch 1997; Jeffery *et al*. 2016; Ruggerone & Irvine 2018). γ_s is the site effect, which is assumed to be normally distributed with mean zero and variance σ_o^2. The effect of chum biomass on ocean age was only modelled for fish with scale age data, whereas site effects were allowed for the prediction of ocean age for all fish (including those with missing scale age data).

3.3.4. Multi-level model: Standard Length Sub-Model

The standard length L_i of a female i in year t was modeled as

$$L_i \sim \text{Normal}(\mu_i, \sigma_l)$$

where μ_i is the expected standard length of a female i in year t and was modeled as a linear model such that:

$$\mu_i = \alpha_l + \boldsymbol{\beta}_\mathbf{l}\mathbf{X}_\mathbf{l} + \gamma_{l,s} + \gamma_{l,t}$$

$$\gamma_{l,s} \sim \text{Normal}\left(0, \sigma_{l,s}^2\right) \text{ and } \gamma_{l,t} \sim \text{Normal}\left(0, \sigma_{l,t}^2\right)$$

where α_l is the intercept, $\mathbf{X}_\mathbf{l}$ is a matrix of environmental covariates, $\boldsymbol{\beta}_\mathbf{l}$ is a vector of effect sizes for those covariates, and $\gamma_{l,s}$ and $\gamma_{l,t}$ are the random effects of site and year, which are assumed to be normally distributed with mean zero and variance $\sigma_{l,s}^2$ and $\sigma_{l,t}^2$, respectively. The matrix $\mathbf{X}_\mathbf{l}$ included variables to test our hypotheses that standard length was associated with various environmental drivers including: (i) ocean age, a binary indicator variable representing ocean age of 2 (0) or 3 (1), (ii) Multivariate ENSO

Index (MEI, https://www.esrl.noaa.gov/psd/enso/mei/) in the year prior to the return to freshwater (Jeffery *et al.* 2016), (iii) the North Pacific Gyre Oscillation (NPGO, http://www.o3d.org/npgo/) during the winter months (November to March) prior to the return to freshwater (Jeffery *et al.* 2017), and (iv) biomass of immature and mature North Pacific chum salmon (Jeffrey *et al.* 2017) caught in commercial fisheries in the year of return to freshwater (Jeffery *et al*. 2017; Ruggerone & Irvine 2018).

3.3.5. Multi-level model: Fecundity Sub-Model

The fecundity F, of female i in year t was modeled as:

$$F_i \sim \mathrm{NegBin}\left(r_f, p_{f,i}\right)$$

where r_f is the size parameter (i.e., overdispersion in egg counts relative to a Poisson process) and $p_{f,i}$ is the success probability parameter for a negative binomial distribution. The parameter $p_{f,i}$ was thus:

$$p_{f,i} = \frac{r_f}{r_f + \mu_{f,i}}$$

where $\mu_{f,i}$ is the expected fecundity of female i in year t. We modelled expected fecundity as a generalized linear model with a log link function such that:

$$log\left(\mu_{f,i}\right) = \alpha_f + \beta_{f,l} \cdot L_i + \beta_{f,e} \cdot x_{f,i,e} + \gamma_{f,s} + \gamma_{f,t}$$

$$\gamma_{f,s} \sim \mathrm{Normal}\left(0, \sigma_{f,s}^2\right) \text{ and } \gamma_{f,t} \sim \mathrm{Normal}\left(0, \sigma_{f,t}^2\right)$$

where α_f is the intercept (i.e., log of the average fecundity), $\beta_{f,l}$ is effect of standard length L_i of female i in year t, $\beta_{f,e}$ is the effect of enhancement, $x_{f,i,e}$ is the enhancement term (0 or 1), and $\gamma_{f,s}$ and $\gamma_{f,t}$ are the site and year effects, which are assumed to be normally distributed with mean zero and variance $\sigma_{f,s}^2$ and $\sigma_{f,t}^2$, respectively.

3.3.6. Model fitting, diagnostics, and parameterization

We fitted our Bayesian MLM model using JAGS Markov-Chain Monte Carlo (MCMC) samplers in R via jagsUI (Plummer 2003; R Core Team 2017; Kellner 2018). Our approach allowed for parameter effect sizes and credibility intervals to be estimated for all parameters in each sub-model. The jagsUI package uses MCMC simulation to iteratively sample from a set of conditional distributions (priors) to produce posterior estimates (posteriors) of the parameters of interest (Table 3.2). We used 3 chains saving 1,000 samples each (thinning every 20 iterations), burning in 80,000 (with an adaptation phase of 10,000) for a total chain length of 100,000 iterations. Posterior convergence was assessed in several complementary ways: (1) visual inspection of MCMC chain traceplots, (2) a Gelman-Rubin diagnostic test on each parameter, with potential scale reduction factors (PSRF) <1.1 indicating convergence to a common posterior distribution and (3) graphical checks of each sub-model's posterior predictive distribution and bias using standardized residuals comparing predicted to observed life-history trait values (i.e., ocean age, standard length, and fecundity; Gelman *et al.* 2013).

Table 3.2 Multi-level model parameter descriptions.

Sub-Model	Parameter	Description
Ocean age	O_i	
	$\beta_{o,chum}$	Chum biomass (at ocean age 2)
	$\gamma_{o,s}$	Site
Standard length	L_i	
	β_l	Environmental covariates: ocean age, chum biomass (at year of return), NPGO, multivariate ENSO
	$\gamma_{l,s}$	Site
	$\gamma_{l,t}$	Year
Fecundity	F_i	
	$\beta_{f,l}$	Standard Length
	$\beta_{f,e}$	Enhancement
	$\gamma_{f,s}$	Site
	$\gamma_{f,t}$	Year

All beta and gamma coefficients were given the same vague normal distribution prior with means of 0 and precision 0.01 (S.D. = 10).

We centered and standardized all non-binary covariates by one standard deviation (i.e. chum biomass, NPGO, MEI, standard length) due to large differences in parameter variance and to estimate standardized effect sizes for each covariate. To improve MCMC mixing, redundant reparameterization, or hierarchical centering, was used (Gelman *et al.* 2008).

3.3.7. Leave-one-out Cross Validation

We tested an alternative hypothesis for the effect of enhancement duration (count of years since initiation of enhancement activities) instead of just enhancement occurrence in the fecundity sub-model of our Bayesian MLM. We competed these models in an information theoretic framework using leave-one-out-cross-validation (Vehtari *et al.* 2017; ‘loo’ package; Gabry 2017). Leave-one-out-cross-validation iteratively removes one datapoint at a time, uses the model estimates to predict that datapoint, and assesses the deviance of those predictions (i.e., predictive accuracy). Thus, it favors models with high goodness-of-fit while penalizing model complexity similar to AIC. In the information theoretic framework, the model with a lower LOO Information Criterion (LOOIC) score is taken as having higher predictive accuracy. Results indicated that the enhancement duration model had lower predictive power (Δ LOOIC = 5.624), as such our results below focus on the enhancement occurrence model.

3.4. Results

Ocean climatic indices and Pacific salmon abundance have fluctuated greatly over the past seven decades (Figure 3.2). The MEI showed a slight positive trend over time, with NPGO seeming to be cyclical but not directionally changing, with increased variability since the early 1990s. Chum biomass declined from about 1.5 million metric tons in the mid 1940s to a low of just over 650 000 metric tons in 1969. Annual biomass has since been climbing to near 3 million metric tons per year. During this same time period, life history traits and size of Pacific sockeye salmon have also been changing (Figure 3.3). Our data suggest that the proportion of sockeye salmon spending two years in the ocean has decreased slightly between 1970 and 2010. Mean annual standard lengths are variable, but roughly stable, with a mean of 53.18 cm and average S.D. of 3.25 cm within years. Mean annual fecundities have ranged from approximately 2700 to 4000. Decadal averages increased during the 1950s to the 1980s (averaging almost 3600 in the 1980s), but have declined to present, falling to less than 3100 after 2010.

