Ecological drivers of variation in juvenile sockeye salmon marine migrations

by

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B.Sc. (Honours), Queen's University, 2012

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Abstract

Animal migrations are often associated with high mortality due to increased energy expenditure, reduced foraging opportunities, and increased predation risk. Migratory traits such as body size, phenology, or use of stopover habitats may moderate individual risk to mortality mechanisms and influence patterns of survival. However, variability in migratory traits is rarely quantified in detail because tracking many individuals over large areas is logistically challenging. In this dissertation, I used otoliths to examine migratory variability among and within sockeye salmon (*Oncorhynchus nerka*) populations, a species that has recently experienced declines associated with poor survival during juvenile marine migrations. Broadly, I examined the individual and environmental drivers of migratory patterns, as well as how variation across ecological scales (individuals, populations, and years) contributed to migratory diversity. First, I conducted a laboratory study to validate the use of otolith microstructure techniques in sockeye salmon post-smolts. Next, I assessed how a suite of ecological processes could interact to create a latitudinal gradient in sockeye salmon body size. By reconstructing individual growth and migration histories I determined that variation in size was correlated with ocean entry size and phenology, rather than differential marine growth or size-selective mortality. I then used estimates of migratory rate from otoliths to demonstrate that juvenile sockeye salmon exhibited distinct migratory phenotypes associated with ocean entry traits. Larger individuals migrated rapidly offshore, while smaller fish reared for several weeks in nearshore regions. Furthermore, a subset of the smallest individuals entered the ocean late in the year, migrated particularly slowly, and may have overwintered on the continental shelf. These linkages between ocean entry and migratory traits suggest juvenile sockeye salmon exhibit substantial migratory plasticity associated with carry-over effects from freshwater residence; however juvenile salmon may also respond strongly to variable conditions in marine habitats. In my fifth chapter, I compared marine growth and migration phenology in years with low and high competitor densities. After accounting for freshwater density-dependent effects, growth rates were similar in both years, but mean migration rates were nearly 50% faster in the high-density year. Migratory behavior may be used to buffer individuals from the effect of competitive interactions. In my final chapter, I sampled 16 Fraser River sockeye salmon populations to explore variation in the timing and duration of early marine migrations. Although populations differed in downstream migration timing, as well as their duration of residence within nearshore habitats, there was substantial variation within each population and between sampling years. These findings suggest individual characteristics and stochastic processes interact with population-specific strategies to shape migratory phenologies in this metapopulation. Management actions should account for and preserve migratory diversity at multiple ecological scales to maintain resilient salmon populations into the future.

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Chapter 1 - Introduction

1.1. Migration ecology

Long-distance migrations are taxonomically widespread, span massive spatial scales, and can shape ecological communities across disparate habitats (Dingle 1996). Migratory populations have evolved to exploit multiple peaks of seasonal productivity or avoid periods of high mortality (Alerstam et al. 2003) and, as a result, are often more abundant than closely related, resident populations (Fryxell et al. 1988, Quinn 2005). Ultimately, as migratory species move between habitats, they couple distinct ecological communities, stabilize networks, and provide unique ecosystem services (Holtgrieve and Schindler 2011, Semmens et al. 2011, Bauer and Hoye 2014).

Unfortunately, the seasonal movements that make migratory species ecologically valuable also increase their vulnerability to natural and anthropogenic disturbance (Runge et al. 2014). Successful conservation strategies must ensure both breeding and wintering habitats remain intact, while simultaneously maintaining migratory corridors that often span multiple political jurisdictions (Runge et al. 2014). Conservation science has begun to recognize the necessity of spatially explicit management plans for highly mobile taxa, yet migratory populations remain at high risk (Wilcove and Wikelski 2008), particularly in the context of climate change (Robinson et al. 2009).

Given finite conservation resources, identifying and protecting life history stages or habitats that disproportionately limit the productivity of migratory populations is essential. Declines in the population size of migratory taxa may be the result of reduced fitness in breeding/wintering habitats (Norris et al. 2004) or effects that accumulate throughout the life cycle (Harrison et al. 2011, Healey 2011). However, mortality during long distance movements is often disproportionately high relative to non-migratory periods due to reduced foraging opportunities, increased energy expenditure or exposure to predators and pathogens (Sillett and Holmes 2002, Cooke et al. 2006, Klaassen et al. 2014, Clark et al. 2016). Therefore, mortality rates in habitats that are only briefly occupied may have large effects on population size, transforming migrations into survival bottlenecks (Parker 1968, Newton 2006, Buehler and Piersma 2008).

Mortality risk typically varies across space or time and, as a result, variation in migratory traits such as phenology or condition can moderate an individual's likelihood of survival. Migratory variation may arise due to phenotypic plasticity, when conditions experienced prior to the start of migration shape physical characteristics or behaviors (Newton 2006). Such carry-over effects are correlated with individual fitness across a range of taxa (Harrison et al. 2011). For example, repeat migrants exhibit experiential learning that results in both greater migration speeds and higher survival rates (e.g., black kites *Milvus migrans*, Sergio et al. 2014; pike *Esox lucius*, Tibblin et al. 2015). In Dolly Varden trout (*Salvelinus malma*) older individuals "retire" from anadromy and experience reduced mortality as a result (Bond et al. 2015). Perhaps most commonly, individuals in better condition are typically able to migrate more rapidly, often with significant benefits to reproductive success or survival (e.g., American redstarts *Setophaga ruticilla*, Marra et al. 1998; pink salmon *Oncorhynchus* gorbuscha, Dickerson et al. 2005; black-tailed godwits *Limosa limosa*, Gunnarsson et al. 2006).

In other instances, migratory traits may vary at larger ecological scales. Selection for migratory traits often varies across breeding grounds, ultimately resulting in the evolution of population-specific strategies (Berthold et al. 1992) that may have considerable impacts on fitness. Populations can experience relatively higher mortality if they utilize risky migratory routes (Hewson et al. 2016) or if migratory phenologies expose them to unfavorable environmental conditions (Cooke et al. 2004). Atlantic salmon (*Salmo salar*) populations exhibit divergent rates of mortality during seaward migrations, which are linked with differences in habitat use (Lacroix 2008). In other instances, however, the link between migration and population dynamics may be subtle. For example, changes in the skewness or synchrony of phenologies can have a large effect on survival (Rasmussen and Rudolf 2016). Consequently, the distribution of migratory phenotypes within a population may play as large a role in regulating dynamics as the median (CaraDonna et al. 2014).

Environmental variability is a third driver of diversity in migratory traits. While habitat quality prior to departure can have strong effects on individual fitness (Marra et al. 1998, Gunnarsson et al. 2006), conditions encountered en route can also exert a particularly strong influence. Severe weather events can delay phenologies (Schaub et al. 2004), cause mass mortality events (Newton 2006), or force individuals to reverse course (Senner et al. 2015). Even when abiotic conditions are optimal for migration, limited prey resources (Schaub et al. 2008) or high competitor densities (Dierschke and Delingat 2001) can force individuals to alter their migratory behavior or utilize different habitats.

Disentangling the relative influence of variation among individuals as opposed to populations, as well as the effect of environmental conditions prior to and during migrations, is complex, but valuable. First, there is a growing consensus that intraspecific diversity can act to stabilize population aggregates by spreading risk among distinct components (Schindler et al. 2010). Accurately identifying the scale and source of variation within metapopulations is a necessary prerequisite to preserving that diversity. Second, management strategies will differ depending on whether diversity is relatively static and maintained at the level of populations or plastic and regulated by environmental stochasticity. In the former, there will be strong benefits to conserving a representative suite of populations with distinct strategies (Anderson et al. 2015), while in the latter it will be advantageous to identify and maintain the processes that generate intra-population diversity.

1.2. Pacific salmon ecology

Pacific salmon (*Oncorhynchus* spp.) are important economically, socially, and ecologically to communities throughout the North Pacific. Many Pacific salmon populations are anadromous, migrating between freshwater and marine systems. These movements increase the relative abundance and body size of anadromous populations (Quinn 2005) and provide substantial nutrient subsidies to impoverished terrestrial systems (Wipfli et al. 1999). As a result of these long distance migrations, Pacific salmon are vulnerable to a range of disturbance pressures and sustainable exploitation requires coordinated efforts to explicitly protect migratory corridors, as well as spawning and rearing habitat (Bottom et al. 2009).

The freshwater migrations of Pacific salmon have been intensely studied for decades, largely due to concerted efforts to re-establish or re-build populations after freshwater habitat was lost due to anthropogenic development (Groot and Margolis 1991).

Numerous studies demonstrate that Pacific salmon populations exhibit considerable variation in freshwater migratory traits including spawning phenology (Groot and Margolis 1991, Hodgson and Quinn 2002), body morphology and energetics (Crossin et al. 2004), migration speed (Hanson et al. 2008), and physiological tolerance (Eliason et al. 2011). Within populations, many of these migratory traits appear to influence individual fitness. Reproductive success is associated with body size and timing of arrival on spawning grounds (Cooke et al. 2004, Dickerson et al. 2005), while juvenile survival varies with downstream migration timing (Scheuerell et al. 2009, Furey et al. 2016)

Meanwhile variation in Pacific salmon marine migratory characteristics has only begun to be closely examined. In part this reflects a shift within salmon ecology towards a paradigm where year class strength is strongly influenced by interannual variation in early marine survival, rather than the capacity of freshwater habitat alone (Pearcy 1992, Beamish and Mahnken 2001). While the specific mechanisms that drive marine mortality remain unclear, they are potentially diverse and may include predator density and community composition, pathogen levels, prey availability, abiotic environmental conditions, and competitor abundance (Healey 2011, McKinnell et al. 2012). Notably each of these factors likely varies in space and time, creating a mechanism by which mortality risk may be moderated by variation in juvenile migratory characteristics.

Previous studies of juvenile Pacific salmon marine migrations have typically depended on population-wide observations or artificial tags. In the first method, movements of focal populations are estimated using changes in catch distribution from research surveys, paired with stock identification techniques. Population-wide observations have been used to determine how salmon populations utilize specific marine rearing areas and migratory corridors (e.g., Morris et al. 2007, Beacham et al. 2014a), as well as provided coarse estimates of migratory phenologies (e.g., Tucker et al. 2009, Preikshot et al. 2012). However, methods based on catch data alone are inherently limited because individual variation in migratory characteristics cannot be separated from the distribution of the population as a whole (Forrest and Miller-Rushing 2010).

Conversely, artificial tags can be used to gather fine-grained ecological data and provide information on individual migratory strategies. In the case of Pacific salmon, artificial tags have been particularly useful in estimating travel speeds (Lacroix 2008, Melnychuk et al. 2010) and identifying regions of high mortality (Welch et al. 2009, Melnychuk et al. 2014, Clark et al. 2016). Despite these breakthroughs, different tagging methods have shortcomings that limit their effectiveness in the marine environment. Acoustic or satellite archival tags provide movement data at the scale of individuals, yet the tags themselves, as well as the associated infrastructure (e.g., receivers, arrays, targeted retrieval), are expensive (Reine 2005). As a result, it is rarely feasible to tag a sufficient number of individuals to make comparisons among multiple populations simultaneously. Though acoustic tags have decreased dramatically in size, they are often still too large to deploy on all sizes of juvenile salmon, leading to concerns that estimates may be biased (Furey et al. 2016). At the other end of the spectrum are lower-priced tags, such as passive integrated transponder (PIT) or coded wire tags (CWTs). Both of these tags can be readily applied to a large number of individuals regardless of size; however, PIT tags are rarely effective in marine habitats due to their short detection range (Reine 2005), while CWTs depend on individuals being recaptured, necessitating high tagging and sampling effort to reach a sufficient sample size.

In certain instances natural markers (e.g., parasites, stable isotopes, calcareous structures) can provide a robust alternative to artificial tags when investigating patterns of migration, dispersal, and connectivity (Gillanders 2010). Otoliths are inner ear bones that grow through the concentric deposition of calcium carbonate and have been particularly useful in studying the dynamics of fish populations (Secor 2010). Since somatic and otolith growth are strongly correlated, individual growth histories and previous size can be readily estimated (Hickling 1933). Many otoliths form visible microincrements at daily intervals that can be used to age juvenile life stages (Pannella 1971). Moreover, certain ontogenetic events (e.g., hatching, habitat transitions) are recorded as visible "checks" on otoliths that can be used to date important life history events (Marshall and Parker 1982). Finally, otoliths, which are inert, incorporate ambient environmental elements into their physical structure (Campana 1999). Movements between distinct habitats can then be reconstructed using these elemental signatures (Macdonald and Crook 2010).

Such characteristics make otoliths a particularly powerful tool for exploring hypotheses about juvenile salmon marine migrations. Stress checks are typically formed when salmon smolts migrate into a saline environment (Neilson et al. 1985, Saito et al. 2007) and can be validated using microchemistry techniques, which detect changes in strontium and barium concentrations due to elemental differences between salt and fresh water (Miller et al. 2010, Stocks et al. 2014). Pairing entry checks with counts of increments provides a robust estimate for the number of days individuals have been in the marine environment (Saito et al. 2007, Claiborne and Campbell 2016). Therefore, otoliths can be used to estimate outmigration phenology, minimum travel speeds, size at ocean entry, and stage-specific growth rates – characteristics that are commonly associated with interannual variation in survival in Pacific salmon (Beamish et al. 2004, Duffy and Beauchamp 2011, Tomaro et al. 2012).

The broad goal of this dissertation was to explore how juvenile sockeye salmon marine migrations vary within and among populations, as well as to identify individual and ecological characteristics that underpin this diversity. To answer these questions I extracted data from otoliths that were collected by collaborators during seven years of Fisheries and Oceans Canada research surveys and were assigned to specific spawning populations using genetic stock identification techniques (Beacham et al. 2005).

In Chapter 2 I present results of a validation study on the use of otolith microstructure techniques in sockeye salmon postsmolts. I reared individuals in captivity, transitioned them from fresh to saltwater, and periodically sampled the population to confirm that otolith microincrements were produced daily. I then tested whether visual marine entry checks were consistent with microchemistry estimates from stable isotopes using inductively coupled plasma mass spectrometry. I observed a visual marine entry check and counts were strongly correlated with the number of days since smolting. Chemical estimates of ocean entry, as indicated by changes in Sr:Ca ratios, were largely consistent with visual checks, but could precede visual estimates by ~9 days. I suggest that the chemical and visual checks are associated with distinct environmental processes that can lead to uncoupling between the two estimates; however, visual estimates are likely a reasonable proxy for first feeding in estuarine or marine environments.

In Chapter 3 I examine the ecological underpinnings of variation in body size during juvenile salmon migrations. Sockeye salmon in British Columbia exhibit a consistent latitudinal gradient in body size during juvenile marine migrations – individuals, within a spawning population, that are caught in northern regions are significantly larger than those caught closer to ocean entry points. I used data collected from four populations to disentangle the effect of individual characteristics that developed during freshwater residence from that of processes occurring during marine residence. I provide evidence that variation in body size during migrations is predominantly driven by ocean entry size and timing, not differential marine growth. Furthermore, by comparing size distributions along the migratory corridor, I demonstrate that larger body size in northern regions is not due to the selective mortality of smaller individuals. This work indicated that the heterogeneity that develops among individual sockeye salmon during freshwater residence persists during marine migrations.

Juvenile sockeye salmon within a population are generally thought to make a relatively uniform and rapid migration offshore. In Chapter 4, however, I present evidence of multiple, distinct migratory behaviours within several British Columbia populations. Specifically, individuals that were captured in northern regions had migrated rapidly, immediately after ocean entry, while the remainder of the population moved away from their ocean entry points slowly over a period of several weeks. Within these two behaviours, travel speed was also positively correlated with ocean entry size and, in the case of fish caught in northern regions, entry date. Furthermore, I found evidence of a potential third migratory behavior whereby individuals that entered the marine environment particularly late in the year and at a small size failed to migrate offshore by late autumn. These divergent migratory patterns result in populations that are highly dispersed during their first marine summer, which may buffer populations from poor rearing conditions encountered en route (Morris et al. 2007).

Chapters 3 and 4 suggest that the conditions juvenile sockeye salmon experience during freshwater residence impact their size and behavior during marine migrations. Yet conditions experienced during marine migration may still moderate juvenile salmon spatial distributions (Burke et al. 2013) and growth (Duffy and Beauchamp 2011, Miller et al. 2014a). In chapter 5 I explore whether juvenile sockeye salmon migratory characteristics are correlated with the abundance of con- and heterospecific competitors. Although competition at sea appears to reduce individual growth and survival in Pacific salmon, previous studies have analyzed interactions across broad spatial and temporal scales (e.g., Peterman 1984, Connors et al. 2012, Ruggerone and Connors 2015). As a result, it is unclear whether density-dependent effects occur throughout marine residence, and which competitor assemblages have the greatest impact. Specifically, I test for density-dependent effects on juvenile sockeye salmon growth and migratory behavior during two years with dramatically different pelagic fish densities in the Strait of Georgia. I demonstrate that the density of the four most abundant species (juvenile sockeye salmon, pink salmon *O. gorbuscha*, chum salmon *O. keta*, and Pacific herring *Clupea pallasii*) was six-fold greater in 2012. After accounting for the influence of freshwater density-dependent effects, I found that juvenile sockeye salmon migrated away from their ocean entry points significantly faster in 2012, however growth rates were stable between years. I suggest juvenile salmon may exhibit shifts in behavior to minimize competitive interactions during early marine residence and ensure sufficient growth.

My first chapters demonstrated that juvenile sockeye salmon exhibit substantial heterogeneity in their early marine migrations, and that this variability is influenced by characteristics that develop during freshwater residence, as well as conditions experienced during early marine residence. In Chapter 6, I explore how the migratory phenologies of a sockeye salmon metapopulation vary across multiple ecological scales. Although Fraser River populations exhibited consistent differences in migration phenology, there was considerable variation within each population that was associated with individual variation in life history, body size, entry date, and growth. Nevertheless, individual and population-scale effects were dominated by inter-annual variation, which suggests that stochastic environmental processes do play a key role in moderating ecological variability.

The results of this dissertation describe how a suite of ecological processes acting across scales shape long-distance migrations. Given that mortality during migrations generally (Sillett and Holmes 2002, Newton 2006), and among Pacific salmon specifically (Pearcy 1992), can regulate population dynamics, these findings are a critical first step to identifying mechanisms of differential survival. Furthermore, if migratory diversity decreases variability in marine survival (Morris et al. 2007), these patterns could demonstrate areas where conservationists and managers can take effective action to increase the long-term sustainability of salmon populations.

Chapter 2 - Validation of daily increments and a marine entry check in the otoliths of sockeye salmon post-smolts

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2.1. Abstract

We reared and smolted juvenile sockeye salmon (*Oncorhynchus nerka*) in laboratory conditions to validate otolith microstructure techniques. We found that otoliths produced daily increments, as well as a consistently visible marine entry check formed during individuals' transition to saltwater. Field-collected sockeye salmon post-smolts of an equivalent age also displayed visible checks; however microchemistry estimates of marine entry date using Sr:Ca ratios differed from visual estimates by approximately nine days suggesting the physiological processes leading to microstructural and –chemical checks may differ.