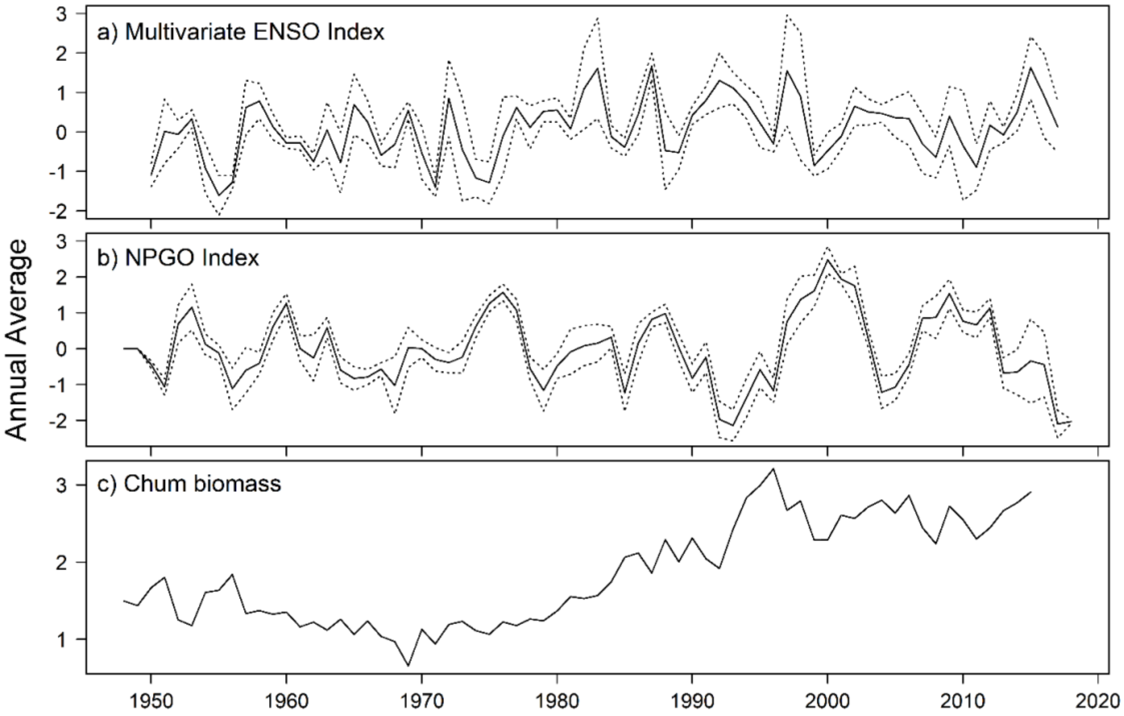

Figure 3.2 Time series of environmental predictor variables used in the ocean age and Standard length sub-models.

Annual average (solid line) is shown for Multivariate ENSO Index (MEI) and NPGO Index, along with +/- 1 S.D. (dashed lines). Total North Pacific chum abundance (adults and immature individuals) is shown in million metric tons.

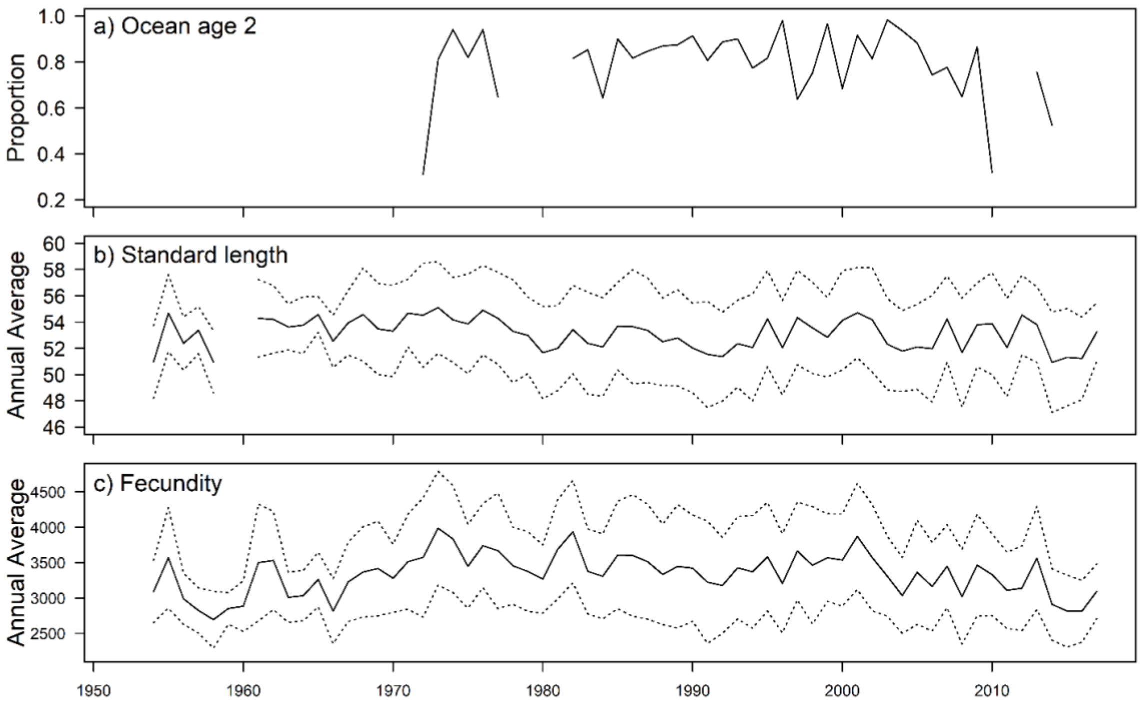

Figure 3.3 **All fish annual averages of a) proportion ocean age 2 years, b) mean (solid line) and +/- 1 S.D. (dashed lines) standard length (cm) and, c) mean (solid line) and +/- 1 S.D. (dashed lines) fecundity for all sampled years.**

From the MLM, estimated effects sizes and credible intervals generally revealed one term having the most substantial effect in each sub-model (Table 3.3; Figure 3.4). Ocean age was strongly influenced by North Pacific chum abundance; standard length was strongly impacted by ocean age; fecundity was strongly influenced by standard length. All 95% fixed effect credible intervals did not cross zero, except the interaction between enhancement and standard length. Thus, our results revealed that for each life history trait, there was a key variable which had strongest influence, and that in some cases, this was not an environmental variable, but another life history trait (e.g. fork length as a master variable which controls fecundity).

Table 3.3 Posterior mean, standard deviation, 95% credible interval and $\widehat{R}$ statistic for each standardized parameter of each sub-model.

Sub-model	Parameter	Mean	SD	Lower bound (2.5%)	Upper bound (97.5%)	Rhat
Ocean age	$\beta_{o,chum}$	0.309	0.049	0.215	0.409	1.000
Standard length	$\beta_{l,o}$	1.633	0.014	1.606	1.660	1.003
	$\beta_{l,chum}$	-0.058	0.030	-0.115	-0.001	1.001
	$\beta_{l,npgo}$	0.071	0.028	0.015	0.126	1.007
	$\beta_{l,mei}$	-0.065	0.029	-0.122	-0.008	1.005
Fecundity	$\beta_{f,l}$	0.127	0.002	0.124	0.130	1.000
	$\beta_{f,e}$	0.027	0.010	0.006	0.045	1.003

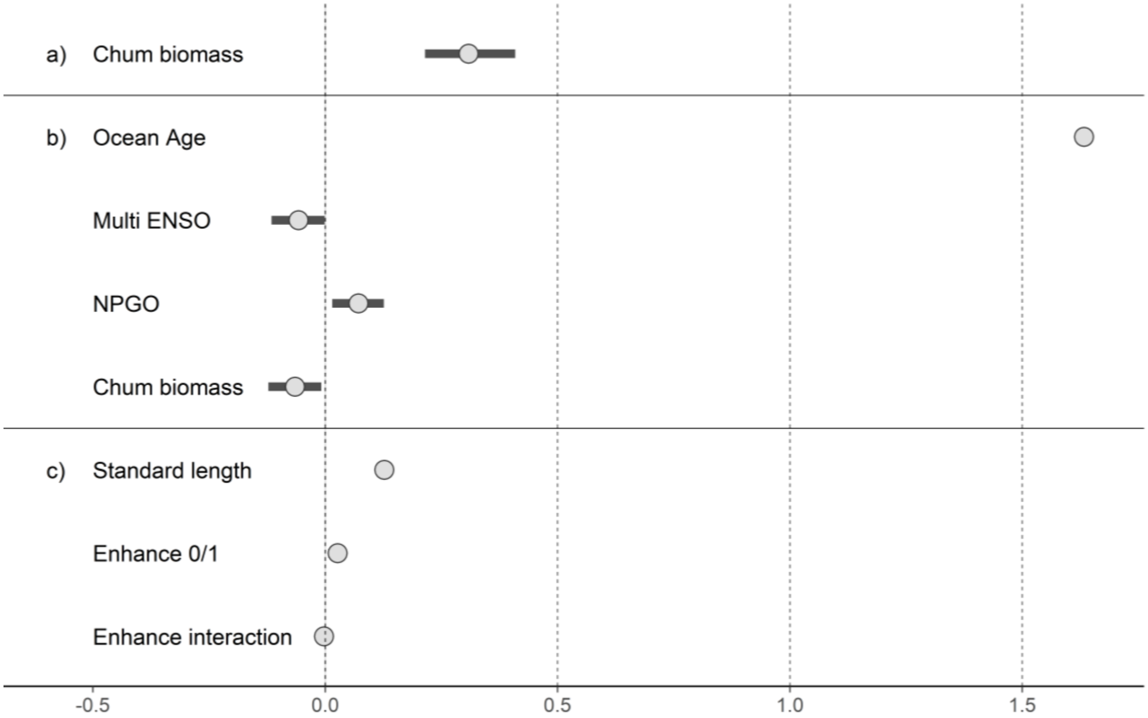

Figure 3.4 Standardized coefficient plots for standardized effect sizes on: a) ocean age b) standard length and c) fecundity.

Mean values of the posterior distribution (points) are shown with 95% CrIs (thick lines).

3.4.1. Ocean Age Sub-Model

In the ocean age sub-model, increased North Pacific chum biomass increased the probability of sockeye salmon spending 3 years in the ocean, to return as 5-year-old mature adults (Table 3.4; Figure 3.4; Figure 3.5). The standardized effect size of chum biomass on ocean age was 0.309 (95% C.I. 0.215-0.409). At low (-2 S.D.), average, and high (+2 S.D.) chum biomass, the probability of spending 3 years in the ocean was 2.5%, 5.2%, and 10.7%.

Table 3.4 Estimated average proportion spending 3 years in the ocean at low, average and high North Pacific chum biomass.

Chum biomass	Low (-2 S.D.)	Average (mean)	High (+2 S.D.)
Proportion ocean age 3	2.5%	5.2%	10.7%

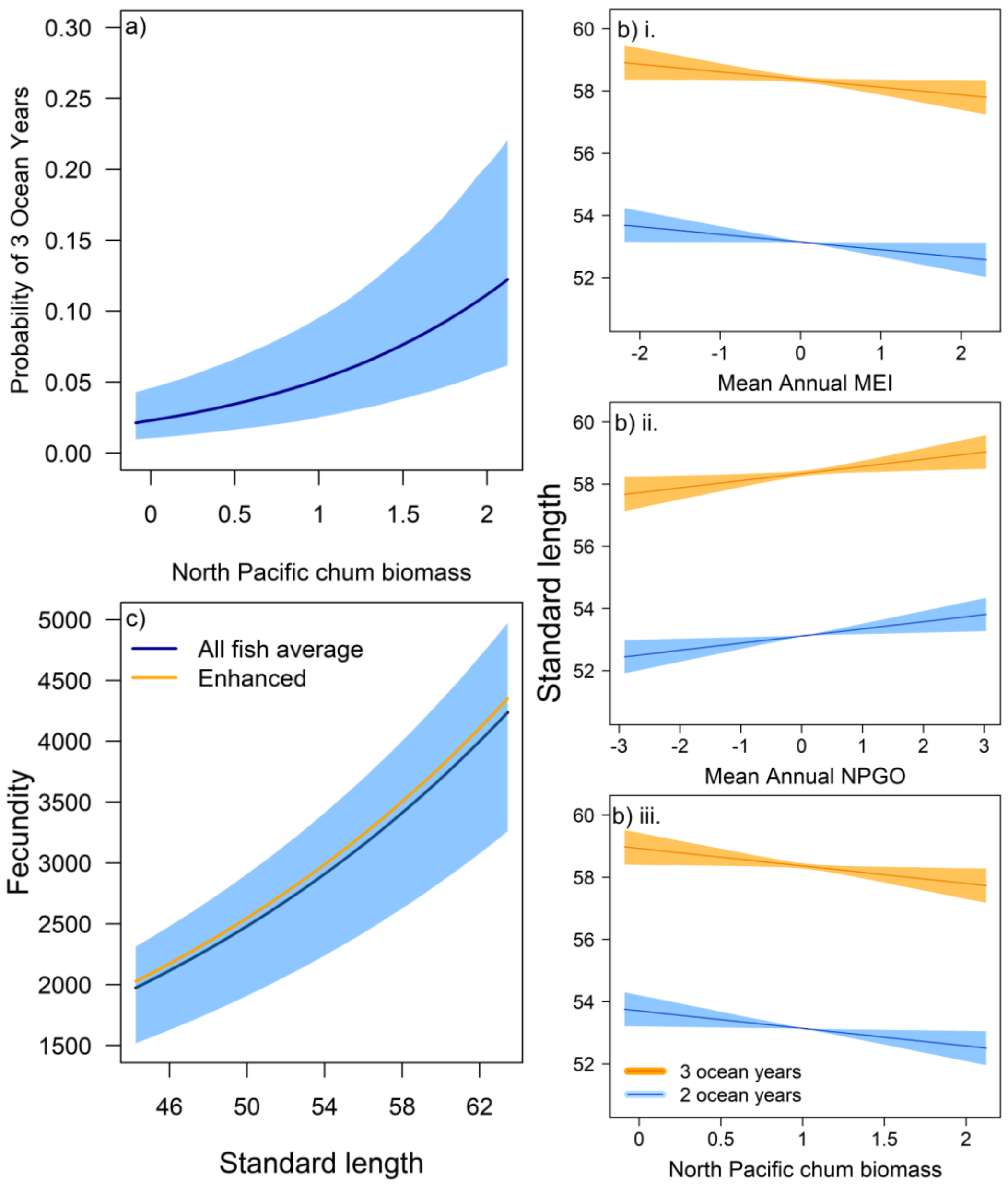

Figure 3.5 Model predictions for each of a) ocean age 3 years, b) standard length and c) fecundity sub-models.

Chum biomass (in million metric tons), MEI, NPGO and standard length (cm). Axes are centered on all fish averages (mean) and range represents approximately +/- 3 S.D.

3.4.2. Standard Length Sub-Model

Standard length was found to be most positively influenced by ocean age, with an average standardized effect size of 1.633 (95% C.I. 1.606-1.660; Figure 3.4; Figure 3.5). Both ocean age and NPGO were positively associated with standard length.

MEI and chum biomass had a negative statistical effect on standard length. Standardized effect sizes for MEI, NPGO and chum biomass were all very similar in absolute values, at -0.058 (95% C.I. -0.115 - -0.001), 0.071 (95% C.I. 0.015 - 0.126), and -0.065 (95% C.I. -0.122 - -0.008), respectively. Ocean age 2 sockeye that experienced average ocean conditions had mean standard length of 53.13 cm (Table 3.5). For a 3-year ocean age individual, experiencing average ocean conditions, this increased to 58.34cm. For sockeye that encountered good ocean conditions (i.e. low MEI and chum biomass, and high NPGO) standard lengths increased by 1.55 cm on average. Poor ocean conditions were associated with 1.55 cm decrease in standard length.

Table 3.5 Estimated average standard length for returning sockeye salmon given ocean age and ocean conditions encountered (including NPSA, NPGO and MEI)

Ocean age	2 years			3 years		
Ocean conditions	**Poor**	**Average**	**Good**	**Poor**	**Average**	**Good**
Standard length	51.58	53.13	54.68	56.80	58.34	59.89

3.4.3. Fecundity Sub-Model

Fecundity increased with increased standard length, and with the effect of enhancement (Table 3.6; Figure 3.4; Figure 3.5), with mean standardized effect sizes of 0.127 (95% C.I. 0.124-0.130) and 0.027 (95% C.I. 0.006-0.045), respectively. The interaction between enhancement and length was not found to have an impact on fecundity (standardized effect size of ~0). Standard length was strongly correlated with fecundities, with large sockeye averaging around 4000 eggs while small fish had only around 2100 eggs (Table 3.6). Small fish (-2 S.D.) were estimated to have an overall average of 2104 eggs, but in enhanced populations, this increases to 2161. For large fish (+2 S.D.), the overall average was 3977 eggs, increased to 4085 in enhanced populations. Enhanced populations were estimated to have only 3% higher fecundity than the whole data average.

Table 3.6 Estimated average fecundity for sockeye given standard length and enhancement

Standard Length	All fish	Enhanced
Small (-2 S.D.)	2104	2161
Average (Mean)	2893	2971
Large (+2 S.D.)	3977	4085

3.5. Discussion

Multiple oceanic stressors explained variability in a suite of life-history traits associated with the fecundity of sockeye salmon (Figure 3.6). Various stressors impacted different aspects of these linked life-histories. The net result of this complicated interplay of factors was that sockeye salmon fecundity has varied substantially over the last six decades. Over the last 40+ years, average decadal fecundities went from 3587 (1970s) to 3508 (1980s) to 3410 (1990s) to 3378 (2000s) to 3097 eggs per female (2010s). Thus, BC sockeye are 14% less fecund on average in recent years compared with 40+ years ago.