2.2. Introduction

Calcified structures often produce periodic increments that can be used to estimate age and growth. Otoliths are frequently preferred in such studies since they are formed early in fish development and cannot be resorbed like scales (Campana and Thorrold 2001). Moreover, periods of physiological stress (e.g., the transition from fresh- to saltwater habitats, first feeding) can cause discontinuities, or 'checks', in the daily increment sequence characterized by increased opacity that allow researchers to estimate when key life history events occur (Pannella 1971). However, the accuracy of age and growth estimates from otoliths depends on a robust relationship between otolith and somatic growth, the consistent deposition of increments at a known rate, and the universal formation of checks of interest within a population (Campana 2001). Importantly, previous studies have indicated that these assumptions do not necessarily hold for all species or age classes (Campana et al. 1987, Wild et al. 1995).

Daily otolith increments have been examined in sockeye salmon (*Oncorhynchus nerka*) fry (Wilson and Larkin 1980, Marshall and Parker 1982), but there are no published accounts confirming the formation of daily increments in sockeye salmon post-smolts. Although visible marine entry check marks have been confirmed in several *Oncorhynchus* species (Volk et al. 1984, Neilson et al. 1985, Zhang and Beamish 2000, Saito et al. 2007, Middleton 2011) and marine residency in a northern population of *O. nerka* has been investigated using microchemistry techniques (Stocks *et al*., 2014), these metrics have not been directly compared. Moreover, since freshwater residency and migration rate through estuaries vary between species and populations, the effectiveness of otolith metrics may differ as well.

Understanding this potential variation is particularly important in Pacific salmon species. Given that Pacific salmon recruitment dynamics are thought to be strongly influenced by conditions experienced shortly after ocean entry (Beamish and Mahnken, 2001), studies that can accurately estimate age and growth relative to marine entry timing will be valuable for identifying mechanisms of mortality. Here we test the hypothesis that sockeye salmon post-smolts produce daily increments and a visible marine entry check by (i) visually validating otoliths of a known age and (ii) comparing visual marine entry check estimates with shifts in barium and strontium concentrations indicative of ocean entry.

2.3. Methods

2.3.1. Laboratory-reared fish

Eggs, collected from adult sockeye salmon in Harrison River in 2011, were fertilized and hatched at the University of British Columbia. Fry were then transported to the University of Victoria's Aquatic Research Facility in March 2013. After transport to the University of Victoria, we smolted fish by gradually increasing the salinity of their tanks to 29 PSU over a period of three days. At both facilities fish experienced a natural seasonal photoperiod, were fed *ad libitum* commercial fish meal pellets twice daily, and reared at temperatures that varied between 10-16°C seasonally.

We selected a 100-day sampling period since it is a conservative estimate of the time an individual would spend migrating from southern British Columbia to the Gulf of Alaska and is thought to encompass much of the early "critical period" in juvenile salmon survival (Beamish and Mahnken 2001, Beamish et al. 2012b). Over this period, we removed a subset of the captive population over 11 sampling events (n = 10 individuals per event) and anesthetized individuals with a lethal dose of tricaine mesylate (MS-222). Fish fork length and mass were recorded (to the nearest 1 mm and 0.1 g respectively) and both sagittal otoliths were removed for further processing.

Otoliths (sagittae) from experimental fish were removed and soaked in deionized water for 10 minutes. Unless the left otolith was damaged or could not be retrieved, only left sagittal otoliths were mounted and analyzed. After soaking, otoliths were dried and fixed to glass microscope slides, sulcal side up, with thermoplastic adhesive (SPI Supplies Crystalbond 509). Otoliths were observed with a compound microscope (Zeiss Universal) at 25x, 110x, and 400x. Images were captured with a digital camera (SPOT

Flex, FX1520) for analysis using Image J (Rasband 1997-2014). The exposed surface was polished with 300, 10, and 3 µm lapping film (Digikey 3M) until primordia and peripheral increments could be observed along the dorsal axis. The slide was then heated, the otolith flipped, and the reverse side polished until increments and the presumed marine entry check were clearly visible along the dorsal axis. Potential marine entry checks were identified by the presence of an especially dark, optically dense daily increment, separated from the otolith core by a distinct translucent zone representing winter freshwater growth (the freshwater annulus). The entry check was also separated from the otolith periphery by clearly defined increments whose spacing gradually increased, rather than the densely packed increments that preceded the first freshwater annuli (Zhang and Beamish 2000, Saito et al. 2007). If the dorsal axis of the otolith was damaged, the otolith was vateritic (an alternative crystalline structure that results in translucent and unreadable otoliths), or a marine entry check could not be identified, the otolith was discarded.

We measured otolith width at the widest point along the dorsal-ventral axis. Otolith length was also measured, but preliminary analysis suggested that width was more strongly correlated with fork length ($r^2_{OL} = 0.77$ vs. $r^2_{OW} = 0.81$). We enumerated all increments between the potential check and the periphery. The distance from primordia to observed marine entry check (check radius) and the distance from primordia to periphery (total radius) were also recorded. All counts and measurements were performed three times per individual and the mean was used for subsequent analyses. If counts differed by more than eight daily rings, the otolith was excluded. We used a regression, followed by a chi-square analysis to test the null hypothesis that the slope and intercept of the relationship between predicted counts (based on known date of smolting) and observed counts were equal to one and zero respectively (Jolicoeur 1991, Trudel et al. 2004). Statistical analyses were conducted in R 2.15 (R Core Team 2012).

2.3.2. Field-caught fish

We used an elemental marker approach to validate the accuracy of visual marine entry check estimates in post-smolts. Previous studies have indicated that strontium and barium are deposited in otoliths proportional to their environmental concentration (Bath et al. 2000). Since Sr is typically positively correlated and Ba negatively correlated with salinity, the relative concentration of each of these elements in otoliths can be used to explore transitions between freshwater and marine environments (Macdonald and Crook 2010).

We used otoliths from 12 sockeye salmon post-smolts collected at sea in June and July 2007-2008 using a rope trawl (Tucker et al. 2009) to validate the formation of marine entry checks by otolith microchemical analysis after polishing and visual measurements (see above). Marine entry checks were visible and appeared similar to those observed in experimentally reared juveniles. Additionally, daily increments tended to become larger and more uniformly spaced following this check. This pattern was less consistent in lab-reared post-smolts, probably due to stable environmental conditions and food availability. DNA analyses (Beacham et al. 2005) performed on these fish indicated that nine *O. nerka* post-smolts were from Great Central Lake and three from Sproat Lake (both stocks enter the ocean on the west coast of Vancouver Island, British Columbia, Canada).

Elemental analysis was carried out at the University of Victoria's School of Earth and Ocean Science's Inductively Coupled Plasma Mass Spectrometry (ICP-MS) Facility in Victoria, BC with an X-Series II ICP-MS and an UP-213 laser ablation system. The laser was set at a pulse rate of 5 Hz with a 15-µm ablation spot size and intervals of 30-µm between ablation spot centers (except for Sample 1, which had a spacing of 50-µm between spot centers). Laser ablation occurred along the central dorsal axis of left otoliths. Prior to ablation, analyte isotopes were measured for 30 s and subtracted from those measured during ablation. Elemental concentrations were calculated using NIST 610, 613, and 615 standard glasses following methods in Miller (2007). Elemental ratios were recorded for Sr and Ba in g kg^{-1} (Ca is used as the internal standard for the analysis) and reported in mmol mol^{-1} for Sr:Ca and µmol mol^{-1} for Ba:Ca. One field-captured otolith was damaged during ablation and was removed from subsequent analyses.

Shifts in elemental concentrations were statistically quantified by estimating breakpoints in the regression between elemental ratios and distance from otolith core. Breakpoint analysis assumes that within the classical linear regression model there are multiple segments where regression coefficients are constant and identifies locations where this relationship shifts to a new state (Zeileis *et al.* 2002). Breakpoints are calculated by minimizing the residual sum of squares for each stable state of the regression model and have been previously used to quantify shifts in the elemental structure of otoliths (e.g., Stocks *et al.* 2014). Breakpoints, along with 95% confidence intervals, were calculated using the *strucchange* package (Zeileis et al. 2002, Zeileis et al. 2003) in R. The breakpoints function in this package is built upon an algorithm for estimating multiple breakpoints described in Bai and Perron (2003) and uses a distribution function for determining confidence intervals from Bai (1997). When models identified multiple breakpoints in a sample (likely due to differences between otolith core, freshwater, and marine zones), the breakpoint closest to the periphery was identified as the "marine" breakpoint and used as the marine entry check estimate. We assessed the accuracy of visual estimates by determining whether they fell within the 95% confidence interval of the estimated breakpoint.

2.4. Results

2.4.1. Laboratory-reared fish

The mean fork length ± S.D. of sockeye salmon post-smolts increased from 93.6 ± 17 mm in the first sampling period to 143.7 ± 14.0 mm in the final. Mean otolith width ± S.D. also increased from 1277 ± 142 µm to 1852 ± 132 µm between first and final sampling periods. Otolith width was linearly and positively correlated with fork length ($n = 94$, $r^2 = 0.81$, $P < 0.001$), suggesting that somatic growth can be back-calculated from otolith growth. Marine entry checks, identified as a particularly dark increment preceded by a translucent region near the otolith periphery, were observed in all experimentally reared *O. nerka* post-smolt otoliths that were undamaged and non-vateritic along the dorsal axis ($n = 94$; Fig. 2.1). Marine entry checks did not differ substantially in appearance from those observed in Chinook salmon (*O. tshwaytscha*; Middleton 2011) or chum salmon (*O. keta*; Saito *et al.* 2007). Sixteen otoliths were discarded due to damage. The number of increments observed was strongly correlated with the number of days since juvenile *O. nerka* were smolted, and the slope and intercept of the regression were not significantly different from zero and one respectively ($n = 94$, $r^2 = 0.99$, $\alpha = 0.99 \pm$

0.01 SE, $\beta = 0.13 \pm 0.39$ SE, $\chi^2 = 0.21$, $P > 0.05$). This relationship suggests that increments are formed daily in *O. nerka* for at least one hundred days after smolting.

2.4.2. Field-caught fish

In all samples of field-captured post-smolts, an increase in Sr:Ca could be observed near the otolith periphery that was consistent with saltwater entry (Figs. 2.1, 2.2); however, the breakpoint models suggested that chemical and visual marine entry estimates varied (Fig. 2.3). Five visual marine entry check estimates fell within the 95% C.I. of marine breakpoints calculated from Sr levels; the remaining visual marine entry estimates were consistently greater than the chemical estimates, suggesting visual entry checks were formed after Sr began to increase (Fig. 2.3).

Plots of Ba concentrations displayed a less consistent pattern than Sr. Although 10 otoliths displayed declines in Ba:Ca coincident with increases in Sr:Ca, breakpoint estimates could not be calculated for two samples (Fig. A2.1). Moreover, the majority of the otoliths examined displayed Ba declines that were strongest in the otolith core, where marine entry is highly improbable. Finally, only two samples had marine breakpoint estimates that were identical to those calculated using Sr:Ca. It is likely that these differences were caused by the extreme variation in Ba:Ca concentrations (up to three orders of magnitude) across otolith transects (Fig. A2.1). Due to the large variation in Ba values and associated improbable estimates of marine entry timing, only Sr:Ca estimates were used when making comparisons between chemical and visual estimates.

2.5. Discussion

We found evidence that otolith increments were produced at daily intervals in juvenile sockeye salmon for at least 100 days after a smolting event. Furthermore, we consistently observed marine entry checks in all otoliths. However, among samples captured in the field, visual estimates of ocean entry date often varied from those estimated using microchemistry by approximately one week. The trend for visual marine entry estimates to be observed after chemical estimates suggests check formation, though correlated with environmental Sr, is not dependent on the incorporation of elemental signatures. One consideration is that the relatively coarse scale at which elemental data were collected influences the precision of breakpoint estimates. We could only estimate confidence intervals across discrete increments (*i.e.* ablation spots) and because breakpoints are defined as the last observations in a segment before a shift, they will necessarily be skewed towards earlier observations.

Yet discrepancies between visual and marine checks were unlikely to be solely the result of statistical bias. Changes in otolith composition can be temporally variable and dependent on local environmental conditions such as temperature (Miller 2011). The field-captured post-smolts used in this study migrated through the Somass River and then Alberni Inlet, an estuary characterized by a relatively strong vertical salinity gradient to 2-10 m depth, for at least 10 km from the river mouth (Waldichuk et al. 1968). Juvenile sockeye salmon captured at sea are generally found at depths <10 m (Welch et al. 1998) and vertical or longitudinal movements through the estuary may result in variation among individuals in their exposure to Sr. Since the formation of increments, and therefore a visual entry check, likely depends on a minimum threshold of somatic growth, differences in spatial distribution coupled with variation in foraging rates could uncouple the formation of visual and chemical checks. Although a lack of detailed water quality metrics made testing these predictions impossible, visual and marine estimates of marine residency may differ due to individual behavior, particularly differences in movement rate through the estuary and individual growth. Indeed, differences in visual and chemical estimates were particularly great in otoliths with gradual increases in Sr levels, suggesting the rate at which elements are incorporated during estuarine residence varies.

After this study was completed, additional microchemical analyses were conducted on juvenile sockeye salmon captured north of Vancouver Island that had migrated through the Fraser River estuary. Preliminary results suggest that ~25% of these otoliths ($n = 15$) had visual entry checks that were underestimated relative to chemical checks by 6-21 days (Lyse Godbout, Fisheries and Oceans Canada, *personal communication*). Therefore, the visual checks of individuals migrating through the Fraser River tended to develop *before* chemical checks, which suggests the relationship between visual and chemical checks may vary between watersheds. If, as predicted, visual checks represent rapid growth after downstream migrations (Neilson et al. 1985, Zhang and Beamish 2000), differences in the amount of tidal intrusion and foraging conditions could underpin these differences. In this case, the Somass River, through which Great Central and Sproat Lake post-smolts migrate to Alberni Inlet, is relatively short and has considerably lower flows than the Fraser River. As a result, the strength of tidal intrusion into the Somass may be relatively greater and may be more likely to result in a chemical signature prior to feeding.

In conclusion, this study indicates that for *O. nerka* post-smolts there is a strong relationship between otolith and somatic growth and that otolith increments are formed daily. Marine entry check estimates were strongly correlated with known smolting date in experimentally reared individuals, but chemical estimates of marine entry from elemental ratios in field caught fish were earlier, on average, than visual estimates. These results suggest that the integration of environmental chemical signatures and the formation of microstructures in otoliths, though correlated, may reflect different physiological processes influenced by individual behaviour.

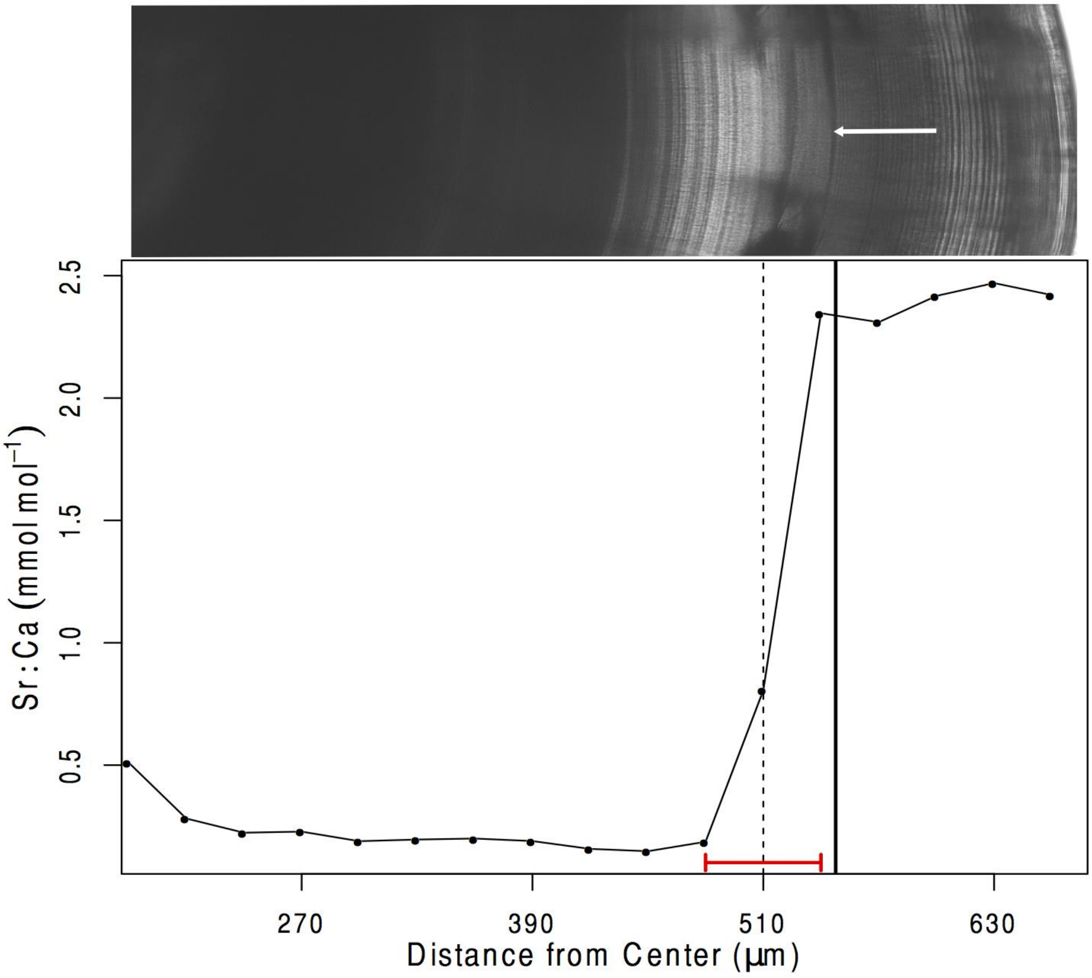

Figure 2.1 Polished sockeye salmon post-smolt otolith and associated Sr:Ca profile. The white arrow on image and black vertical line on Sr:Ca profile indicate the visual marine entry check estimate. The irregular, light zone immediately preceding the visual estimate represents the freshwater annulus. The dashed vertical line on the element profile represents the chemical estimate with associated 95% C.I. as determined by breakpoint analysis.