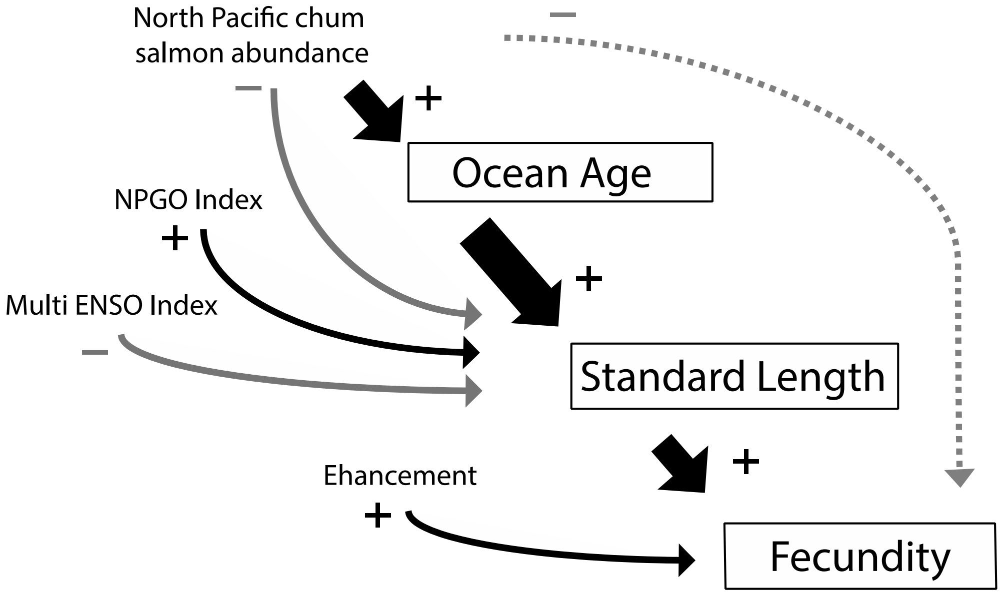

Figure 3.6 Diagram of direct and indirect factors that are positively (+) and negatively (-) correlated with different life history stages and traits. Thicker arrows indicate stronger standardized effect sizes.

When there was greater biomass of chum salmon in the North Pacific during the second year of ocean residence, sockeye salmon were more likely to delay migration. In high biomass years, an average of 10.7% of sockeye returned to freshwater as 3-year-olds, while in low biomass years only 2.5% of sockeye migrated as 3-years-olds. Upon return to freshwater, these ocean-age-3 sockeye were, on average, 5.2 cm longer than the ocean-age-2 fish. In addition, good ocean conditions, characterized by low MEI and chum biomass, and high NPGO increased standard lengths by 3.1 cm, when compared to poor ocean condition years. Standard lengths controlled fecundities, with large sockeye averaging around 4000 eggs while small fish had only around 2100 eggs. In addition, enhancement was associated with smaller magnitude increase in fecundity of approximately 60 to 120 eggs, for small and large sockeye, respectively.

We found that competition made fish smaller for their age, and older at maturity. Later maturation can increase opportunity for growth, body size and fecundity, but can also decrease the probability of survival to reproduction (Roff 1984). Thus, increases in ocean age may decrease productivity of populations if decreased individual survival is not matched by increased individual size and fecundity.

Although we believe this modelling approach greatly strengthens the explanatory power of both indirect and direct pressures on life history characteristics, there are also weaknesses in our model and data. A complete model set, competed with Bayesian model comparison techniques, may help identify the model with best possible explanatory power. For example, in our multi-level model, we did not include all potential predictor variables in all sub-models as this would lead to singularity issues and prevent model convergence. We used best available science to inform placement of ocean conditions and competition into specific sub-models, instead of applying them to all sub-models and reporting on all effect sizes and inclusion probabilities. In addition, we recognize the unbalanced nature of our dataset. Different locations and populations had different sampling intensities and sampling durations. This is due largely to the availability of data, and the fact that complete, long-term datasets are rare. While one of the strengths of the MLM modeling approach is building from linked datasets that can contain gaps and holes, the certainty of our model outputs could be strengthened with additional data from throughout British Columbia.

The trade-off between egg size and egg number is a well-known and well-studied life history process whereby energy is allocated between few, large eggs or many, small eggs (e.g. as examined in Smith & Fretwell 1974; Sargent *et al.* 1987; Fleming & Gross 1990; Beacham *et al.* 1993; McGurk 2000; Quinn *et al.* 2004). The data used in this analysis however, did not include egg size information for the large majority of individuals. Thus, while we acknowledge that inferences regarding population productivity would be strengthened with the inclusion of egg size data; these datasets are limited to our knowledge. Thus, our analyses cannot directly assess variation in egg size or other aspects that might influence offspring quality. Additional modelling that incorporates egg size and egg number information would likely provide powerful information on the reproductive success of individuals and populations. We found relatively long-term datasets for egg number from across the province, but egg size data has been much more varied in terms of collection methods and protocols. Going forward, a standardized method of fecundity and egg size sampling would greatly improve the potential for comprehensive models that provide reproductive success predictions with greater certainty.

Here, we provide novel data about variability in sockeye fecundity and the potential drivers of these shifts. On average, Fraser and Skeena River sockeye salmon have exhibited large-scale declining trends in productivity, since the 1980s and 1990s. Some of the largest declines have been observed in the Early Stuart, Bowron and Birkenhead populations, where productivity has declined by 75-85% since the mid 1960s (as measured by recruits per spawner ratios). For the Early Stuart populations, this represents a decline from about 20 to only 3 recruits per spawner (Peterman and Dorner 2012). This large-scale decline in productivity could have been driven by shifts in patterns of survival or abundance, or by changes in fecundity. We found that fecundities have declined by 14% over the same time period. It thus appears that declining fecundity may be contributing to some of the observed trends in declined productivity. However, declines in fecundity do not fully explain these trends; other processes such as shifting survival appear to drive the majority of these trends (e.g. Peterman & Dorner 2012, Ruggerone & Connors 2015, Malick *et al.* 2017).

There was some evidence that enhanced populations had relatively higher fecundity than non-enhanced populations. We suggest that this is evidence that enhancement via spawning channels may shift fecundities, perhaps by decreasing egg size due to lifting of natural selective pressures towards larger juveniles. Previous research on hatcheries has observed similar trends in some hatchery populations and populations heavily supplemented by hatcheries (e.g., Fleming & Gross 1990, Beacham & Murray 1993, Heath *et al*. 2003, Beacham 2011). While the magnitude of the shift in fecundity observed in our dataset was fairly small, it suggests that enhancement may have the unintended consequences of driving trait evolution. If enhanced fish stray to nearby non-enhanced populations, they may introduce maladaptive traits. Quantifying these potential unintended consequences could help inform management of enhancement activities.

Here we fit linked life-history trait sub-models that collectively incorporate multiple drivers of shifting sockeye salmon fecundities. Understanding the relationships between factors contributing to productivity requires the complex integration of multiple stressors on linked life-history traits. Salmon fecundity determines one aspect of an individuals' reproductive fitness, but is influenced by a variety of environmental conditions and other life-history characteristics. On-going work to build similar sub-models for other life-stages (e.g., egg-smolt survival; marine survival) will aid in fitting increasingly complex nested Bayesian models to consider the cumulative effects of multiple stressors across the sockeye salmon life-cycle. In this way, we can continue to characterize and understand the ways in which environmental conditions, that are changing in increasingly novel ways, will shape the future productivity of salmon populations.

Chapter 4. General Discussion

In this thesis, I examined multiple stressors across ontogenetic shifts in sockeye salmon. The complex life-cycles of salmon allow them to exploit resources from different habitats, including rivers, lakes and the ocean, but also exposes individuals and populations to varied conditions and challenges. In my second chapter, I found that, for lake-outlet spawning sockeye, increased river discharge created more areas of challenging water velocities for fry migrating upriver to the rearing lake. Lake rearing habitat was, however, associated with larger fry (30% longer and 150% heavier) that increased in size at almost twice the rate of those sampled in downriver habitats. Collectively, these results suggest the importance of upriver migration in lake-outlet spawning sockeye salmon as well as their sensitivity to habitat and hydrologic change. In my third chapter, I examined multiple pathways of stressors on life history traits from a broad temporal and spatial perspective. I analysed a nearly 7-decade dataset from Fraser and Skeena River sockeye salmon, in conjunction with time series of ocean conditions and climatic indices. I found that i) at higher biomass of Northeast Pacific chum salmon, sockeye are more likely to spend 3, rather than 2 years foraging in the ocean, ii) good ocean conditions, namely high NPGO index values, low MEI index values, and low Northeast Pacific chum salmon biomass are associated with larger sockeye, and iii) the largest sockeye are 50% more fecund than average size individuals, and enhanced populations were found to have an additional 3% increase in egg number. Together, this research further illuminates the intricacies in the effects of multiple environmental stressors on sockeye salmon across their complex life cycle. In this chapter I further examine these findings as well as discuss their potential management and conservation implications.

4.1. Ontogenetic habitat shifts and vulnerability of juvenile sockeye salmon

A number of core findings were discovered in my second chapter. Both seasonal and spatial patterns were identified in water velocity across the lake outlet reach, with increased high velocity areas during higher river discharge. This suggests that velocity barriers exist for upstream migrating fry, increasingly so during high discharge events such as spring freshet. Although juvenile salmon are known to temporarily use interstitial space as visual and velocity refuge habitat, between boulders or other river substrate (Bjornn & Reiser 1991), I suggest that the lake-outlet reach may function as a one-way check valve during high discharge, preventing some fry from accessing the upstream rearing lake.

The rearing lake was associated with larger juveniles, specifically 30% longer and 150% heavier than those in downriver habitat. This suggests that lake habitat provides superior growth conditions, and that failure to reach this habitat could decrease growth, with potential risk for decreased abilities for individuals to compete for resources, evade predators, and ultimately survive. Importantly, it appears that there is little rearing habitat downstream; populations of fry below the lake do not persist and likely have low fitness. This is relevant because massive numbers of fry are transported downstream each year, from 18% (7.5 million fry from the 1965 brood; Clarke & Smith 1972) to 67% (2.5 million fry from the 2015 brood; LBNF, 2016) of total fry production in the lower Babine River. The Lower Babine River population has decreased by approximately 85% since the 1950s, with two counts of less than 2000 spawners in the last ten years (Fisheries and Oceans Canada 2018).

It is quite possible that that anthropogenic habitat changes at this site may exacerbate this migration challenge. This section of river has areas where no riparian vegetation provides nearshore visual or hydrologic cover and where the banks have been armoured to protect in-river infrastructure (e.g. the installation of cement foundations, steel beams and sheet piling, and large, angular, riprap boulders). These types of alterations decrease the capacity of the shoreline to dissipate energy and facilitate access to flooded riparian refugia (Strayer & Findlay 2010). There are on-going efforts to perform restoration in this reach to address this challenge.

I suggest that the physical geography of lake outlets may be extremely sensitive and vulnerable to land-use alterations that change patterns of flow across space. This could exacerbate vulnerability of species with complex life cycles that use lake-outlet habitats to fulfill ontogenetic requirements. Further, within complex landscapes and life cycles, the conditions and configuration of a specific location could have population-level effects. It has been suggested that targeted conservation activities, specific in the time and place of implementation, can account for the dependencies of populations on complex habitat types (Runge *et al.* 2014). Some examples of this include restrictions of fisheries around endangered sea turtle rookeries during the breeding season (James *et al.* 2005), the shutdown of wind turbines during peak bat or bird migrations (Drewitt and Langston 2006) or hydrologic engineering to provide adequate and appropriate flows for anadromous fish during critical life stages (Jager & Rose 2003).

4.2. Drivers of shifting sockeye salmon life-history traits

In chapter 3, I found that ocean environmental conditions and Pacific salmon life-history traits have fluctuated greatly over the seven decades. Chum biomass declined between the 1940s, 1950s, and 1960s (1.5 to 0.65 million metric tons) but has since climbed to an annual average of near 3 million. The Multi-decadal El-Niño Southern Oscillation Index (MEI) has shown a slight positive trend over time and the North Pacific Gyre Oscillation (NPGO) Index was found to be cyclical, but not changing directionally, with increased variability since 1990s.

The proportion of sockeye spending three years foraging in the ocean has increased slightly between 1970 and 2010, and while size has been relatively constant, decadal averages of fecundity have fallen by approximately 15% since the 1980s. I found that the biomass of chum is positively correlated with ocean age, where an increase from low (-2 S.D. from mean) to high (+2 S.D. from mean) chum biomass increases the probability of spending 3 years in the ocean from 2.5% to 10.7%. Although it is well studied that ocean age is a large driver of size at maturity, I found additional impacts of ocean climatic indices and chum salmon biomass on size as well. The MEI, NPGO, and biomass of Northeast pacific chum were similar in magnitude of absolute effect size. The experience of poor (-2 S.D.) versus excellent (+2 S.D.) ocean conditions was associated with a 3 cm increase in fork length at maturity. Finally, I found that fecundity was largely driven by body size, a relationship well studied in Pacific salmon (e.g. Fleming & Gross 1990; Beacham & Murray 1992). I found that the increase from small (-2 S.D.) to large (+2 S.D.) body size was associated with a near doubling of egg number, from around 2100 to 4000, on average. Enhancement further increased fecundity of an individual by about 3%, which was the equivalent of about 110 eggs in large females. This modelling approach highlights the intricacies in direct and indirect pathways of multiple stressors on linked life history traits. Thus, this chapter provides an analyses of a large data set to quantified how multiple stressors impact linked life-history traits.

Future modelling efforts using the same hierarchical Bayesian modeling framework could similarly unpack how multiple stressors influence performance of sockeye salmon life-stages (e.g. egg-to-fry survival, marine survival). Ultimately, these different sub-models could be integrated across the entire life cycle. Large shifts in the productivity of sockeye have been observed in both the Fraser and Skeena systems, but questions remain regarding the relative importance of different stressors and life-stages as well as interaction of stressors driving these shifts. Increasingly comprehensive modelling approaches will allow further characterization of the ways in which environmental conditions, that are changing in increasingly novel ways, will shape the future productivity of salmon populations.

4.3. Conservation Implications

This thesis contributes to the understanding of complexities of environmental impacts on species that utilize multiple habitats throughout migratory life histories. Evaluating the value of conservation options for vulnerable species, isolated geographically, politically or temporally, is not possible without an understanding of the magnitude of threats and impacts across the complete life cycle (Martin *et al*. 2007; Iwamura 2013). I suggest that migration and movement corridors are crucial areas used within complex life cycles that also warrant investigation and protection. Although these locations may be used for only a short period of time, the reliance of a species on a particular pathway, such as a river, means that a small amount of habitat loss or degradation could have population-level consequences (Weber *et al.* 1999)

The application of dynamic species management has also been suggested as an appropriate approach to complex life-cycle conservation (Runge *et al.* 2014; Reynolds *et al.* 2017). This approach uses system state-specific actions, targeted in space and time, to address critical population needs or vulnerabilities (Reynolds *et al*. 2017). Incorporation of habitats needed for all life stages, and the migratory or movement corridors between those habitats, can tailor habitat management or rehabilitation to provide environments specifically when and where populations need them (Martin *et al.* 2007; Reynolds *et al.* 2017). This targeted approach may be increasingly important as the global climate crisis renders existing protected areas insufficient to provide the type, distribution, and amount of habitat required by species with complex, migratory life cycles (Mora & Sale 2011). Thus, there is a need to build on the existing network of available, suitable, protected habitat (Poiani *et al*. 2000), which may be done a dynamic approach of adjustable, scalable and cost-effective conservation (Reynolds *et al.* 2017).

Cooperation between local communities, government agencies and individual stakeholders can greatly increase the effectiveness of management strategies for species with complex life cycles (Runge *et al.* 2014). Local experts may bring an intimate understanding of local climate patterns, threats from industry or development and the natural history of the landscape, and identification of multiple local threats (Runge *et al.* 2014) and broad description of problems that one or more life stages may face (Martin *et al.* 2007). Community-based resource management capitalizes on the co-evolution of humans and complex ecosystem dynamics, and the local and traditional knowledge built over long periods of time regarding baselines and shifts in the system (Gadgil *et al.* 1993; Berkes & Folke 1998; Berkes *et al.* 2003). The knowledge and practices about ecosystem dynamics, including the complex ways species interact within it, can enable effective management and conservation (McLain & Lee 1996; Johannes 1998; Berkes 1999; Ludwig *et al.* 2001; Berkes & Jolly 2001; Gadgil *et al.* 2003). Further, Indigenous knowledge has been shown to differ substantially from Western ways of knowing, and to have measurable benefits to science and conservation (Ward-Fear *et al.* 2019). Ecosystems or habitats managed by local or indigenous communities is also declining less rapidly (e.g., decreased biodiversity or ecosystem functioning) than areas under the jurisdiction of corporate or national institutions (IPBES 2019). It follows that the employment of Indigenous and local motivations to maintain and conserve local resources (Anderson 2005; Deur & Turner 2005; Turner & Berkes 2006) could greatly benefit conservation of diverse and dispersed habitats required by species with complex life cycles.