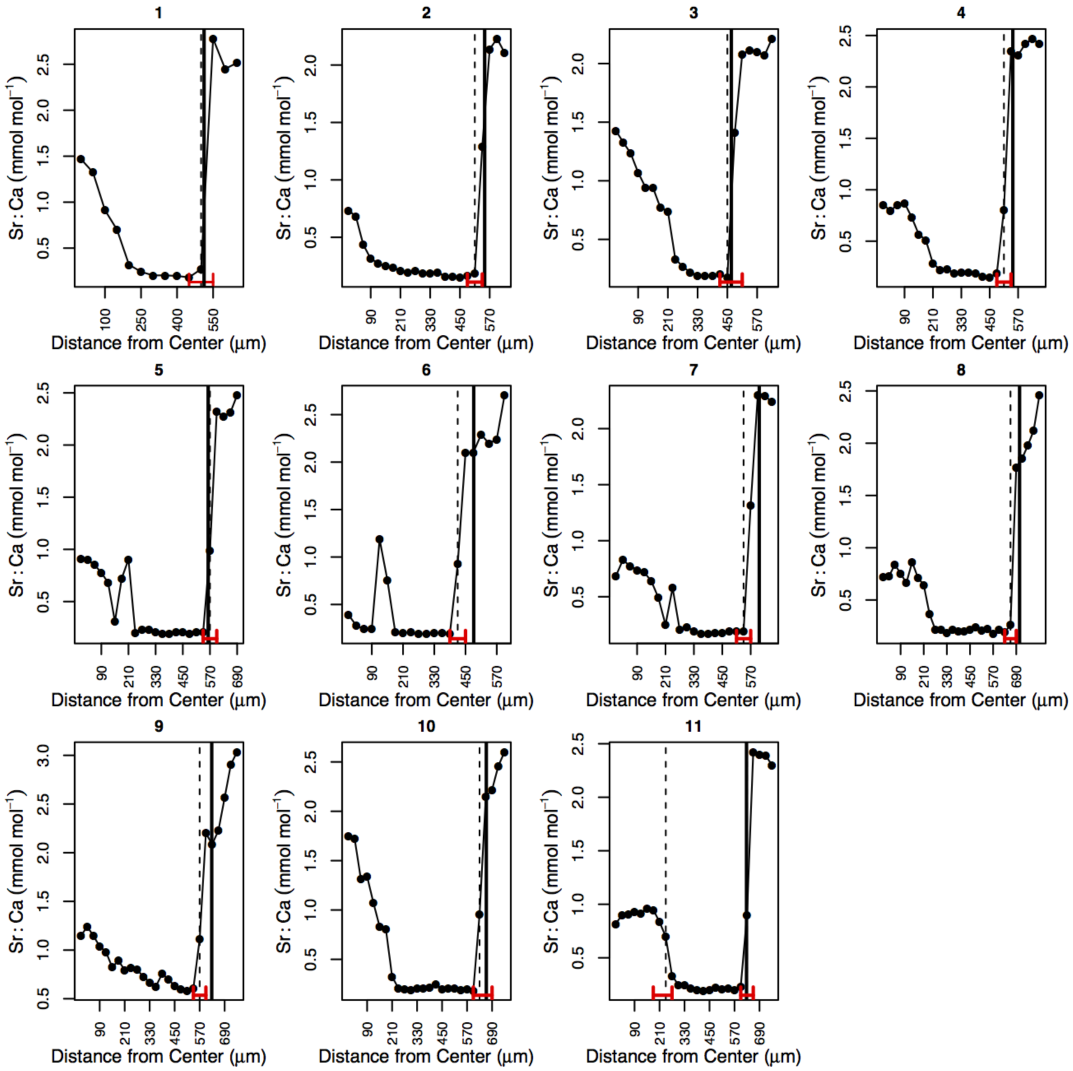

Figure 2.2 Sr:Ca concentrations of ICP-MS laser transects. Transects run from otolith primordia to dorsal periphery The zone representing transition to saltwater is characterized by an increase in Sr:Ca. Visual marine entry check estimates are represented by solid black vertical lines. Breakpoint estimates and 95% C.I. are represented by dashed vertical and horizontal red lines respectively. Note Sample 11 has two breakpoint estimates since the model failed to converge when restricted to one.

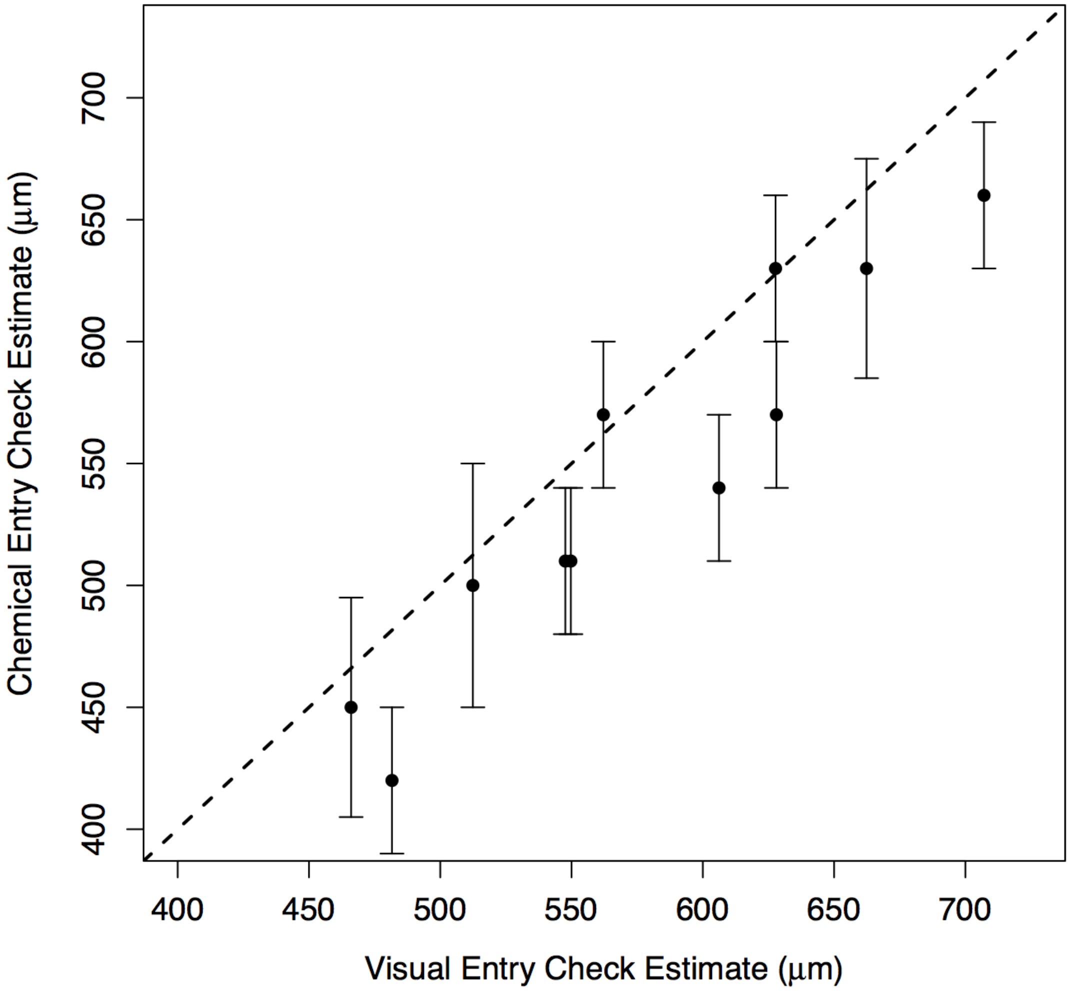

Figure 2.3 Visual and chemical estimates of marine entry measured as µm from the otolith core. Chemical estimates have 95% C.I. calculated using breakpoints in the regression of element concentrations across the otolith transect.

Chapter 3 - Disentangling individual- and population-scale processes within a latitudinal size-gradient in sockeye salmon

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3.1. Abstract

We examined how individual processes contribute to a latitudinal gradient in body size within populations of migrating juvenile sockeye salmon (*Oncorhynchus nerka*) while simultaneously testing for size-selective mortality, a potentially confounding population scale process. Using otolith microstructure techniques and structural equation modeling, we determined that ocean entry size and phenology had strong, direct effects on size at capture. Population identity and freshwater age also had strong indirect effects, moderated by size at entry. Conversely, marine growth rates immediately after entry or before capture were relatively weak predictors of size during migration. We tested for shifts in size distribution indicative of selective mortality, but found no evidence that smaller individuals experienced lower survival during early marine migrations. These results indicate that the migratory distributions of juvenile sockeye salmon are influenced by body size and that this variation is predominantly driven by traits present prior to freshwater outmigration, rather than marine growth or differential survival. We suggest integrating individual variation in migratory characteristics with the effects of environmental conditions experienced en route to provide an improved understanding of migratory species.

3.2. Introduction

Due to the strong link between body size and a wide range of ecological patterns, quantifying and interpreting variation in size within populations is often a critical step to understanding their dynamics (Peters 1983, Brown et al. 2004). This is particularly true in migratory species where body size is positively correlated with both travel speed (Ware

1978) and energy stores (Huss et al. 2008). Although differences in body size are strongly influenced by genetics and life-history strategy, from a proximal perspective they are a function of an individual’s previous size, growth rate, and age. However the frequency of size classes within a group can also be strongly influenced by size-dependent mechanisms, such as selective mortality, that act on the population as a whole (Sogard 1997). As a result, the size distribution of a migrating population may be predominantly static and driven by individual traits that are present prior to departure or moderated by the conditions the population experiences during long distance movements.

Sockeye salmon (*Oncorhynchus nerka*) is an anadromous species with a broad geographic distribution, distinct life history strategies at several biological scales (Burgner 1991), and evidence of differential migration between and within populations (Beacham et al. 2014a, Beacham et al. 2014b). After rearing in freshwater systems, juvenile sockeye salmon migrate from coastal rivers to maturation grounds in the north Pacific Ocean and Bering Sea over a period of several months (Burgner 1991). Juveniles travelling along the coastal migration corridor exhibit a consistent latitudinal gradient in body size. Individuals captured in northern regions are significantly larger and in better condition than those captured at approximately the same time further south (Tucker et al. 2009, Beacham et al. 2014b). Furthermore, this pattern persists from May through the following March each year, across more than a decade of survey data (Tucker et al. 2009, Beacham et al. 2014b). Since this gradient is present within a given population aggregate, differences in body size are not an artifact of northern regions simply producing larger fish *sensu* Bergmann’s rule (Tucker et al. 2009, Beacham et al. 2014b).

Instead, larger body size in northern regions is expected to be correlated with individual traits influenced by both freshwater and marine rearing environments. Specifically, greater size at ocean entry (smolt size), a longer period of time at sea, more years spent rearing in freshwater, faster growth during migration, or a combination of several of these traits could create a gradient in body size (Tucker et al. 2009). Populations that produce larger smolts are typically distributed further north and earlier in the year, which supports the hypothesis that size at ocean entry can shape spatial variation in size (Beacham *et al.* 2014b). Yet it is unknown whether there is sufficient variation in smolt size to create a latitudinal gradient within populations and the effects of ocean entry timing, age, and marine growth are untested altogether.

Alternatively, changes in the size distribution of a migrating population may be the result of processes acting on that population as a whole, rather than the differential migration of individuals. Mortality is estimated to be especially high among juvenile Pacific salmon at sea (Beamish and Mahnken 2001) and appears to be size-selective in several populations (Holtby et al. 1990, Henderson and Cass 1991, Bond et al. 2008, Claiborne et al. 2011, Duffy and Beauchamp 2011); however, it remains unclear whether this mortality is greatest during juvenile migrations, during the first winter at sea, or is stable throughout ocean residency. If mortality rates of sockeye salmon are particularly high during northward migrations, an increase in the mean size of the population with latitude could occur due to the selective removal of the smallest individuals independently of individual variation in migratory characteristics.

Tucker et al. (2009) and Beacham et al. (2014b) observed an increase in juvenile sockeye salmon body size with latitude; however, the nature of their data prevented them from examining individual populations in a given year. Therefore, our first objective was to test the hypothesis that body size of sockeye salmon varies consistently with latitude while controlling for inter-annual and population effects. Next, we tested the relative importance of size at ocean entry, length of ocean residency, marine growth, and age in creating a body size gradient. Since migratory phenology and size often vary between years (Kovach et al. 2013) and populations (Beacham et al. 2014b), we also accounted for inter-annual and population effects in our models. Finally, we tested for the presence of size-selective mortality (SSM) to determine whether population scale processes could be interacting with or masking individual differences.

3.3. Methods

3.3.1. Drivers of variation in body size

At the level of the individual, the final body size of an organism (L_t) is a function of its previous size (L_0), growth (G), and time (t) where:

$$L_t = L_0 + G*t \qquad \text{Eq. 3.1}$$

To gauge the relative importance of variation among individuals, each of these parameters must be estimated during the period of interest. In this study, L_0 represented size at the beginning of migration (i.e. ocean entry) and G represented growth during a time period of days (t). We examined growth during two distinct periods. First, we estimated growth during the initial week after ocean entry because of its association with the duration of nearshore residency and migratory rate of other salmonids (Healey 1980). The second period represented growth in the week immediately prior to capture and was chosen to encompass potential spatial variation in growing conditions that could result in divergent body sizes developing en route (Tucker et al. 2009, Ferriss et al. 2014). Depending on population and life history, sockeye salmon can enter the marine environment as sub-yearlings or after a variable number of years of freshwater rearing. Since freshwater age may be correlated with body size and phenology (Bugayev 2000), we also estimated its indirect effect on capture fork length via size at ocean entry and length of marine residency.

Conversely, tests of size-selective mortality (SSM) require repeated sampling of a population over time or space so that size distributions before and after potential mortality events can be compared. In juvenile fishes SSM is generally directional so that larger individuals have higher survival rates (Sogard 1997). As smaller individuals are removed via SSM, the size distribution of the population should exhibit decreased variance, increased kurtosis, and negative skewness (indicative of a rightward shift), as well as an increase in mean size (Gagliano et al. 2007).

3.3.2 Field sampling and data collection

We collected juvenile sockeye salmon in 2007 (June 22 – July 5) and 2008 (June 21 – July 3) from seven sampling regions along a south-north gradient from southern British Columbia to the Alaskan border (Fig. 3.1; Table A3.1). Fish were captured with a mid-water rope trawl hauled at the surface for 15-30 minutes at 5 knots (~9.8 km/h) by *CCGS W.E. Ricker* and *F/V Viking Storm*. Up to 30 juvenile sockeye salmon were randomly selected from each net tow for sampling. We recorded fish length and mass and removed both sagittal otoliths at time of capture. Tissue samples were removed from the operculum and preserved for population identification. Individuals were identified to the population level using 14 microsatellite loci (Beacham et al. 2005). A 50% probability was used as a lower limit when assigning individuals to populations and the false assignment rate was estimated to be 5% (Beacham et al. 2005).

To ensure a sufficient sample size, our analysis focused on individuals belonging to four of the most abundant populations. Lower Adams River (LA) and Chilko Lake (CH) are populations that are located in the Fraser River drainage, approximately 484 km and 629 km, respectively, from their ocean entry point in the southern Strait of Georgia (Crossin et al. 2004). After ocean entry, both populations generally migrate north through Johnstone Strait (Tucker et al. 2009; Beacham et al. 2014a, 2014b). Great Central Lake (GC) and Sproat Lake (SP) populations spawn in central Vancouver Island (26 km and 8 km from the coast, respectively), enter the ocean on the west coast via Barkley Sound, and undertake a similar northward migration along the continental shelf (Wood et al. 1993, Tucker et al. 2009, Beacham et al. 2014a). North of Vancouver Island, all four populations are commonly captured together and appear to exhibit similar migratory pathways to their maturation grounds in the Gulf of Alaska (Tucker et al. 2009; Beacham et al. 2014a, 2014b; Fig. 1).

We used otolith microstructure techniques to estimate the growth and migration history of captured fish. Otoliths are calcareous structures found in many teleosts that are commonly used in age and growth studies because of their incremental formation. Otolith and somatic growth are strongly correlated in juvenile sockeye salmon and individuals form a distinct marine entry check mark after transitioning to saltwater (Freshwater et al. 2015). Therefore otolith size at this check can be used as a proxy for body size at ocean entry. By enumerating and measuring the spacing between otolith micro-increments that are formed daily after the marine entry check mark, it is possible to estimate length of ocean residency and marine growth rates, respectively (Neilson et al. 1985, Zhang and Beamish 2000). Finally, annual age can be inferred by counting annuli, large opaque bands that represent periods of slower, winter growth (Neilson et al. 1985, Zhang and Beamish 2000).

The otolith microstructure of approximately one third of the captured individuals (*n* = 367) was examined. Microstructure observations were made after otoliths were polished by hand following methods in Freshwater et al. (2015). cellSens Imaging Software (Olympus Scientific Solutions America) was used to measure several otolith microstructure characteristics: 1) marine entry check radius, 2) number of daily circuli after entry mark, 3) length of first marine weekly increment, 4) length of last marine weekly increment, and 5) freshwater age. We measured radii from the otolith core to the marine entry check. We enumerated increments between the marine entry check mark and the otolith periphery to estimate days at sea. To estimate weekly growth, we measured the distance between the marine entry check and the seventh daily ring after marine entry (first week of growth) and between the seventh to last daily ring and the otolith periphery (last week of growth). Individuals with one freshwater winter annulus were classified as age-1 and those with two as age-2. All measurements were made dorsal and perpendicular to the anterior-posterior centerline of the otolith (Fig. 3.2) and were completed three times per otolith with the average used in subsequent analysis. If measurements could not be completed due to damage or if counts differed by more than eight daily rings, the otolith was discarded (18 out of 367).

Otolith width was positively and linearly related to fork length at capture (r^2 = 0.80, *n* = 367, *P* < 0.001), suggesting the radius of the marine entry provides a reasonable estimate of fork length at ocean entry. However since estimates of size are necessarily calculated using fork length at capture (e.g., Neilson et al. 1985), we were concerned that using back-calculated estimates of entry size in the SEMs could falsely inflate the correlation between size at ocean entry and size at capture. Therefore, raw otolith microstructure measurements were used in model construction.

3.3.2. Statistical analyses

Juvenile sockeye salmon captured in the Strait of Georgia in 2007 were not stock identified and were excluded from this analysis. Therefore, we conducted all analyses on two distinct datasets to spatially and temporally balance the sampling design. The first dataset included Vancouver Island populations (GC and SP) sampled in both 2007 and 2008 (subsequently referred to as VI dataset), while the second included Fraser River populations (CH and LA) captured in 2008 (subsequently referred to as FR dataset).

We used linear models to test the hypothesis that fork length at capture increased with latitude, while controlling for the effects of population identity and year of capture (set as fixed effects and coded as dummy binary variables). Since fork length at capture was not normally distributed, it was log transformed before constructing linear models.

Next, we used structural equation modeling (SEM) to examine the relationship between fork length at capture and early marine characteristics estimated from otolith microstructure (see methods above). In SEM, several interacting processes are simultaneously modeled to assess their cumulative effects (Grace and Keeley 2006). Given that variability in body size, phenology, age, and growth can have cascading effects on one another, SEM provides an ideal framework for disentangling causal pathways among individual traits. We specified, evaluated, and adapted models following guidelines developed for ecological systems in Grace et al. (2010). We developed *a priori* models based on observational and theoretical evidence (Fig. 3.3; detailed justifications for paths provided in Table A3.2). Note that we did not initially include direct effects linking population and year to size at capture; however, these SEMs fit poorly and direct links between population and year to capture size were included in all final models. Differences between the FR and VI datasets (populations, years, and age effects) forced us to specify unique SEM structures for each dataset.

To compare the relative importance of early marine characteristics that differed substantially in unit of measurement and variance, all continuous variables were centered and reduced to a mean and variance of zero and one, respectively. Although fork length at capture and marine entry check radius measurements were not normally distributed, we estimated SEMs using either weighted least-square with mean and variance corrected (WLSMV; VI dataset) or robust maximum likelihood techniques (MLR; FR dataset). Since both are robust to deviations from normality (Brown 2006, Rosseel 2012), we standardized, but did not transform all data. WLSMV was required for the VI dataset SEM since it included an endogenous categorical variable (i.e. freshwater age).

We confirmed adequate model fit with a chi-square goodness of fit index, which compares the implied model covariance structure to that of the raw data ($P > 0.05$ indicates adequate fit), and secondarily tested fit with four additional indices (Table A3.4): Normed Fit Index (Bentler and Bonett 1980), Non-Normed Fit Index (Hu and Bentler 1998), Root-Mean-Square Error of Approximation (MacCallum et al. 1996), and Comparative Fit Index (Bentler 1990). We calculated the indirect effects of explanatory variables on capture size by multiplying coefficients from compound significant paths (Grace and Keeley 2006).

To test for the presence of SSM, we estimated three metrics associated with size distributions: variance, Pearson’s kurtosis coefficient, and Pearson’s skewness coefficient. We calculated each metric for each subpopulation, i.e. a unique combination of population, sampling region, and year (regions denoted in Fig. 3.1; catch breakdown in Table A3.1). Specifically, we predicted that if SSM was the principal mechanism of a latitudinal increase in mean size, variance would decrease, kurtosis would increase, and skewness would decrease (indicating a rightward shift) with increasing latitude. To test these hypotheses, we compared the performance of a suite of hierarchical linear models testing for correlations between each SSM metric and latitude, while controlling for the effects of population identity and sampling year.

Since variance typically decreases with sample size before stabilizing, we preliminarily tested for the potential confounding effect of small sample sizes within subpopulations. We sampled with replacement from four different subpopulations, calculated the variance at sample sizes ranging from 5-150 individuals, and repeated this procedure 10,000 times. Depending on the subpopulation, variance estimates stabilized at 20 – 40 individuals (Fig. A3.1). We next constructed models for three different datasets that consisted of subpopulations containing at least 20, 30, or 50 individuals. Model selection indicated the results were qualitatively similar regardless of the sample size threshold and our explanatory power was increased when a larger number of subpopulations could be included (i.e. a threshold of $n = 20$). Therefore, we only present those results here.

We used an information theoretic approach to test for the effect of latitude on fork length at capture and on the three SSM metrics (Burnham and Anderson 2002). Akaike Information Criteria adjusted for small sample sizes (AICc) were used to assess model performance with different combinations of predictor variables, beginning with a null model containing no explanatory variables (Zuur et al. 2009). Since AIC selection often ranks complex models with little additional explanatory power as equivalent to simpler, nested models, we selected the most parsimonious model (i.e. fewest explanatory variables) with a ΔAICc < 2 (Burnham and Anderson 2002, Richards 2008). We used histograms of residuals, Shapiro-Wilks tests, and QQ plots to verify models met normality and homoscedasticity assumptions.

All statistical analyses were performed with the statistical software R (R Core Team 2012) using the *moments* (Komsta and Novometsky 2012) and *lavaan* (Rosseel 2012) packages.

3.4. Results

3.4.1. Latitudinal size gradient

We examined variation in fork length at capture in 1011 juvenile sockeye salmon (n_{VI} = 684; n_{FR} = 327). As previously observed (Tucker et al. 2009, Beacham et al. 2014b), the mean fork length of individuals captured increased with latitude across all sampled populations and years (Fig. 3.4, Table 3.1). AICc model selection indicated saturated models incorporating latitude, population, and year effects had the greatest support in both datasets (ΔAICc of next best model > 2; Table A3.3). Among VI individuals, juveniles from Great Central Lake were smaller than those from Sproat Lake (mean ± SD: FL_{GC} = 117 ± 19.5 mm; FL_{SP} = 140 ± 23.1 mm), and individuals were smaller in 2007 than 2008 (FL_{2007} = 120 ± 20.5 mm, FL_{2008} = 140 ± 23.8 mm). In the FR dataset, Lower Adams River individuals tended to be smaller than juveniles originating from Chilko Lake (FL_{LA} = 112 ± 10.8 mm, FL_{CH} = 123 ± 14.4 mm). Finally, capture size increased more quickly with latitude among VI individuals than FR individuals (Table 3.1).

3.4.2. Individual-scale processes

We analyzed the otoliths of 367 of the 1011 juvenile sockeye salmon captured in 2007 and 2008 (n_{VI} = 262; n_{FR} = 105; Table A3.5). The range of values observed across otolith metrics was similar for both datasets, although VI juveniles exhibited greater variation in ocean entry size and duration of marine residency (Table 3.2). Chi-square goodness of fit tests indicated the SEMs fit the observed data well (VI dataset: χ^2 = 8.48, DF = 5, P = 0.13; FR dataset: χ^2 = 0.92, DF = 2, P = 0.61; additional indices also suggested good fit (Table A3.4)). Both SEMs explained a substantial proportion of the variation observed in body size during the juvenile migration of sockeye salmon (r_{VI}^2 = 0.86; r_{FR}^2 = 0.51). In both models juvenile body size was directly and indirectly affected by multiple individual characteristics; however, the importance of different traits, as well as how individual traits interacted with one another, differed between VI and FR individuals (Fig. 3.5).

Among VI juveniles otolith radius at the entry check, a proxy for ocean entry size, had the greatest direct effect on size at capture (Fig. 3.5a, Table 3.3). Since size at ocean entry was significantly correlated with freshwater age, age also had strong positive, but indirect, effects on body size at capture (Fig. 3.5a, Table 3.3). The model identified strong, positive correlations between duration of marine residency and size at capture; however, there was no significant relationship between size at ocean entry and the timing of ocean entry (Fig. 3.5a). Although Great Central Lake individuals were typically smaller during migration than Sproat Lake juveniles, population identity did not influence size at capture directly. Rather, Great Central Lake individuals exhibited significant differences in entry size, age structure, and ocean entry timing (Fig. 3.5a) and, as a result, the total effect of population identity on body size was considerable (Table 3.3). The VI SEM indicated strong inter-annual effects on body size at capture and population age structure, as well as correlations with growth immediately prior to capture and the timing of ocean entry (Fig. 3.5a, Table 3.3). Finally, early marine growth was a weak, but significant predictor of final body size, while marine growth immediately prior to capture was not significantly correlated with final body size (Fig. 3.5a, Table 3.3).

To test whether age-2 juveniles were disproportionately influencing the model we also constructed an SEM including only age-1 VI individuals. Although the overall fit of this model was moderately weaker ($r^2 = 0.74$), the pathways identified as significant were similar (Fig. A3.2), indicating that entry size and timing are strong drivers of body size variation during migration independent of age structure.

Variation in fork length at capture of Fraser River juveniles was also strongly correlated with size at ocean entry and inter-population differences (Fig. 3.5b, Table 3.3). Unlike the VI dataset, there was support for a direct effect of population identity on final body size and this effect was magnified by indirect effects via differences in marine growth (Fig. 3.5b, Table 3.3). Growth immediately prior to capture and duration of marine residency were also significantly correlated with size during migration, albeit more weakly (Fig. 3.5b, Table 3.3). As in the VI dataset there was no significant correlation between duration of marine residency and size at entry (Fig. 3.5b).

3.4.3. Population-scale processes

After restricting our analysis to subpopulations with at least 20 individuals, we examined changes in variance, kurtosis and skewness across a latitudinal gradient with 17 unique combinations of population, capture region, and year. Based on AICc model selection, none of the proposed explanatory variables improved model fit relative to a null model including only an intercept term (Fig. 3.6, Table 3.4; all models shown in Table A3.6). Thus variance, kurtosis, and skewness did not consistently vary with latitude.

3.5. Discussion

In this study, we predicted that latitudinal shifts in the size distribution of juvenile sockeye salmon would be correlated with variation in individual characteristics, as well as ecological processes that act upon populations as a whole. We tested these hypotheses using four populations of juvenile sockeye salmon captured along a marine migratory corridor. Specifically, we examined the relative importance of different early marine characteristics (smolt size, phenology, age, and marine growth) on the formation of a latitudinal gradient in size, while controlling for inter-population and inter-annual effects. We also tested for the presence of size-selective mortality (SSM) during this period, which could independently create an apparent increase in mean size. We determined that the size of migrating individuals is more strongly related to individual traits present prior to long distance movements than growth en route. Similarly, there was no evidence that the latitudinal gradient in size we observed was associated with SSM.

3.5.1. Latitudinal size gradient

Previous studies have used catch data pooled across years to demonstrate that the fork length and energy density of juvenile sockeye salmon increases with latitude within a population (Beacham *et al.* 2014b) or population aggregate (Tucker *et al*. 2009). Ours is the first study, however, to confirm consistent increases in fork length with latitude while controlling for both population and year effects. The presence of a latitudinal gradient across several populations and years indicates juvenile sockeye salmon do not move north as a homogeneous group. Instead migratory rate, phenology, or both appear to be influenced by body size.

3.5.2. Individual-scale processes

The Vancouver Island (VI) and Fraser River (FR) structural equation models (SEMs) indicated that size during migration was directly and indirectly related to several ecological characteristics. In both VI and FR individuals, otolith radius to the marine entry check (a proxy for size at ocean entry) had the greatest direct effect on variation in size at capture. While it is intuitive that initial fork length will influence subsequent length, at some point during development body size becomes more dependent on growth than previous size (Thanassekos et al. 2012). Our findings suggest that most of the juveniles in these populations maintain their initial size differences for several weeks after ocean entry, despite the accelerating growth rates of other individuals (next paragraph). Furthermore, these size differences are strongly correlated with the spatial distribution of individuals. While it is likely that larger juveniles are able to migrate more rapidly due to the direct effect of body size on optimal swimming speeds (Ware 1978), movement rates may also be influenced by size-specific behavioral differences, for example foraging activity and predator avoidance (Mittelbach 1981).

Size at capture was also positively associated with the length of marine residency in all four populations. Such a pattern is likely driven by the rapid acceleration in growth that typically occurs in sockeye salmon after ocean entry (Burgner 1991). In several salmon species entry timing appears to be earlier among individuals that are larger at ocean entry (Irvine and Ward 1989, Weitkamp et al. 2012); however, in this study marine entry check radius was not correlated with the number of days individuals had been at sea. Since migration phenology (i.e. the timing of ocean entry) was significantly correlated with capture size, independently of size at entry, early ocean entry may be an alternative strategy that allows smaller individuals to compensate for poor growth in freshwater and reach a relatively large size during migration.

The spacing of weekly increments, which served as indicators of marine growth, was a less consistent predictor of size during migration than other otolith metrics. Among VI individuals capture size was significantly, although weakly, correlated with early marine growth, but was not linked to growth prior to capture. Conversely, the capture size of FR juveniles was directly correlated with growth in the week prior to capture, but not growth immediately after entry. The relatively weak effect of increment spacing on capture size observed here contrasts with previous work that identified strong spatial variability in salmonid marine growth rates (Ferriss et al. 2014). This discrepancy may have been caused by differences in the specific locations, years, or populations that were sampled. Alternatively, residual variation associated with the otolith-body size relationship may result in weekly increments providing a relatively weak signal compared to other otolith metrics; however, these weak relationships do not appear to be limited to weekly estimates of growth. Preliminary analyses indicated that average marine growth rate (i.e. the average spacing of daily increments) was also a relatively poor predictor of size at capture. After accounting for the effects of capture year and population identity, a model containing average marine growth rate had similar performance relative to a model containing either the first or the first and last weekly increments as explanatory variables (Table A3.7).

Size or growth advantages present in early developmental stages can have cascading impacts on subsequent life history stages, particularly in gape-limited taxa such as many fishes (Fuiman and Higgs 1997, Post 2003). Therefore, it was unsurprising that we observed indirect effects of freshwater traits on size during migration in all four populations. VI juveniles that were larger at ocean entry grew more rapidly immediately after river out-migration and this early marine growth had significant effects on marine growth prior to capture, as well as size at capture. Similarly, although no direct path between freshwater age and size at capture existed, its total effect was large because of the close correlation between age and entry size. In some cases traits also moderated one another – in the FR dataset greater early marine growth was correlated with later ocean entry, ultimately weakening the normally positive direct effect of marine residency on migration size.

Despite many structural similarities, the effect size of paths in the VI and FR SEMs differed. Some of these differences may be a result of the smaller, one-year sample size of the FR dataset. Others, however, may be due to the unique freshwater rearing habitats, marine entry environments, and initial migratory routes used by these distinct population groups. For example, VI individuals displayed greater variation in entry size and phenology than FR populations – characteristics that may be related to lower densities during freshwater rearing (Connor et al. 2013).

3.5.3. Inter-population and inter-annual effects

Population identity had strong effects on size at capture via intervening freshwater and marine variables. Such effects are broadly supported by previous observations of substantial variation among salmonid populations in migratory patterns at sea (Trudel et al. 2011, Lacroix 2013, Beacham et al. 2014a, Beacham et al. 2014b). Consistent with findings in Beacham et al. (2014b), migrating Great Central Lake juveniles were typically smaller than other VI populations; however, this study clarifies that these size differences are likely residual effects due to growth during freshwater rearing and the timing of marine entry. Conversely, differences in size at capture between FR populations were not strongly correlated with entry size or phenology, but were related to population-specific marine growth rates. Therefore, while inter-population variation is likely common in many salmonid populations, the influence of distinct freshwater rearing habitats relative to differences in early marine distributions may vary.

Although we could not evaluate temporal differences in the FR dataset, we observed significant inter-annual effects among VI individuals. Inter-annual differences in size and phenology are likely a function of several biological processes that can influence growth in both freshwater rearing grounds and en route to overwintering regions including: primary production and prey community composition (Bi et al. 2011, Tomaro et al. 2012), density-dependent interactions (Peterman 1984), and temperature (Welch et al. 1998).

Direct effects of sampling year (VI dataset) and population (FR dataset) on size at capture were not included during initial construction of SEMs, but were added post hoc to achieve adequate model fit. These variables may represent differences not captured by other metrics, for example, the residual variation unexplained by the otolith-body size relationship.

3.5.4. Size selective mortality

Selective mortality can strongly influence the size distribution of fish populations in general (Sogard 1997) and such shifts been observed during the marine period in several populations of Pacific salmon using hard structures (*O. kisutch*, Holtby et al. 1990; O*. nerka*, Henderson and Cass 1991, Farley *et al.* 2007; *O. tshawytscha,* Claiborne *et al.* 2011; *O. gorbuscha*, Cross *et al.* 2011; *O. mykiss,* Bond *et al*. 2008). Yet identifying when and where selective mortality occurs during marine residency is not possible using hard structures from returning adults alone. As a result, a precise understanding of when and where bottlenecks in Pacific salmon survival occur remains unclear.

We did not detect any evidence of size-selective mortality in juvenile sockeye salmon during their initial offshore migration. Although kurtosis was weakly correlated with latitude, the relationship was negative indicating the size distribution was becoming less peaked as migration progressed – the opposite of what would be expected if smaller individuals were selectively removed. We stress that our study was not intended to rigorously explore whether or not differential survival occurs during the marine residency of sockeye salmon, but rather to determine if it co-occurred with the formation of a latitudinal size gradient. Therefore, we cannot reject the possibility that SSM occurs in these populations, but it is unlikely that differential survival drives an increase in mean size with latitude.

Several caveats limit our ability to apply our findings regarding patterns in SSM more broadly. First, we would not detect SSM if mortality is episodic and a variety of sizes are selected against at different periods. For example, while Rhinoceros Auklets preferentially target smaller juvenile sockeye salmon in poorer condition (Tucker et al. 2016), these predation events are spatially restricted and may not be representative of mortality during migration overall. Instead mortality during migration, a period of several months, will be a function of a wide range of predators (Christensen and Trites 2011) and pathogens (Miller et al. 2014b). If various mortality mechanisms remove specific size ranges of juvenile salmon during their migration, the selective effects of any one source of mortality may be masked. Similarly, we would not detect SSM if it is most severe overwinter (i.e. after our final sampling event in mid-July), after juvenile sockeye salmon have moved offshore to maturation grounds and are thought to be energetically stressed (Farley et al. 2011). Finally, the impact of SSM on salmon populations may vary inter-annually so that its effects are only apparent in years of poor survival (Woodson et al. 2013). As a result, selective mortality may intermittently drive body size variation in these populations, but be absent during our sampling years because marine survival rates were average or high (DFO 2012, 2014a).

Long distance migrations occur in many taxonomic groups and have been identified as periods with especially high fitness costs (Alerstam et al. 2003). Although migrations are influenced by many biological traits, body size may be particularly important due to its effect on maximum movement rates (Ware 1978), foraging breadth

(Mittelbach 1981), energy storage (Huss et al. 2008), predator avoidance (Sogard 1997), and future reproductive fitness (Peters 1983). Our findings indicate that the distribution of juvenile sockeye salmon during marine migration varies predictably with body size, at least during the initial migratory period. Furthermore, variation in body size during migration among the studied populations and years was predominantly driven by individual traits present prior to freshwater emigration, specifically initial size and phenology, rather than processes occurring en route, i.e. differential growth or selective mortality. While the importance of individual variation to migration has been widely recognized in terrestrial systems, it has been relatively rarely studied in aquatic species (with the exception of partial migration; e.g., Brodersen et al. 2008). Our results strongly suggest that aquatic migrations cannot be viewed as simple, homogenizing events that influence populations and individuals uniformly. To successfully manage and conserve migratory species a detailed understanding of their ecology during these long-distance movements is essential.

Table 3.1 Parameter estimates of linear models examining fork length at capture (log transformed) from Vancouver Island and Fraser River datasets. Population identity and year were coded as dummy variables. Model parameters were estimated relative to Sproat Lake individuals in 2007 (VI dataset) and Lower Adams individuals in 2008 (FR dataset). All parameters are statistically significant (CI does not overlap 0).

Dataset	Explanatory Variable	Estimate (± 95% CI)
Vancouver Island	Latitude	0.07 ± 0.004
n = 684	Great Central	-0.05 ± 0.015
	Year	0.15 ± 0.013
Fraser River	Latitude	0.05 ± 0.006
n = 327	Chilko	0.02 ± 0.019

Table 3.2 Means ± SD of individual juvenile sockeye salmon traits estimated from otolith microstructure across datasets and years. Data ranges are shown in parentheses.