Climate warming further complicates the conservation of migratory species with complex life cycles. In freshwater systems, ecosystem change related to climate warming is predicted to primarily impact characteristics of the hydrologic cycle and water temperature (Dodds *et al*. 2015). Global temperature increase facilitates increased water vapour storage in the atmosphere, which leads to more extreme hydrologic events; droughts will be drier and longer, and precipitation and flooding will increase (Crozier *et al.* 2008). Periods of extreme high or low flows and temperature increases, especially during migration and key life history events, such as spawning, will increase mortality (Hellmuth *et al.* 2002; Hoffman *et al.* 2003; Stillman 2003; Crozier *et al*. 2008). Mediation of climate change impacts and threats may be dependent on understanding their interaction throughout life stages and traits, such as fecundity or survival (Webster 2002; Cox 2010).

In summary, this thesis highlights direct and indirect impacts of multiple stressors across ontogenetic shifts in sockeye salmon. The complex life cycles of salmon, and migration between habitats required for developmental stages, expose them to diverse conditions and varied threats. Due to their reliance on multiple habitats, salmon use large geographic areas and must contend with varied types and intensities of anthropogenic impacts (Runge *et al.* 2014). Thus, consideration of direct and indirect pathways of multiple stressors on the complex, migratory life cycles of sockeye salmon is an increasingly important area of research for the conservation of this commercially, socially and culturally important species.

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Appendix A. Supplemental Material for Chapter 2

Table A.1 Complete model sets for each response variable. Marginal R_2 (Marg R_2; proportion of variance explained by fixed factors alone) and Conditional R_2 (Cond R_2; proportion of variance explained by fixed and random factors).

Response	Model number	Covariates	AICc	Marg R_2	Cond R_2
ln(Abundance)	3	Habitat + Q	282.8	0.267	0.269
	7	Q	283.1	0.212	0.271
	6	Week	285.2	0.194	0.230
	1	Habitat + Q + Habitat * Q	287.2	0.274	0.274
	4	Habitat + Week	287.7	0.222	0.227
	2	Habitat + Week + Habitat * Week	291.5	0.232	0.234
	5	Habitat	299.3	0.063	0.063
	8	-	299.7	-	0.018
Length	2	Habitat + Week + Habitat * Week	10434.5	0.564	0.588
	4	Habitat + Week	10554.1	0.531	0.560
	6	Week	10564.8	0.411	0.553
	1	Habitat + Q + Habitat * Q	10701.7	0.492	0.520
	3	Habitat + Q	10859.1	0.447	0.478
	7	Q	10868.2	0.330	0.462
	5	Habitat	11700.2	0.140	0.187
	8	-	11709.1	-	0.195
ln(Weight)	2	Habitat + Week + Habitat * Week	1541.7	0.574	0.590
	4	Habitat + Week	1640.1	0.546	0.569
	6	Week	1649.2	0.457	0.0.559
	1	Habitat + Q + Habitat * Q	1991.5	0.452	0.476
	3	Habitat + Q	2112.6	0.413	0.559
	7	Q	2120.4	0.317	0.431
	5	Habitat	2891.1	0.114	0.153
	8	-	2899.3	-	0.155
Condition Factor	2	Habitat + Week + Habitat * Week	-1509.1	0.115	0.142
	4	Habitat + Week	-1483.2	0.100	0.134
	6	Week	-1482.6	0.057	0.125
	1	Habitat + Q + Habitat * Q	-1463.9	0.091	0.124
	3	Habitat + Q	-1419.6	0.068	0.106
	7	Q	-1417.6	0.023	0.107
	5	Habitat	-1376.4	0.044	0.077
	8	-	-1374.9	-	0.071
Energy Density	1	Habitat + Q + Habitat * Q	1460.7	0.307	0.362
	2	Habitat + Week + Habitat * Week	1461.9	0.300	0.354
	4	Habitat + Week	1462.3	0.252	0.301
	5	Habitat	1463.6	0.229	0.276

6	Week	1465.0	0.024	0.274
3	Habitat + Q	1465.7	0.230	0.277
8	-	1466.3	-	0.248
7	Q	1468.3	0.001	0.249

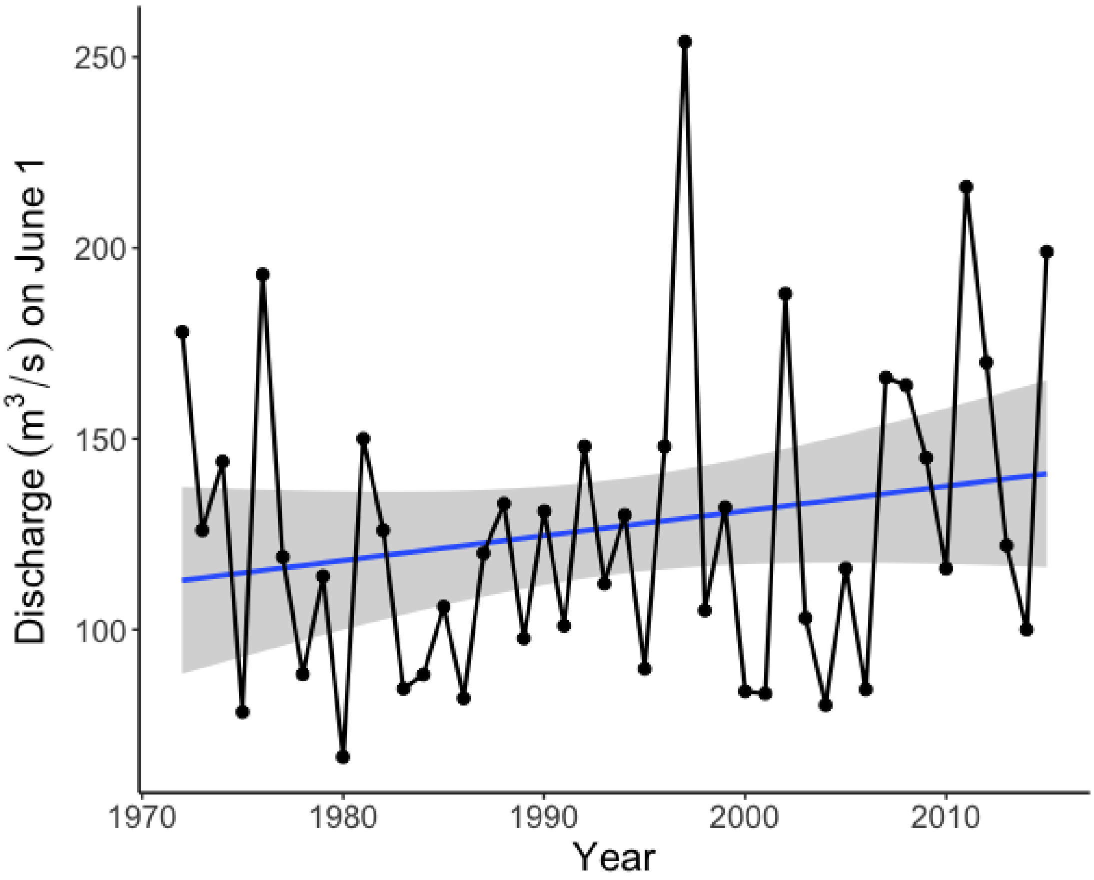

Figure A.1 Babine River discharge on the average observed peak emergence date for Lower Babine River sockeye salmon (*Oncorhynchus nerka*). Data were recorded at the Water Survey of Canada station, located on the west bank, approximately 25 m below the enumeration weir. Note: In 1964 and 1965, downstream travel peak was observed on June 15th. In 1966, the peak was observed June 7th. In 2015 and 2016 the peak was observed between May 29th-June 1st