Estimated Variable	Fraser River	Vancouver Island	
	2008	2007	2008
	(*n* = 103)	(*n* = 113)	(*n* = 149)
Size at Capture (mm)	123 ± 13 (94 – 175)	125 ± 22 (86 – 205)	145 ± 25 (91 – 200)
Marine Entry Check Radius (μm)	569.7 ± 46.9 (500.0 – 766.5)	562.8 ± 56 (451.51 – 774.87)	602.0 ± 65.5 (449.3 – 813.4)
Marine Residency (days)	47 ± 6 (31 – 59)	58 ± 8 (38 – 59)	56 ± 9 (32 – 84)
First Weekly Increment (μm)	16.4 ± 3.1 (8.1 – 25.5)	13.6 ± 3.1 (6.9 – 22.2)	14.3 ± 2.8 (7.4 – 21.0)
Last Weekly Increment (μm)	19.6 ± 2.9 (13.7 – 27.3)	21.7 ± 3.3 (12.6 – 33.6)	20.9 ± 3.1 (12.7 – 28.8)

Table 3.3 Estimates of direct, indirect, and total effects of standardized explanatory variables on fork length at capture based on significant paths identified in structural equation models. Blank spaces represent paths that were not included or not significant in the final SEMs.

	Explanatory Variable	Direct Effect	Indirect Effect	Total Effect
Vancouver Island	Population		-0.783	-0.783
	Year	0.423	0.188	0.611
	Age		0.461	0.461
	Entry Radius	0.662	0.031	0.692
	Days at Sea	0.378		0.378
	Early Growth	0.125		0.125
Fraser River	Population	-0.370	-0.056	-0.427
	Entry Radius	0.612		0.610
	Days at Sea	0.208	-0.011	0.197
	Early Growth		0.068	0.068
	Late Growth	0.208		0.208

Table 3.4 AICc rankings and the estimated fit of top size selective mortality models (ΔAICc < 2). If multiple models had equivalent rankings, the top ranked model (bolded) was the model with the fewest number of parameters (Burnham and Anderson 2002). Models with no explanatory variables include only an intercept term.

SSM Metric	Explanatory Variables in Model	ΔAICc	Log-likelihood	r^2
Variance	**None**	0.00	-88.01	NA
	Year	1.03	-87.03	0.05
Skewness	**None**	0.00	-4.64	NA
Kurtosis	**None**	0.00	-22.06	NA
	Latitude	0.54	-20.83	0.07
	Year	1.19	-21.16	0.04

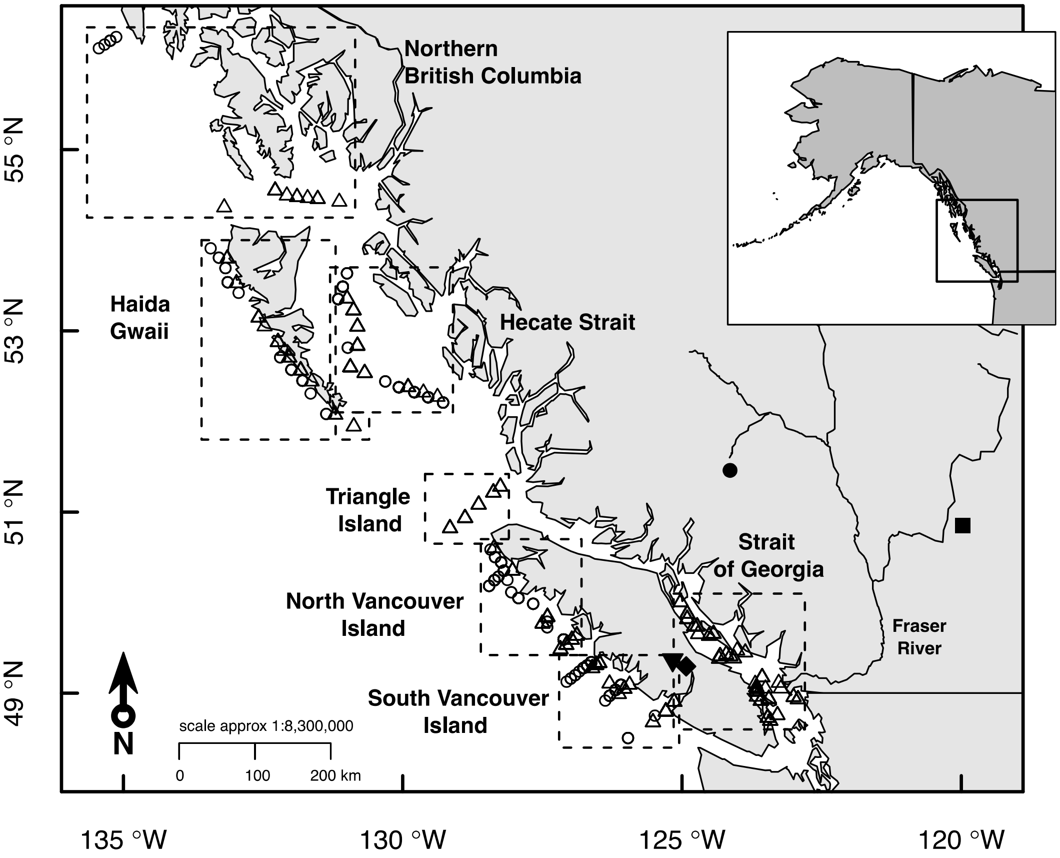

Figure 3.1 Map of study area showing approximate trawl locations (open circles 2007; open triangles 2008) and sampling regions (dashed line polygons) of juvenile sockeye salmon used in otolith microstructure analyses of this study. Symbols for 2007 and 2008 are offset by 0.075° west and east, respectively. Locations of spawning populations are: Great Central Lake (inverted triangle), Sproat Lake (diamond), Chilko Lake (circle), and Lower Adams River (square).

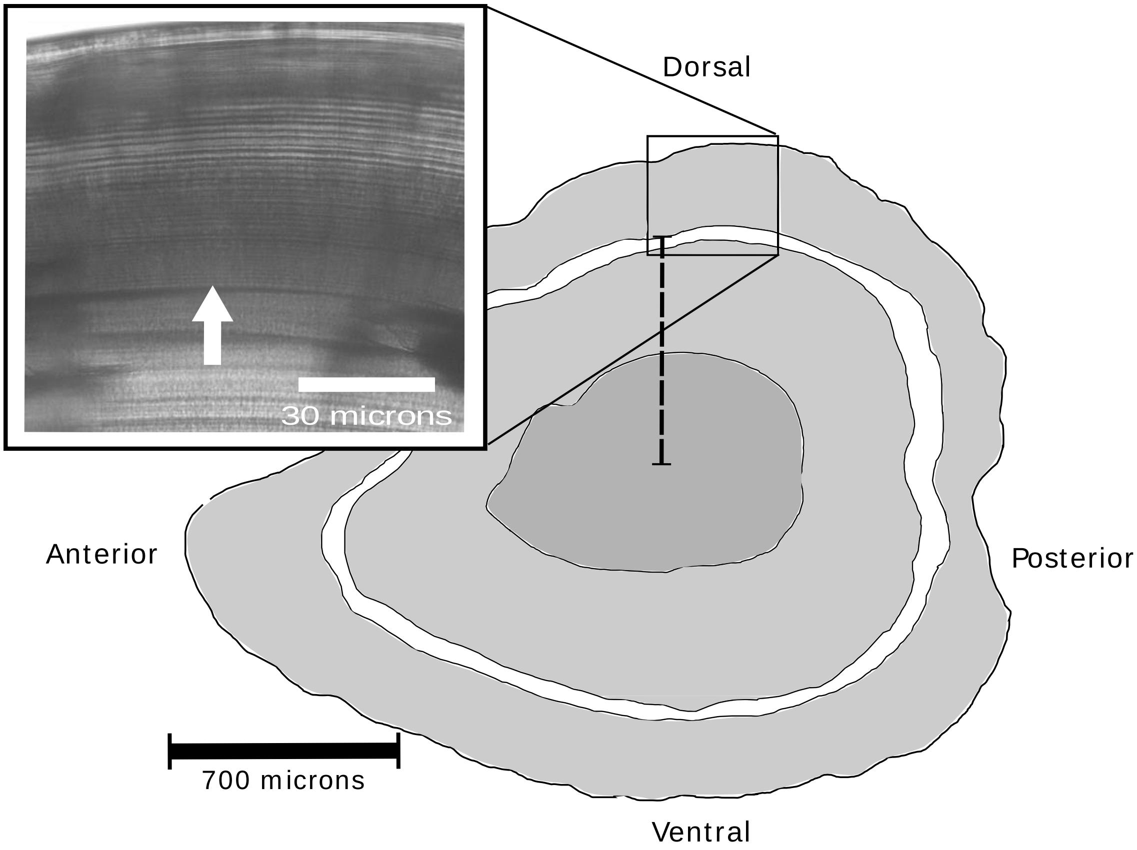

Figure 3.2 Stylized representation of juvenile sockeye salmon otolith. Dark grey zone near core represents larval growth, the white band represents a winter annulus that divides periods of normal growth occurring during the first year in freshwater (inner light grey zone) and marine (outer light grey zone) periods, respectively. Dashed line represents radius measurement to the marine entry check. The inset photograph is a 400x image of a polished otolith showing the marine entry check (indicated by white arrow) and daily micro-increments.

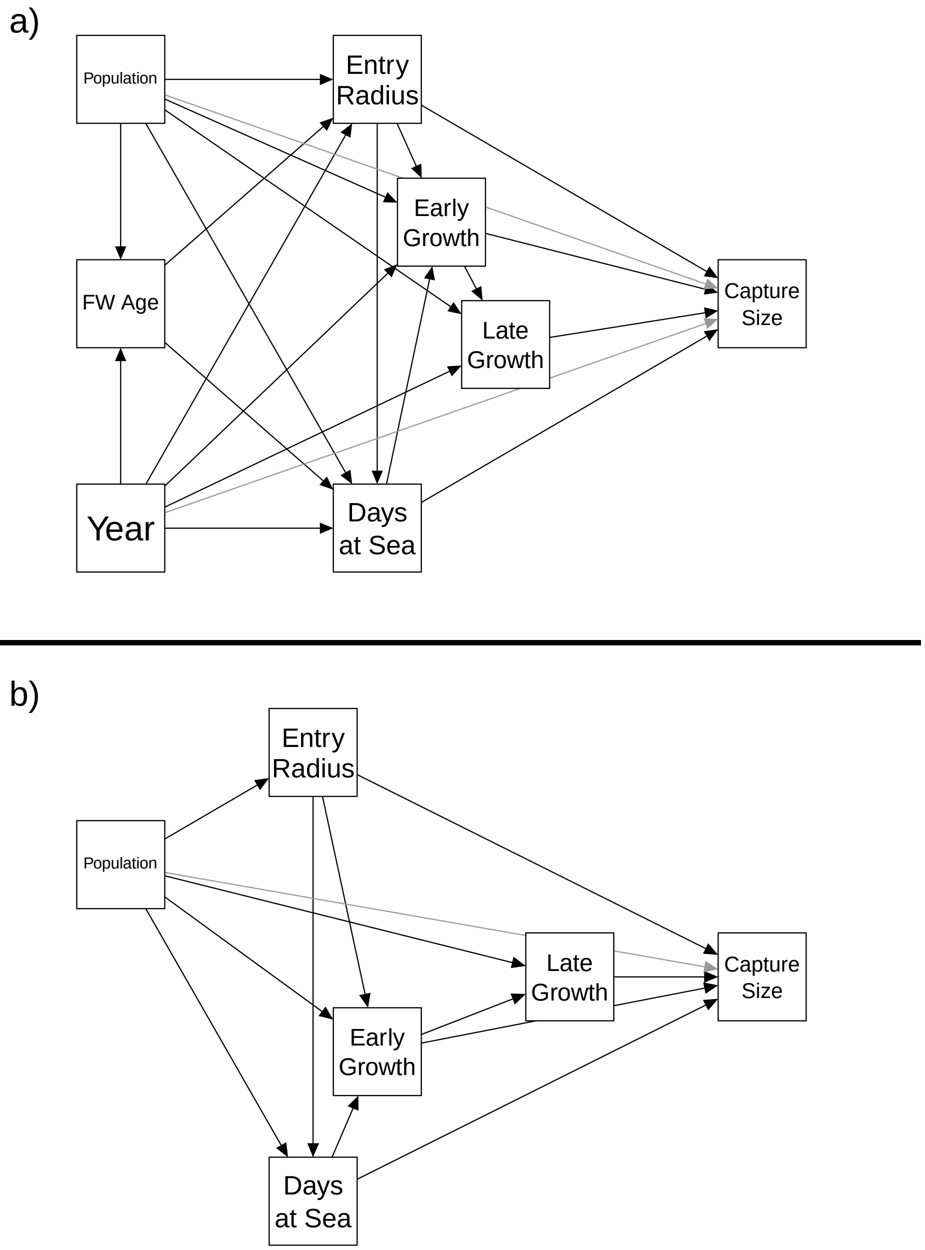

Figure 3.3 Path diagram representing the hypothesized relationships between population, year, early marine characteristics, and size at capture for (a) Vancouver Island and (b) Fraser River juvenile sockeye salmon. Direct paths from population and year to size at capture (shown in grey) were added post hoc to achieve adequate model fit.

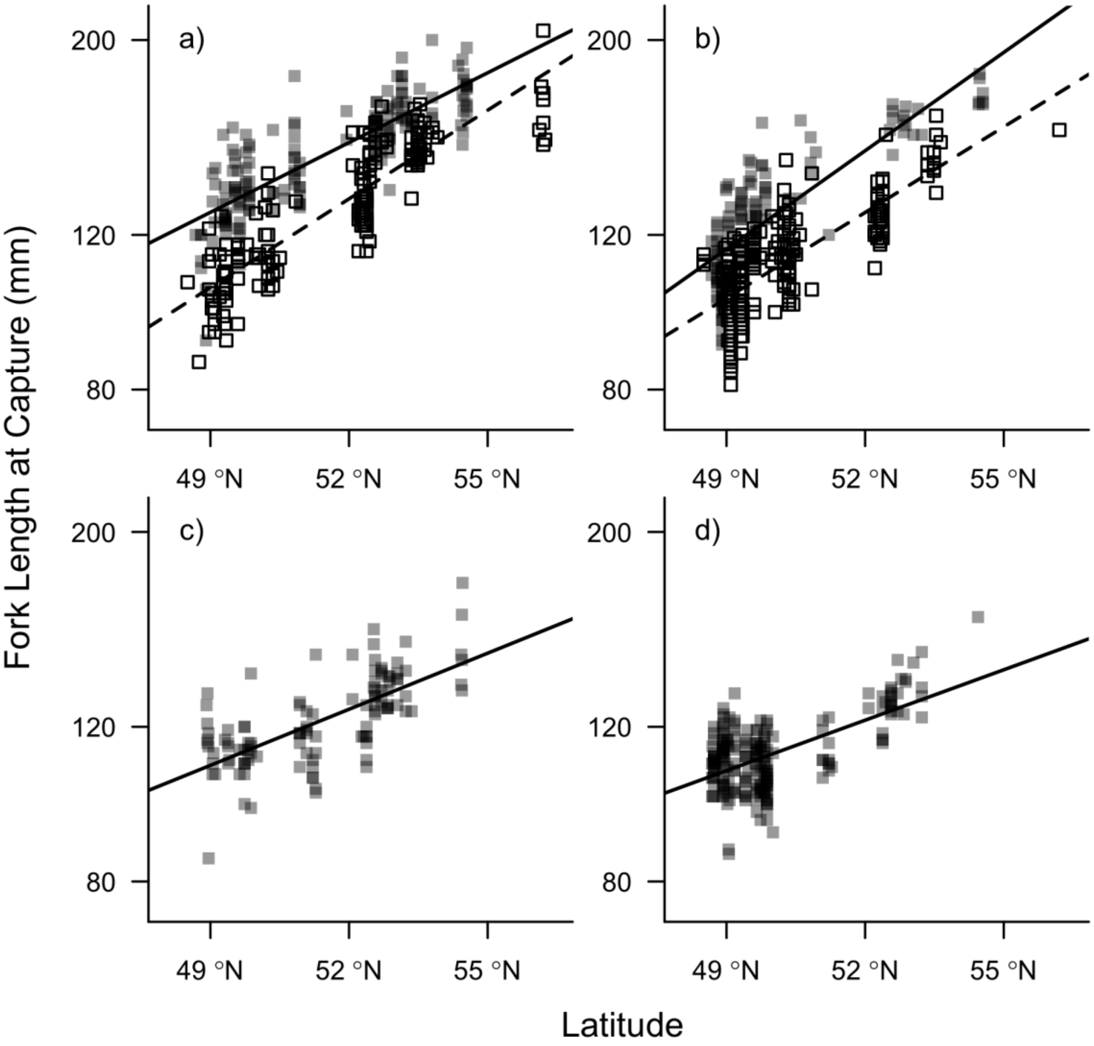

Figure 3.4 Latitudinal gradient in the body size of Sockeye Salmon post-smolts originating from four southern BC populations: (a) Sproat Lake, (b) Great Central Lake, (c) Chilko Lake, and (d) Lower Adams River. Black lines represent linear models regressing log-transformed fork length against latitude. Open squares and dashed lines represent individuals captured in 2007, closed squares and solid lines individuals captured in 2008. Note log scale used on y-axis.

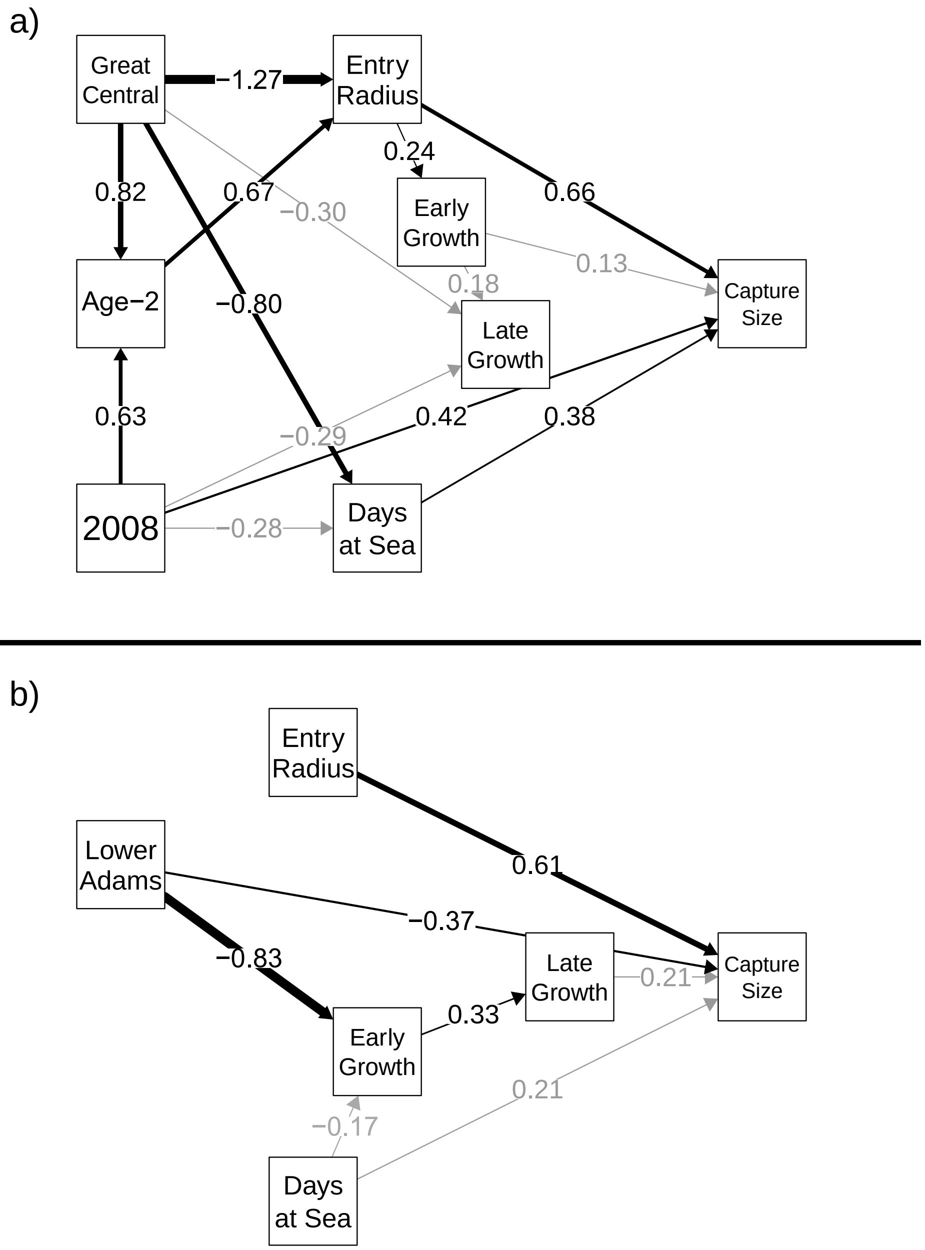

Figure 3.5 Structural equation models examining the direct and indirect effects of population identity, year of capture, and early marine characteristics on size during migration of juvenile sockeye salmon originating from (a) Vancouver Island and (b) Fraser River. Non-significant predictor variables and paths are not shown to improve

readability (see Fig. 3.3 for full tested models). Population identity, year, and freshwater age were coded as dummy binary variables; however, no Fraser River juveniles were collected in 2007 and too few Fraser River age-2 juveniles were included to estimate the effect of age in this dataset. Therefore estimates in (a) are relative to age-1, Sproat Lake individuals captured in 2007 and in (b) are relative to Chilko Lake individuals. Path coefficients reflect standardized variables. Grey and black lines represent significant relationships with standardized effect sizes ≤0.3 and >0.3, respectively; line width reflects the relative strength of the correlation.

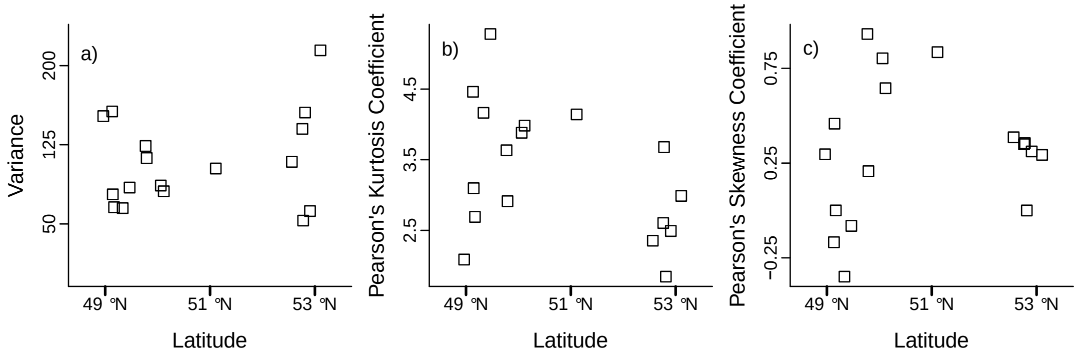

Figure 3.6 Relationship between latitude and size-selective mortality metrics: (a) variance, (b) Pearson’s kurtosis coefficient, and (c) Pearson’s skewness coefficient. Each sampling point represents the catch of a specific population in a given capture region for one year.

Chapter 4 - Divergent migratory behaviours associated with body size and ocean entry phenology in juvenile sockeye salmon

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4.1. Abstract

Survival during early marine life stages is hypothesized to contribute disproportionately to variation in salmon recruitment, yet estimates of cumulative mortality during this period are constrained by uncertainty as to how long juveniles reside in specific regions. We used otolith microstructure techniques to examine the relationship between migratory rate and ocean entry characteristics of juvenile sockeye salmon. We observed differences in migratory rate between catch locations that are consistent with divergent migratory behaviours. Individuals captured in northern regions were typically older, larger at ocean entry, and migrated more rapidly. Migratory rate was also correlated with entry size, phenology, population group, and year. Next, we compared “lingering” individuals captured nearshore during fall surveys to juveniles from the same populations captured during the peak, summer migratory period. We determined that individuals that entered after May 24 and at smaller sizes (<85 mm) had a greater probability of being captured late in the year. Our findings demonstrate that the ocean entry characteristics of juvenile sockeye salmon are strongly correlated with migratory variation within populations and suggest these traits may directly influence juvenile behaviour.

4.2. Introduction

Long distance migrations are associated with high fitness costs that can result in variation across a suite of characteristics (Dingle 1996) – one manifestation of this variability is differences in migratory rate. Migration rate directly determines the ecological environment an individual encounters, including predator and prey communities, pathogen sources, and dynamic abiotic conditions. Simultaneously, migration rate can influence individual condition through physiological processes such as heightened energy demands or transitions to novel physical environments (Hinch et al. 2006). As a result, estimates of migratory rate or the duration of residency in specific regions are valuable when studying migratory species, especially for those taxa that experience bottlenecks in survival during long distance movements.

Sockeye salmon (*Oncorhynchus nerka*) is an anadromous species exploited by commercial, recreational, and First Nations fisheries. Populations in the southern portion of the species' range have experienced variable, but generally poor recruitment in recent years that appears linked to low marine survival rates (Peterman and Dorner 2012). Although sockeye salmon productivity is correlated within regions (Peterman and Dorner 2012), the environmental predictors of marine survival rates differ among populations across relatively small spatial scales (Ye et al. 2015). Since populations do not migrate homogeneously at sea (Tucker et al. 2009, Beacham et al. 2014a), temporal and spatial variability in the distribution of juveniles may influence population-specific mortality rates via differential interactions with predators (Christensen and Trites 2011), pathogen sources (Miller et al. 2014b), or foraging conditions (Mackas et al. 2004, McKinnell et al. 2014). Therefore, quantifying differences in migratory rate among and within sockeye salmon populations will be particularly important to understanding their dynamics.

Variation in migratory rate in salmon may be linked to several ecological characteristics. First, evidence from terrestrial systems suggests age can have strong effects on migratory ability in repeat migrants (Marra et al. 1998, Sergio et al. 2014). Sockeye salmon, being semelparous, lack the opportunity to improve their individual migratory behaviours over time. However, juveniles that have spent multiple years rearing in freshwater may exhibit different behaviours (e.g., timing of out-migration; Jonsson et al. 1990, Kovach et al. 2013), which could result in older individuals migrating more rapidly (Fisher et al. 2014). Second, migratory rate may be associated with body size so that larger juveniles move north more rapidly. Although maximum relative swimming speeds decline with body size due to bioenergetic and physical constraints, absolute swimming speeds are predicted to be consistently greater in larger individuals (Brett 1965, Ware 1978, Trudel and Welch 2005). Movement rates may further diverge as migration progresses due to size-dependent differences in foraging and risk taking behaviours (Mittelbach 1981, Werner et al. 1983, Walters and Juanes 1993). Third, evidence suggests that Pacific salmon marine distributions are influenced by environmental conditions that change seasonally (Burke et al. 2013). Ocean entry phenology will determine the environment that juvenile sockeye salmon initially encounter and may, as a result, moderate migratory rate. Finally, the migration speeds of adult sockeye salmon typically vary between populations and reflect the distances they must travel to reach spawning sites (Crossin et al. 2007). If similar processes influence juveniles, the migratory rates of populations at sea may vary by ocean entry location or migratory route.

While sockeye salmon generally appear to migrate rapidly from ocean entry points (Burgner 1991, Welch et al. 2009, Welch et al. 2011), estimates of nearshore residency and migratory rate are relatively rare and, in some cases, conflicting. Uncertainty in how long juveniles utilize specific areas may have contributed to the lack of consensus as to whether marine mortality rates are greatest within nearshore environments (e.g., the Strait of Georgia, Beamish et al. 2012a), offshore regions (Welch et al. 2011), or both (McKinnell et al. 2014). The majority of previous work has focused on Fraser River populations, which enter the ocean in the Strait of Georgia and then typically migrate north through Johnstone Strait (Tucker et al. 2009). Residency estimates within the Strait of Georgia from tagging studies that utilize the Pacific Ocean Shelf Tracking (POST) array are 9-34 days, depending on population and year (Welch et al. 2009, Welch et al. 2011, Rechisky et al. 2015). These acoustic tagging studies have also estimated migration rates to be 15-24 km day^{-1}, or approximately 1 bl sec^{-1} (Welch et al. 2009, Melnychuk et al. 2010, Rechisky et al. 2015). Conversely, nearshore residency estimates calculated from the catch-per-unit-effort (CPUE) of research surveys in the Strait of Georgia are longer (31-54 days; Preikshot et al. 2012). While Preikshot et al. (2012) did not explicitly calculate migratory rate, their residency estimates suggest considerably slower movements of approximately 4 km day^{-1} or less than 0.5 bl sec^{-1}.

While these studies provide valuable information, both approaches have limitations. First, due to tag burden concerns, acoustic telemetry studies can currently only target larger smolts (Welch et al. 2009, Welch et al. 2011, Rechisky et al. 2015). Tagged individuals are typically two year old smolts, which are generally 60-80 mm larger than the population average (Welch et al. 2009) and often make up less than 5% of the out-migrating group each year (Irvine and Akenhead 2013). Although Melnychuk et al. (2010) determined that sockeye salmon size was not correlated with migratory rate at sea, their analysis was restricted to tagged smolts that were at least 150 mm long and it is possible that smaller fish exhibit different migratory behaviours (Welch et al. 2011, Preikshot et al. 2012, Beacham et al. 2014b).

Second, estimates of migratory rate based on CPUE are driven by the relative abundance of an entire population and cannot identify individual variation in migratory patterns. However, juvenile sockeye salmon belonging to a given population are widely distributed at sea (Tucker et al. 2009), which suggests considerable individual variation in migratory rate or ocean entry timing. Of particular interest are a “lingering” group of individuals that are captured in southern regions in October and November – well after the majority of their cohort has migrated north (Tucker et al. 2009). Since juvenile sockeye salmon survival is predicted to improve with early arrival at maturation grounds in the Gulf of Alaska (McKinnell et al. 2011), it is unclear why a fraction of the population is consistently found inshore, late in the year, where mortality rates are likely higher. We predict that these individuals may be constrained by body size or ocean entry phenology to migrate after the bulk of their cohort.

We used otolith microstructure techniques to estimate individual variation in the migratory rate of four populations of BC sockeye salmon originating from Vancouver Island or the Fraser River. Next, we tested a series of hypotheses to identify potential drivers of this variation: i) that two year old individuals exhibit different spatial distributions and migration rates as one year old juveniles, ii) migratory rate is correlated with ocean entry size and phenology, and iii) the early marine characteristics of juveniles captured in the fall differ from those captured in the summer. Finally, since Pacific salmon can exhibit stock- and year-specific early marine characteristics we also tested for inter-population and inter-annual differences in migratory rate.

4.3. Methods

4.3.1. Juvenile fish collection and population information

In addition to the samples used in Chapter 3, this analysis included juvenile sockeye salmon collected in fall 2008 (Oct 9 – 19) (Fig. 4.1). The fish sampling, body size data collection, genetic stock identification, and otolith selection and processing protocols for this analysis were identical to those reported in Section 3.3.1. As before otolith measurements were repeated three times per otolith and the average was used in subsequent analysis. If any measurements could not be completed, the otolith was discarded (40 out of 443).

Unlike in Chapter 3, in this analysis we used back-calculated estimates of body size to estimate relative migration rate. Body size is commonly back-calculated from hard structures by regressing otolith or scale size at capture against body size at capture. However, these techniques fail to account for how individual, body-structure relationships may deviate from the population average and can introduce additional error (Francis 1990). Therefore we estimated size at ocean entry from marine entry check radii by using scale proportional (SPH) and body proportional hypotheses (BPH) as described in Francis (1990), then used the mean of these two methods as our entry size estimate. Although these techniques are distinct from direct correlations between body size and otolith size, they do use this relationship to provide initial model parameters and therefore require a strong correlation between these two metrics. In this dataset the correlation between otolith radius and size at capture was significant ($r^2 = 0.79$, DF = 419, $P < 0.001$; Fig. A4.1).

4.3.2. Data analyses

We conservatively estimated migration distance as the linear distance in km between an individual's ocean entry point (based on population identity) and capture location, after accounting for the Earth's curvature. In the case of Vancouver Island juveniles, this distance was measured from the mouth of Barkley Sound to the capture location with the length of the Sound added afterwards. We then divided linear migration distance by the number of days since ocean entry to use as an estimate of migratory rate. We also converted migratory rate in km day^{-1} to body lengths per second (bl sec^{-1}) using estimates of fork length at ocean entry; however, we did not account for changes in size during migration.

We used a chi-squared analysis to test the hypothesis that the observed number of age-2 smolts at each capture location during the summer surveys was not significantly different from a random distribution. Next, we used Mann-Whitney tests to determine whether mean migratory rate, size at entry, and phenology differed between age-1 and age-2 juveniles. Since only two age-2 Fraser River juveniles were captured, all analyses examining differences between age groups focused only on Vancouver Island populations (i.e. Great Central Lake and Sproat Lake individuals).

To examine the effects of ocean entry characteristics on migratory rate, we fit linear regressions with migratory rate in km day^{-1} as the response and fork length at ocean entry, entry date, population aggregate (Fraser River or Vancouver Island), and year as explanatory variables. We chose to aggregate populations because we had data for only two populations per watershed and because initial analyses showed migratory rates within an aggregate were similar; however, we speculate differences between populations may be important when examining diverse population assemblages within regions. Preliminary analyses also indicated that migratory rate was strongly bimodal, with each distribution well defined by capture location (Fig. 4.2). Therefore, we included capture region (whether an individual was caught north or south of Vancouver Island's north-western point, Fig. 4.1) as an explanatory variable to account for this underlying variation and ensure adequate model fit. To determine whether the ocean entry characteristics of northern and southern caught fish differed, we also tested for interactions between capture region and all other explanatory variables. Since freshwater age was strongly correlated with entry fork length it was not included as an explanatory variable. We only included summer-caught fish in this analysis to minimize temporal variability and pseudoreplication within regions.

We used Box-Cox power law transformations to identify the optimal exponent to meet normality assumptions for the response variable and raised migratory rate data to the 0.7 power before we fit linear models. To avoid misinterpreting interactions when comparing models, we centered all categorical explanatory variables, and centered and scaled to a standard deviation of one all continuous explanatory variables (Schielzeth 2010). We confirmed explanatory variables were not collinear using variance inflation factors (VIF < 3 indicates minimal collinearity) and tested for adequate model fit by examining quantile-quantile plots and the distribution of residuals.

Next, we used Mann-Whitney tests to compare migratory rates of individuals captured in fall surveys to those captured in northern and southern regions during the summer. We used generalized linear models (GLMs) with a binomial response variable to determine whether early marine entry characteristics could be used to distinguish individuals captured in the summer from juveniles of the same population captured in the same region during fall surveys. The only sampling regions where at least 8 individuals were captured in both seasons were Hecate Strait (HS) and northern British Columbia (N-BC) in 2008 – therefore, all samples collected in other regions and in 2007 were excluded from this analysis. Since no Sproat Lake individuals were captured in fall surveys, we also excluded this population from the analysis. To account for quasi-separation in the initial GLMs we used a bias-reduction estimator developed by Firth (1993) and implemented with the *logistf* package (Heinze et al. 2013) in R version 3.1.3 (R Core Team 2014). We included size at ocean entry, entry date, and population identity as explanatory variables and season of capture (summer or autumn) as the binomial response variable in the saturated model.

For both linear models and binomial GLMs, we used an information theoretic approach to identify top ranked models with AIC adjusted for small sample sizes. If several models had equivalent AICc scores (i.e. ΔAICc < 2), the most parsimonious model was retained (Burnham and Anderson 2002, Grueber et al. 2011). We conducted all statistical analyses in R version 3.1.3 (R Core Team 2017).

4.4. Results

4.4.1. Summer-caught juveniles

Among Vancouver Island juveniles, age-2 individuals were not distributed uniformly across sampling regions ($\chi^2 = 22.6$, DF = 5, $P < 0.001$) and older juveniles were nearly four times more abundant in northern sampling regions (Table 4.1). Age-2 fish had a significantly faster mean migratory rate (W = 1569, $P < 0.001$; Fig. 4.3a). Older individuals were also significantly larger at ocean entry than age-1 juveniles (W = 1004, $P < 0.0001$; Fig. 4.3b) and tended to enter later in the year, with this difference approaching statistical significance (W = 2629, $P = 0.056$; Fig. 4.3c).

Estimates of migratory rate ranged from 0.8 – 21.3 km day^{-1} (0.1 – 2.5 bl sec^{-1}). The distributions were bimodal and were strongly associated with capture region (Fig. 4.2). The mean migratory rate of individuals captured south of Vancouver Island was significantly slower than those captured in northern sampling regions (3.1 ± 1.4 vs. 12.1 ± 3.0 km day^{-1} ± SD; W = 31191, $P < 0.0001$; Figs. 4.2, 4.4, 4.5) and individuals were significantly smaller at ocean entry (75 ± 13 vs. 95 ± 18 mm ± SD; W = 26255, $P < 0.0001$; Fig. 4.4a). Although differences between regions were less extreme, southern-caught fish typically also had been at sea for significantly shorter periods (55.6 ± 10.0 days ± SD in northern regions vs. 51.9 ± 7.3 days in southern regions; W = 19322, $P < 0.001$; Figs. 4.4b, A4.3).