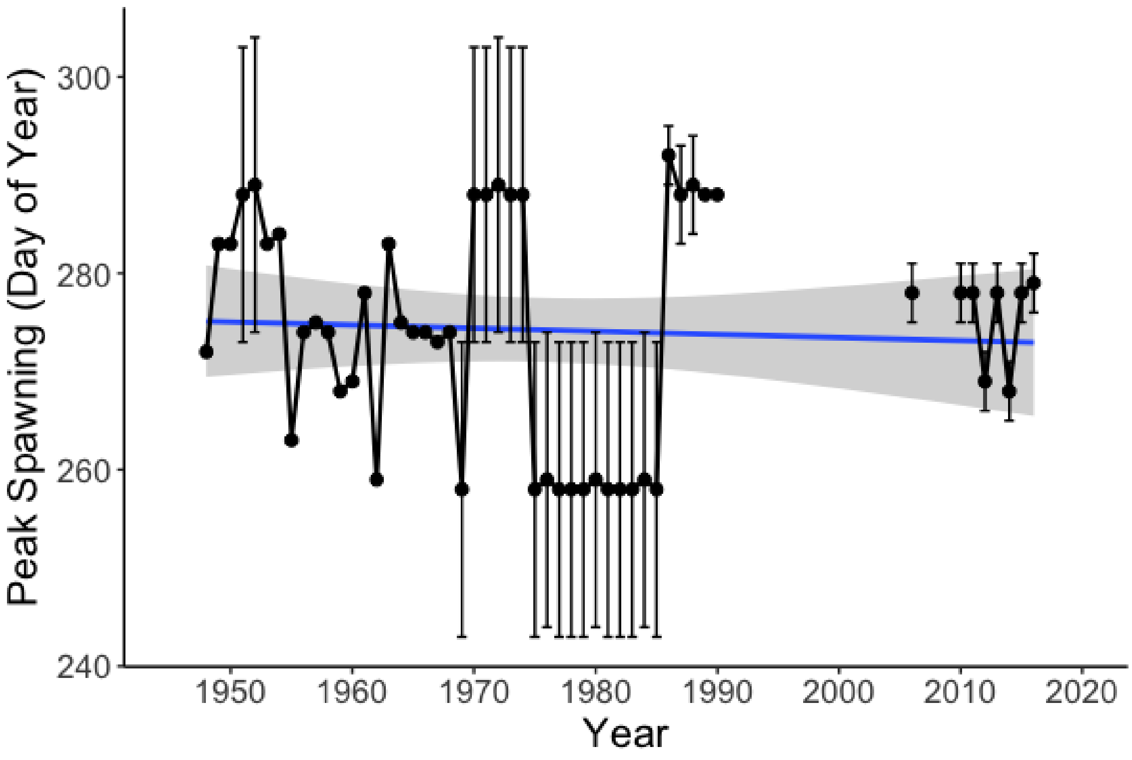

Figure A.2 **Historical spawn timing for Lower Babine River sockeye salmon (*Oncorhynchus nerka*).**

Points without error bars are precise date recordings, error bars added when only week or month are recorded in historical archives

Appendix B. Supplemental Material for Chapter 3

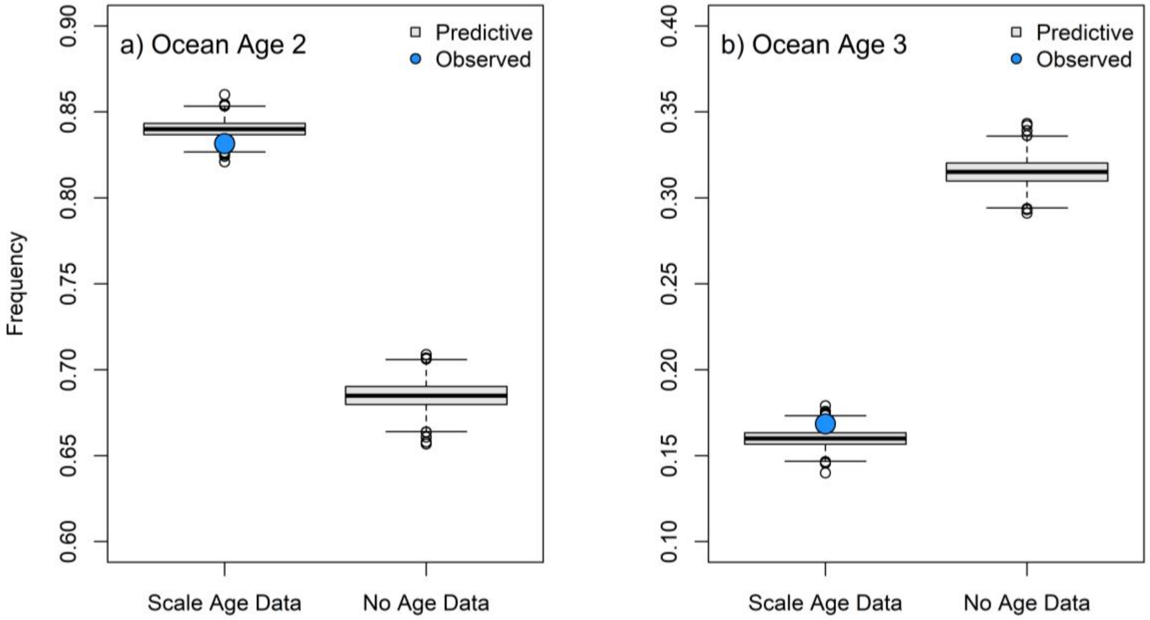

Figure B.1 **Posterior predicted frequency of a) ocean age 2 and b) ocean age 3 individuals where scale age data was available and missing (boxplot shows 25th to 75th percentile and median line at 50th percentile), compared to true data count (blue point) for individuals with scale age data.**

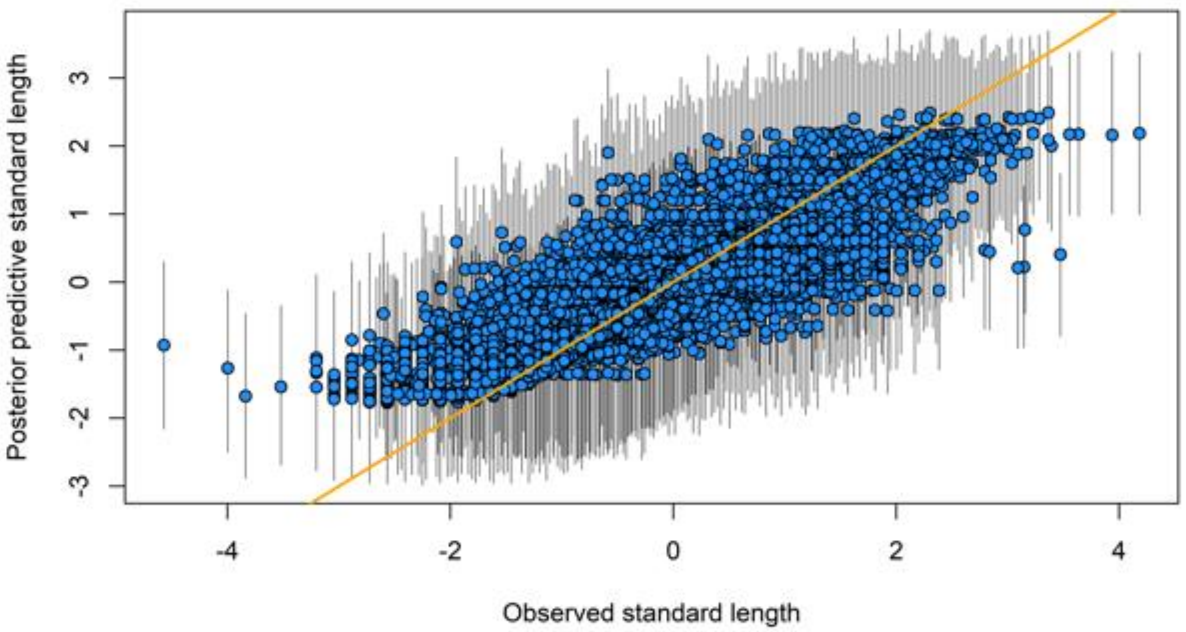

Figure B.2 Posterior predicted standard length values versus observed data

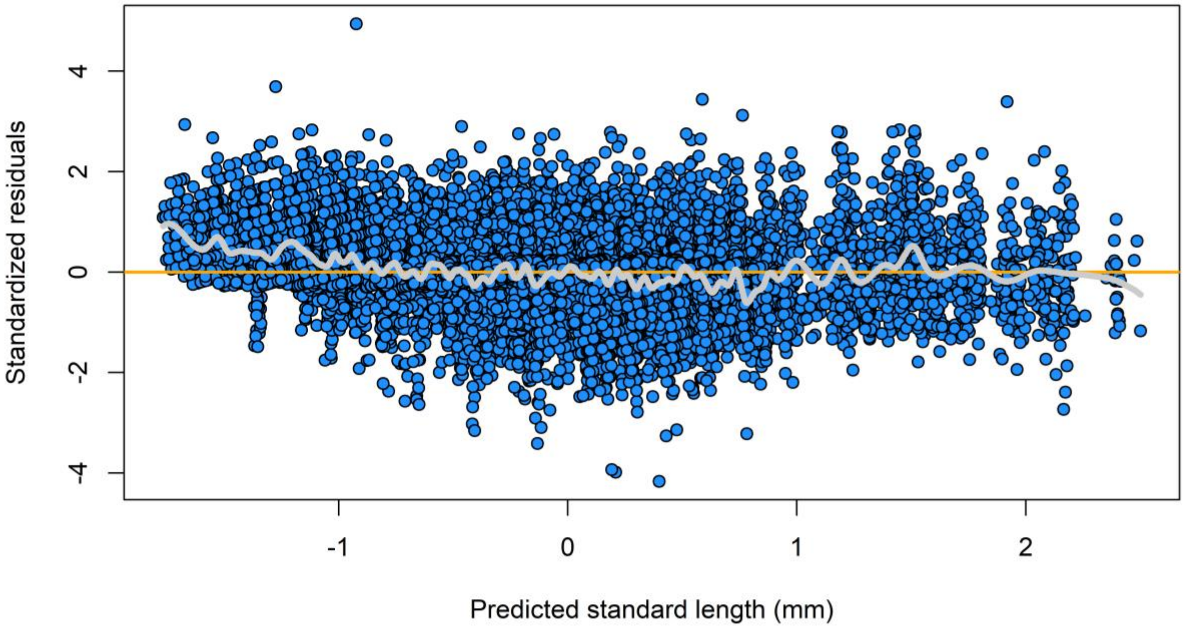

Figure B.3 Standardized residuals for standard length model.