In the top ranked model, entry size, phenology, population aggregate and capture year were significantly correlated with migratory rate after accounting for the underlying variation in migratory rate associated with capture location ($r^2 = 0.91$; Figs. 4.4, 4.5, Table A4.1). The fastest migrants were juveniles that entered at large sizes, relatively late in the year, and originated from Fraser River populations. Although the correlation between body size and migratory rate was consistent between capture regions, there were significant interaction effects between capture region and the other explanatory variables (Fig. 4.5; Table A4.1). As a result, the effects of entry date and population aggregate on migratory rate were greater among fish captured in the north, while the effect of sampling year was stronger in southern regions.

4.4.2. Fall-caught juveniles

Individuals captured in HS and N-BC during fall surveys and retained in this analysis were identified as belonging to Great Central Lake, Lower Adams River, and Chilko Lake population groups. Fall-caught juveniles migrated at a significantly slower rate than individuals from the same populations caught in similar locations during the summer (14.7 ± 2.6 vs. 5.7 ± 0.9 km day^{-1} ± SD; W = 0, $P < 0.0001$), but more rapidly than those captured in southern regions during the summer (3.1 ± 1.4 km day^{-1} ± SD; W = 6849, $P < 0.0001$). Furthermore, marine entry characteristics could be used to identify summer and fall-caught juveniles captured in the same region. The top ranked GLM for predicting season of capture (ΔAIC of next best model > 7) included back-calculated estimates of entry date and entry size as explanatory variables ($\beta_{\text{Entry Date}} = 0.39$, 95% CI = 0.18 – 2.01; $\beta_{\text{Entry FL}} = -0.36$, 95% CI = -2.96 – -0.07; Fig. 4.6, Table A4.2). Population was not retained as an explanatory variable in the top model (Table A4.2).

Juvenile sockeye salmon entering after approximately May 24 and at less than 82 mm FL had a greater probability of being captured in fall than in summer surveys. Although the size distributions of summer and fall-caught fish overlapped considerably, fall captures exhibited significantly lower variance in size at ocean entry (70.6 vs. 379.6 mm; Levene's test: F-value = 40.0, $P < 0.0001$; Fig. 4.6b).

Characteristics estimated from otolith microstructure are summarized by population aggregate, year, and sampling period in Table A4.3.

4.5. Discussion

We observed extensive individual variation in the marine distribution and migratory rate of sockeye salmon juveniles originating from both the Fraser River and Vancouver Island. Individuals exhibited at least two distinct migratory patterns – either migrating rapidly from ocean entry points or residing for several weeks in southern regions while moving north more slowly. Older, age-2 juveniles tended to be more common further north and larger juveniles migrated more rapidly. Lingering juveniles captured in Hecate Strait and northern BC during fall surveys migrated more slowly than individuals captured in the same regions during summer and, like southern-caught juveniles, may have reared for several weeks relatively close to ocean entry points. Additionally, fish caught during fall surveys differed from individuals captured in the same regions during the peak summer migration period by entering the marine environment later in the year and at a smaller size. The heterogeneity we observed suggests that individual variation in ocean entry characteristics *within* populations may influence the migratory behaviour of juvenile sockeye salmon and, as a result, how they interact with their marine environment.

4.5.1. Summer-caught juveniles

Our estimates of migratory rate were bimodal for both Vancouver Island and Fraser River juveniles captured in summer, indicating differences in spatial distribution are associated with variation in travel speed, rather than differences in ocean entry timing alone. Since variation in migratory rate was strongly associated with capture location, even after accounting for individual differences in ocean entry characteristics, we suggest each mode may represent a distinct migratory phenotype. In the first, relatively large juvenile sockeye salmon appear to undertake a directed and rapid migration from their ocean entry points that is similar to results from studies tagging large, age-2 juveniles (Welch et al. 2009, Melnychuk et al. 2010, Welch et al. 2011, Rechisky et al. 2015). Conversely, smaller individuals that enter the marine environment at approximately the same time appear to move away from their entry points more slowly – a pattern consistent with highly dispersed catches of juvenile sockeye salmon in the Strait of Georgia (Preikshot et al. 2012, Neville et al. 2013).

Size-dependent variation in migratory behaviour has been reported in several Pacific salmon. For example, the smaller individuals in populations of pink salmon (*O. gorbuscha*) and steelhead trout (*O. mykiss*) rear in estuarine environments for relatively longer periods (Mortensen et al. 2000, Bond et al. 2008). Similarly, coho (*O. kisutch*) and Chinook salmon (*O. tshawytscha*) juveniles either migrate rapidly offshore or overwinter on the continental shelf, with larger fish consistently observed further from ocean entry points (Morris et al. 2007, Fisher et al. 2014). Finally, juvenile salmon originating from hatcheries appear to move out of nearshore environments more rapidly than wild individuals (Rice et al. 2011, Sturdevant et al. 2012), a pattern that may be linked to the larger mean size of hatchery fish.

Pacific salmon survival is thought to improve with early arrival on maturation grounds (McKinnell et al. 2012), however delaying migration may be adaptive for smaller individuals if it allows them to substantially increase size and energy stores prior to moving offshore. This behaviour may be particularly important for Fraser River populations since foraging conditions immediately outside the Strait of Georgia appear poor (Ferriss et al. 2014, McKinnell et al. 2014). Furthermore, Morris et al. (2007)

hypothesized that variation in migratory rate could create a portfolio effect by ensuring a fraction of individuals encounter adequate rearing conditions during their migrations and by reducing intra-specific competition en route. While there is no evidence that the populations of sockeye salmon we studied overwinter in large numbers in nearshore environments, subtle variation in migratory patterns within populations may act to stabilize marine mortality rates.

Even though we observed differences between age classes in spatial distribution and migratory rate, we suggest migratory behaviour is more strongly associated with size than age. Age-2 sockeye salmon were more common in northern sampling regions and migrated more rapidly than age-1 juveniles; however, both age groups were captured in concurrent sampling events, exhibited overlapping variation in migratory rate, and entered the marine environment at approximately the same time. Instead the most consistent difference between age classes was body size, with age-2 juveniles being, on average, significantly larger.

The relatively strong correlation between migratory rate and back-calculated estimates of fork length at ocean entry across all populations provides additional evidence that migratory behaviour at sea is associated with body size. This pattern is also consistent with observations that larger juvenile Pacific salmon are typically observed further from shore, earlier in the year (Morris et al. 2007, Tucker et al. 2009, Beacham et al. 2014a,b, Freshwater et al. 2016a). Migratory rate may be intrinsically associated with fork length since both optimal cruising and foraging swimming speeds are positively correlated with body size in salmonids (Ware 1978, Trudel and Welch 2005). Alternatively, larger individuals may exhibit size-specific behaviours, such as greater risk taking (Werner et al. 1983) or more efficient foraging (Mittelbach 1981), that secondarily result in faster rates of migration.

Previous evidence of a strong relationship between fork length and swimming speeds (e.g., Ware 1978) does not make our findings novel in the broader context of fish behaviour; however, these results contrast with evidence from acoustic tagging studies on juvenile salmon in which coastal migration rates were not correlated with size (Melnychuk et al. 2010). We suggest that these divergent results are driven by differences in the initial size ranges that each study sampled (155-250 mm in Melnychuk et al. 2010; 45-150 mm in this study). Since migratory rate appears to be correlated with size only in smaller individuals, we suggest the relationship between fork length and migration speed may decouple past a threshold size. Beyond this limit, behaviour may be principally driven by other characteristics (e.g., growth, local foraging conditions). More broadly, our findings indicate that the movements of large, age-2 juveniles may not be representative of all southern BC sockeye salmon juveniles, many of which are age-1 (Irvine and Akenhead 2013) and less than 120 mm when caught in nearshore waters (Neville et al. 2013).

This size-dependent variation in migratory behaviour becomes particularly important when using movement rates to estimate stage-specific survival. Since smaller individuals move north more slowly, they may be more sensitive to poor foraging conditions or high predator densities in nearshore environments. Ultimately, these individuals may experience relatively greater rates of mortality in regions such as the Strait of Georgia or Barkley Sound. Such differences may explain why evidence of high rates of nearshore mortality in juvenile sockeye salmon is currently mixed (Welch et al. 2011, Beamish et al. 2012a, McKinnell et al. 2014).

Juveniles captured in northern regions that entered the marine environment later in the year also migrated more rapidly (e.g., individuals that entered in mid-May migrated ~5 km day^{-1} faster than those entering in late April). Seasonal increases in migratory rate may indicate that the relative benefits of arrival on maturation grounds increase as summer progresses, perhaps due to reduced zooplankton abundance in southern regions, which tends to peak in May-June on the west coast of Vancouver Island and Strait of Georgia (Harrison et al. 1983, Mackas et al. 2004). However, since there are also substantial energetic costs associated with faster swimming speeds (Ware 1978), these late entry fish may arrive on maturation grounds in poor condition and experience reduced survival as a result. The relationship between entry phenology and migratory rate was only significant among juveniles caught in northern regions, which may suggest that smaller, southern individuals are constrained to slower migratory rates or longer nearshore residency, perhaps due to greater costs from offshore movements (e.g., mortality, Healey 1980).

Since salmon migratory behaviour appears to be influenced by physical and biological conditions at multiple spatial scales (Burke et al. 2013), it was unsurprising that migratory rate varied with ocean entry location. For example, Vancouver Island populations captured north of Vancouver Island migrated at a significantly slower rate (~2 km day^{-1}) than Fraser River juveniles. Johnstone Strait may be particularly important in driving differences between Fraser River and Vancouver Island juveniles, as well as between Fraser River fish caught in northern or southern regions. Johnstone Strait is a narrow passage separating Vancouver Island and the BC mainland that is located immediately north of the Strait of Georgia. It is characterized by extreme tidal flows that create low levels of primary productivity and is hypothesized to be a region of poor growth and low survival (McKinnell et al. 2014). Fraser River juveniles may accelerate to pass through these poor foraging conditions or utilize prevailing surface currents, which tend to flow out of the Strait of Georgia through Discovery Passage via Johnstone Strait (Waldichuk 1950). If this is the case, the migratory rate of Fraser River fish may increase relative to Vancouver Island juveniles, which migrate through the weaker and predominantly southerly currents that are present off the west coast of Vancouver Island in early summer (Freeland et al. 1984).

Differences in migratory route may also ultimately influence survival. For example, variation in migratory route *within* salmonid populations is correlated with nearshore mortality rates (Furey et al. 2015) and more extreme differences in migration pathways between populations are thought to influence population specific survival patterns (Ye et al. 2015). Unfortunately accurate estimates of juvenile marine survival are lacking for most sockeye salmon populations; however it is possible that differences in migratory route or the energetic requirements of migration have contributed to high returns to Vancouver Island populations relative to Fraser River stocks in recent years (DFO 2012, 2014a).

Although mean migratory rate was significantly greater in 2007 than 2008, the many variables that may influence migratory behaviour that were not accounted for in this study make it impossible to isolate specific drivers of interannual differences. This is particularly true with regards to juvenile salmon, which can alter their movements due to a range of physical (e.g., flow, temperature) or biological conditions (e.g., density-dependence, primary productivity) in freshwater (Sykes et al. 2009) and marine rearing habitats (Burke et al. 2013). Biophysical models specific to conditions on the BC shelf could be used to examine the relative importance of these processes to sockeye salmon.

Our estimates of juvenile sockeye salmon entry size, timing, and migratory rate from otolith microstructure are broadly consistent with field observations, as well as experimental and theoretical studies. On-going rotary screw trap surveys in the lower Fraser River capture out-migrating smolts of similar size ranges, from late April to mid-June with peak catches occurring in early to mid-May (C. Neville, *unpublished data*). The migratory rates we report are also within the ranges calculated from other studies (Welch et al. 2009, Melnychuk et al. 2010, Welch et al. 2011, Preikshot et al. 2012, Rechisky et al. 2015). Finally, our estimates of migratory rate do not appear to be physiologically unrealistic since they are below maximum sustainable speeds obtained in laboratory experiments (3.3 – 8.2 bl sec^{-1}; Brett and Glass 1973) or theoretical optimal cruising speeds obtained from models of oxygen consumption (3 – 5 bl sec^{-1} at 10 – 20 °C; Trudel and Welch 2005), and within the range obtained from coded wire tag (CWT) recoveries (mean 2.6 bl sec^{-1}; Tucker et al. 2015).

4.5.2. Fall-caught juveniles

Fall-caught individuals migrated at slower rates than individuals captured in the same regions during summer surveys and this delayed migratory behaviour was strongly associated with marine entry characteristics. Specifically, individuals entering the ocean after May 24th had a high probability of being captured in fall surveys, while those that entered during peak out-migration periods in early to mid-May were likely to be caught in summer surveys. Although there was considerable overlap between seasons, entry size was also a significant predictor of season of capture. Fall-caught individuals tended to be smaller than 85 mm at ocean entry and exhibited variation in body size than fish caught in northern regions during the summer. Conversely, population identity was a poor predictor of capture season and the probability of individuals migrating in the fall did not differ among the three populations we examined. The absence of Sproat Lake individuals in fall surveys is one exception and may be related to their relatively large juvenile size (Beacham et al. 2014b).

The nearshore distribution of juvenile fish captured during our fall survey suggests a migratory behaviour that is fundamentally different from that of the majority of juvenile sockeye salmon, which move offshore well before their first marine winter (Burgner 1991, Tucker et al. 2009). We suggest that there are two likely explanations for this pattern. First, though fall-caught individuals enter late in the year, they may still co-migrate with juveniles captured during summer surveys. After reaching the coast of southeastern Alaska, these individuals may then delay or halt their migration. Alternatively, fall-caught juveniles may represent a migratory behaviour that is distinct from either group of summer-caught fish. While the ocean entry dates of fall-caught fish preceded our summer surveys and indicate they must have been at sea when we were sampling, fall-caught juveniles entered the marine environment nearly a month after summer-caught juveniles and may not strongly overlap spatially with the bulk of their cohort. If a late ocean entry date results in fall-caught fish remaining further inshore, these individuals may not be vulnerable to summer surveys and ultimately migrate north independently.

Interestingly, a delayed northern migration by small juvenile sockeye salmon that enter late in the year would represent an intermediate strategy within the species. The majority of sockeye salmon populations enter the marine environment after rearing for several years in natal lakes, but several populations (e.g., the Harrison River stock) are dominated by “sea-type” individuals (Burgner 1991). No sea-type populations were included in our study, however among Fraser River populations sea-type juveniles enter the ocean without extensive freshwater rearing, late in the year (~July), and reside for several months in the Strait of Georgia (Tucker et al. 2009, Beacham et al. 2014a, Beamish et al. 2016). The lingering, fall-caught juveniles we describe here may move north after the peak migration in early summer, but before sea-type individuals. Such an expanded temporal and spatial distribution is consistent with widespread catches of juvenile sockeye salmon across the north Pacific (Tucker et al. 2009, Beacham et al. 2014a).

While some sea-type populations have returned at high rates in recent years (Beamish et al. 2016), it appears unlikely that fall-caught individuals would experience improved survival by delaying their migration. First, since fall-caught fish make up a small fraction of the overall catch (Tucker et al. 2009), more rapid offshore migration appears to be more common and may typically be a more successful strategy. Second, fall-caught juvenile sockeye salmon from Vancouver Island and the Fraser River fish co-occur with relatively high densities of juveniles from Rivers Inlet (Tucker et al. 2009). This pattern is noteworthy because the Rivers Inlet stock strongly declined in the early 1990s, with poor marine survival identified as a key driver (McKinnell et al. 2001). If lingering individuals from southern BC populations rear in the same environment as Rivers Inlet juveniles, they may experience similarly high rates of mortality.

We observed considerable variation in the distribution and migratory rate of juvenile sockeye salmon that was corrrelated with age, as well as ocean entry size, phenology, and population aggregate. It is possible that the entry characteristics we estimated directly contribute to differences in migratory behaviour. Alternatively, size, phenology, and migratory behaviour may simply covary with one another; perhaps as genetically related subgroups within a population diverge. Regardless of the mechanisms that create variation in migratory behaviour, our results support growing evidence that the salmon marine migrations are far from homogeneous (Byron and Burke 2014). Unfortunately, since little is known about what drives differential survival during marine rearing, we can only speculate as to how variation in migratory behaviour will influence mortality. Yet older or larger sockeye salmon juveniles that are caught in northern regions have the potential to experience fundamentally different conditions than those further south. Differences in migration speed will influence how long individuals are exposed to specific predator communities (Christensen and Trites 2011), the prey community that they encounter (Mackas et al. 2004, McKinnell et al. 2014), the pathogens they are exposed to (Miller et al. 2014b), and the energy they accumulate to complete migrations and successfully overwinter (Trudel et al. 2007). Future work should seek to identify mechanisms of mortality throughout the migratory corridor and examine how they may differentially affect juvenile Pacific salmon that differ in entry size and timing.

Table 4.1 Number of age-1 and age-2 Vancouver Island juveniles captured in each sampling region. Regions are shown in Fig. 4.1 and abbreviations are as follows: S-VI = southern Vancouver Island, N-VI = northern Vancouver Island, TI = Triangle Island, HS = Hecate Strait, HG = Haida Gwaii, and N-BC = northern British Columbia.