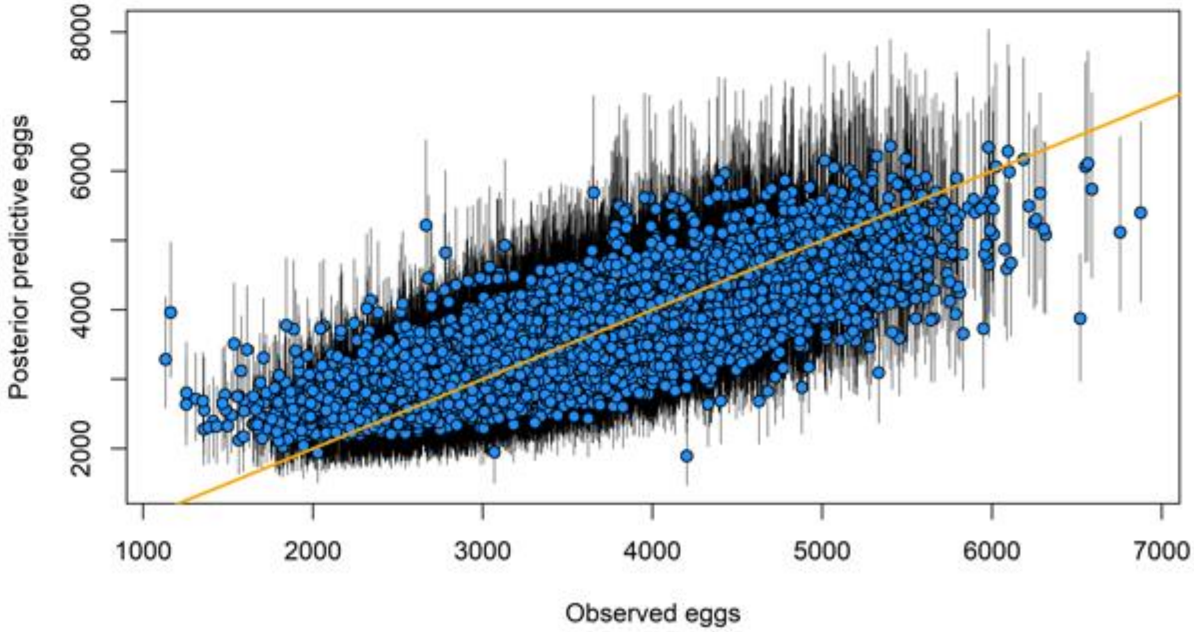

Figure B.4 **Posterior predicted fecundity values versus observed data**

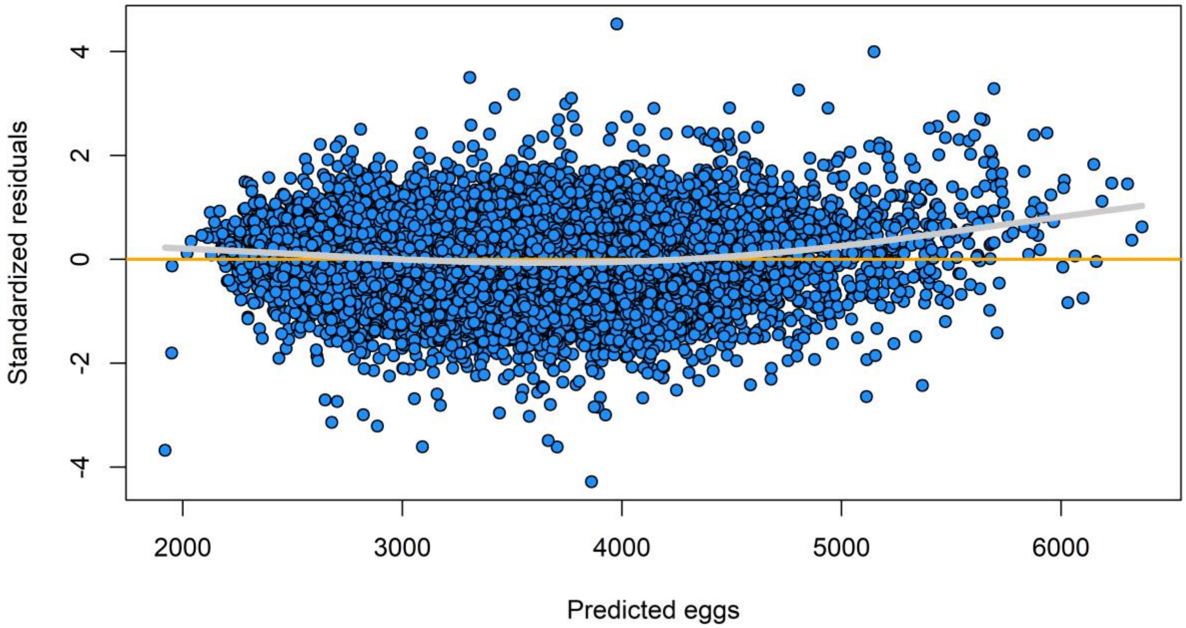

Figure B.5 **Standardized residuals of predicted fecundity values over observed fecundity data.**

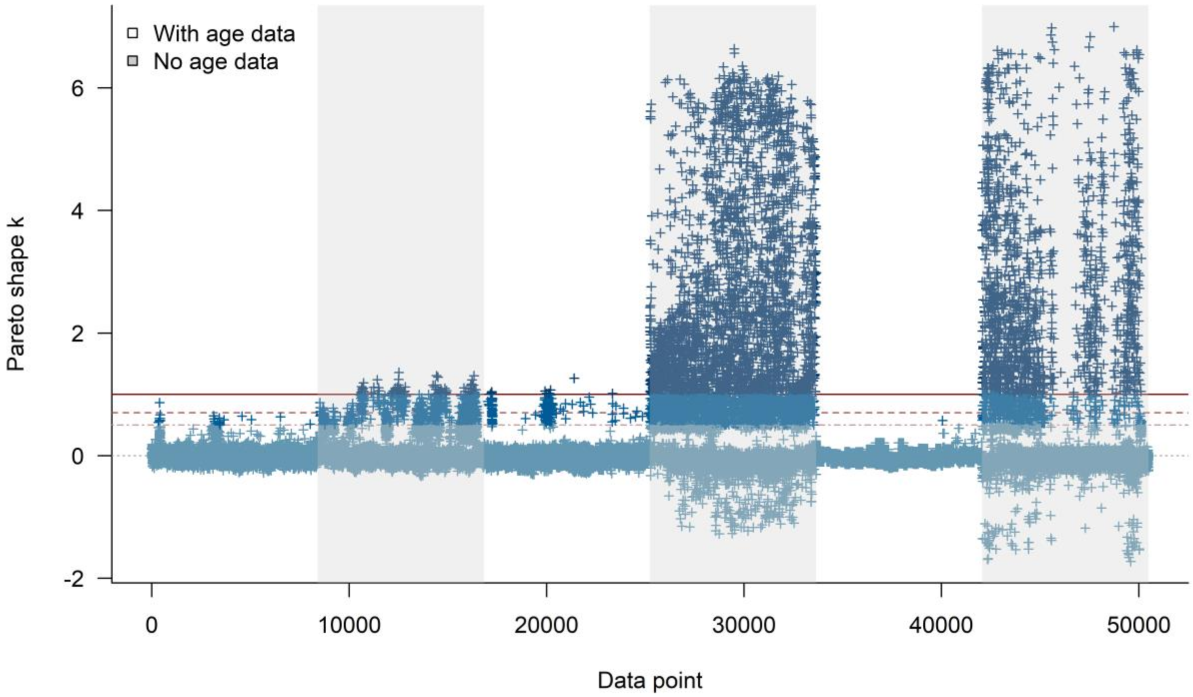

Figure B.6 Log-likelihood estimation of model performance for fecundity (Data points <17 000), standard length (17 000 < Data points < 34 000) and ocean age sub-models (Data points > 34 000). Grey shaded areas indicate data for which scale age data was missing.