	S-VI	N-VI	TI	HS	HG	N-BC
Age-1	64	55	11	52	29	21
Age-2	2	4	0	10	3	10

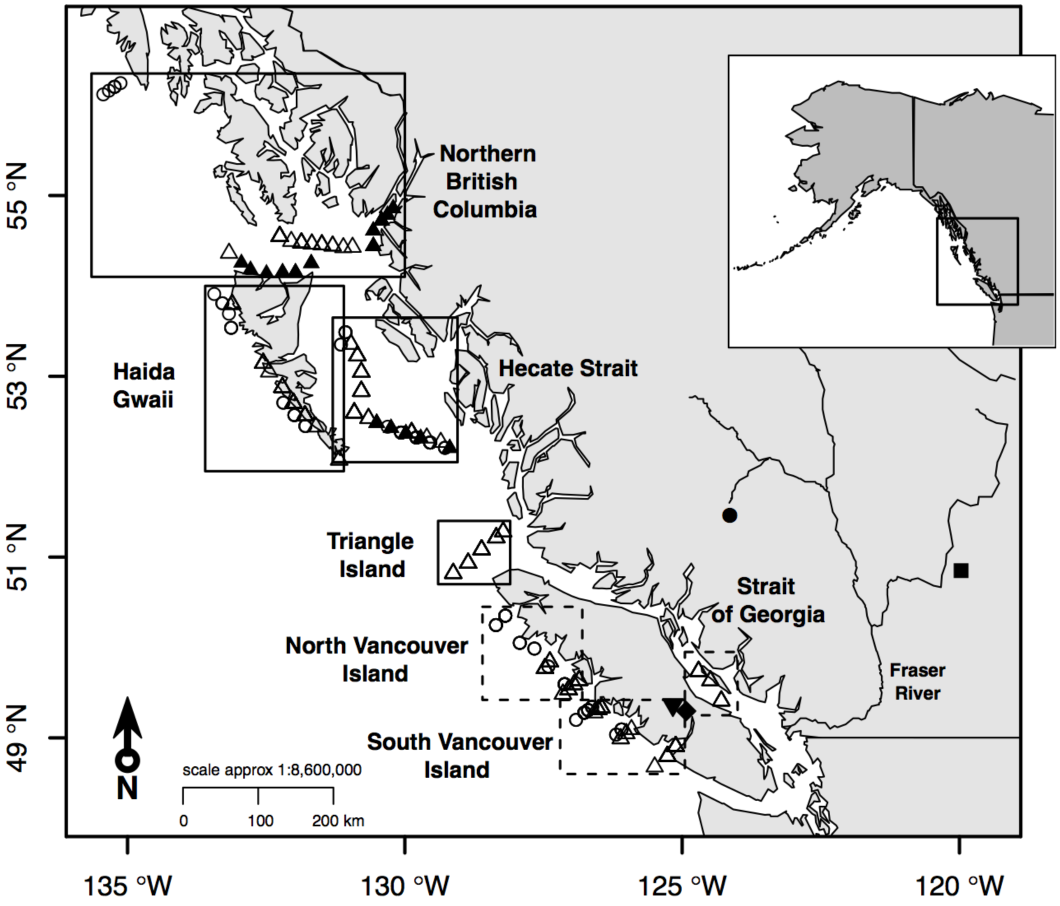

Figure 4.1 Map of study area showing approximate trawl locations and sampling regions of migratory study. Open circles represent summer 2007, open triangles represent summer 2008, and closed triangles represent autumn 2008 sampling events. Solid and dashed polygons represent northern and southern sampling regions, respectively. Symbols for 2007 and 2008 are offset by 0.075° west and east, respectively. Locations of spawning populations are: Great Central Lake (inverted triangle), Sproat Lake (diamond), Chilko Lake (filled circle), and Lower Adams River (square).

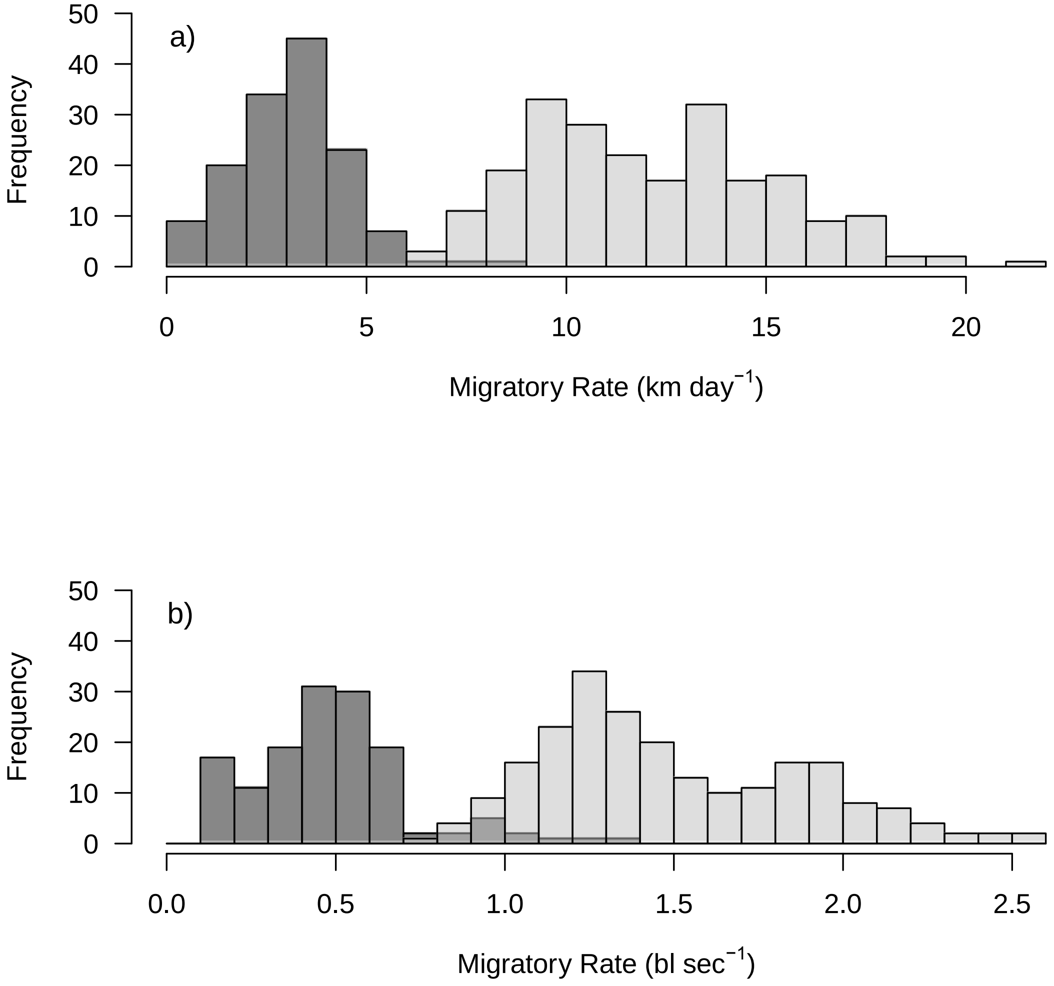

Figure 4.2 Migratory rate of Vancouver Island and Fraser River juvenile sockeye salmon captured during summer surveys. Dark grey and light grey bars represent individuals caught in southern and northern sampling region respectively.

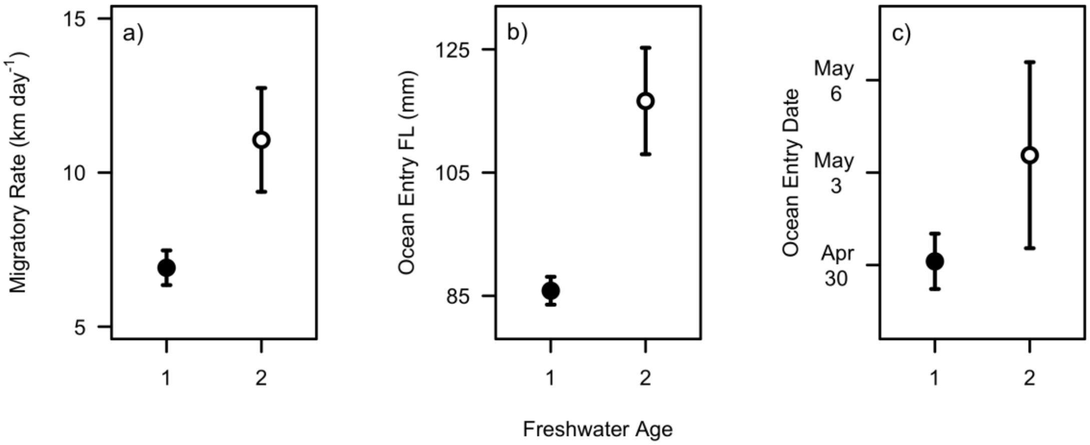

Figure 4.3 Mean a) migratory rate, b) size at ocean entry, and c) entry date of age-1 and age-2 juvenile sockeye salmon. All are summer-caught fish. Error bars represent 95% confidence intervals.

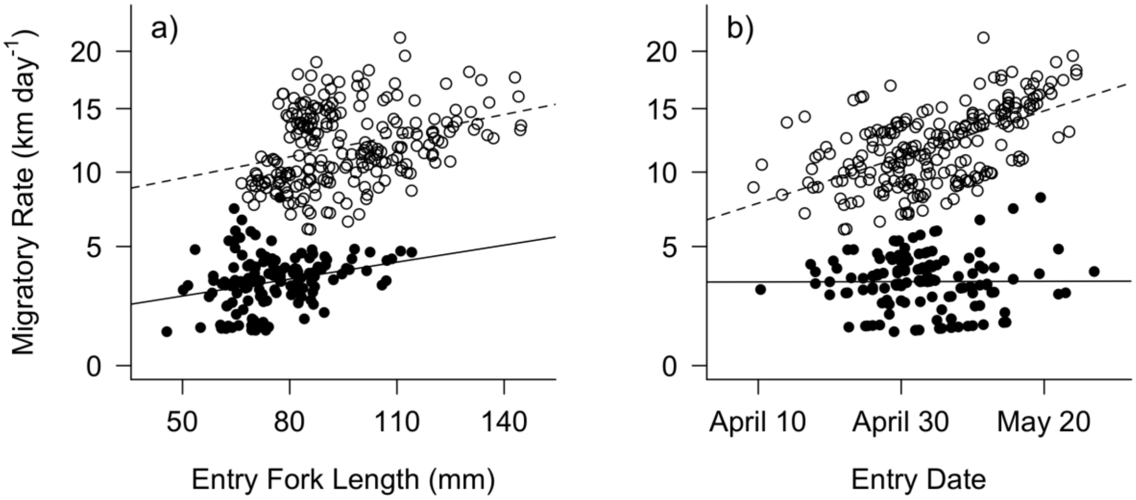

Figure 4.4 Relationship between migratory rate (km day^{-1}) and (a) back calculated size at ocean entry or (b) entry date for juveniles captured during summer surveys. Dashed and solid lines represent regressions for northern (open symbols) and southern (closed symbols) respectively. Note that the y-axes are power law transformed with an exponent of 0.7 and that explanatory variables are represented by raw data, rather than scaled and centered as in models.

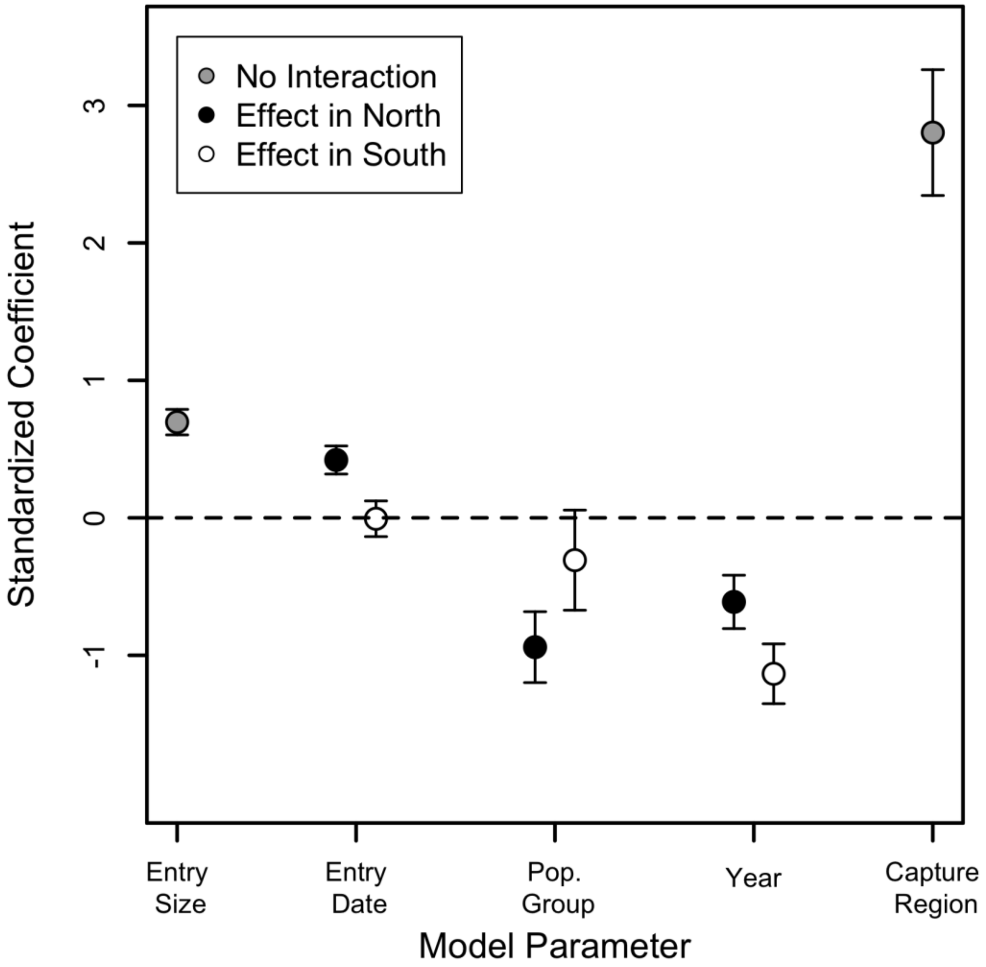

Figure 4.5 Standardized coefficient estimates top migratory rate model for summer-caught juvenile sockeye salmon. Grey circles represent parameters with no significant interaction with capture region. Black and white circles show parameters estimates for northern and southern caught juveniles, respectively (i.e. account for significant interaction effects). Categorical variables were estimated relative to individuals from Fraser River populations, fish that migrated in 2007, or fish that were captured in southern regions, negative values are associated with those juveniles migrating more quickly.

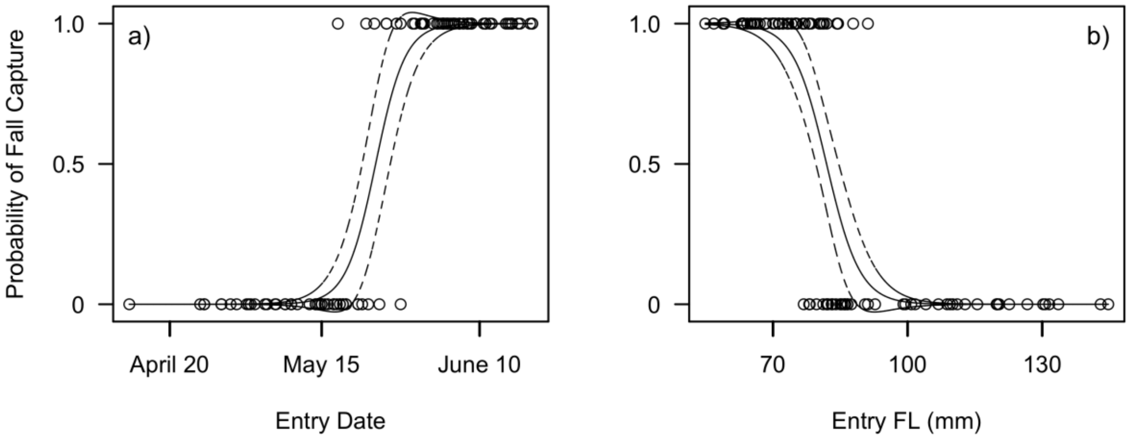

Figure 4.6 Predicted probability of juvenile sockeye salmon being captured in fall surveys. The fitted model in each panel contains the explanatory variable shown on the x-axis when the second is held at its mean value. Sampled individuals were collected in 2008 and belonged to Chilko Lake, Great Central Lake, and Lower Adams River populations.

Chapter 5 - Effects of density during freshwater and early marine rearing on juvenile sockeye salmon size, growth, and migration

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5.1. Abstract

We tested for density-dependent effects on the body size, ocean entry date, growth rate, and migration speed of juvenile sockeye salmon (*Oncorhynchus nerka*) in two years with contrasting competitor densities during freshwater rearing (intraspecific), as well as the first two months of marine residence (intra- and interspecific). Juvenile sockeye salmon entering the marine environment during a year with high competitor densities (conspecifics and nine other pelagic species groups) were, on average, 11% smaller and entered the ocean almost a week earlier. Differences between the high- and low-density years in entry size, but not entry date, were strongest in nursery lakes with high parental spawner abundance, consistent with density-dependent effects on freshwater growth. Mean daily growth rates of sockeye salmon during early marine residence did not vary between years after accounting for variation in ocean entry size and timing, even though the catch-per-unit-effort of the most abundant juvenile salmon species increased more than five-fold. However, juvenile sockeye salmon entering in the high-density year did migrate away from their ocean entry points significantly more rapidly (estimated ~40% increase in bl sec^{-1}). Our results suggest that juvenile sockeye salmon growth during early marine residence may not be strongly limited by competition and that shifts in migration speed or spatial distribution may buffer individuals from competitive interactions.

5.2. Introduction

The effect of competition on the dynamics of animal populations varies with the abundance of competitor populations and the ecosystem's carrying capacity. When abundances are high and resources are limited, intraspecific competition intensifies, often leading to increased mortality rates and reduced growth (Sinclair 1989). Yet identifying periods when individual traits are moderated by density can be complicated by ontogenetic variation in ecological characteristics (e.g., body size, resource requirements, habitat use) that may influence competitive interactions (Ratikainen et al. 2008). Despite these difficulties, quantifying the strength of density-dependence and its impact on population dynamics is important to support the sustainable use and conservation of animal populations (Hilborn and Walters 1992).

In salmon, intraspecific density-dependent effects during freshwater rearing are widely recognized. Large numbers of returning adult salmon can exceed the capacity of available spawning habitat, resulting in high rates of egg mortality due to nest superimposition (McNeil 1964). Similarly, high juvenile salmon abundance during freshwater rearing has been associated with slower growth (Foerster 1944, Schindler et al. 2005), displacement to suboptimal habitats (Gibson et al. 2008), altered downstream migration phenologies (Connor et al. 2013), and reduced survival (Jonsson et al. 1998).

Once salmon enter the marine environment density-dependent effects can be relatively difficult to detect, particularly in highly migratory species or populations. Competitive interactions in the marine environment occur across large geographic areas and coincide with ontogenetic shifts in resource use (Brodeur et al. 2007, Hertz et al. 2016). Furthermore, the composition of marine communities varies across space and time (Orsi et al. 2007), altering the suite of species with which migrants interact. Despite these issues, length-at-age data and reconstructed growth histories from spawners suggest that high densities of conspecifics (Peterman 1984) or other salmon species (Ruggerone et al.

2003, Ruggerone and Connors 2015, Debertin et al. 2017) can depress growth or survival, particularly during offshore residence. Similar density-dependent effects have been hypothesized to also occur early in marine life (Beamish et al. 2010), potentially resulting in size selective mortality and reduced spawner abundance (Beamish et al. 2004)

We examined the potential for density-dependent effects on a suite of individual traits during freshwater and early marine residence in juvenile sockeye salmon (*Oncorhynchus nerka*) originating from the Fraser River in British Columbia. After downstream migration, Fraser River sockeye salmon enter the Strait of Georgia, which lies between Vancouver Island and the British Columbia mainland and is connected to the northeast Pacific Ocean via Johnstone Strait in the north and Juan de Fuca Strait in the south (Fig. 5.1). Most Fraser River sockeye salmon migrate north through the Strait of Georgia ecosystem over a one to two month period (Preikshot et al. 2012, Freshwater et al. 2016b, Neville et al. 2016). Despite the relatively small size of the Strait of Georgia (6,800 km^2), hundreds of salmon populations enter and rear in this ecosystem for several months, resulting in high juvenile salmon densities (Groot and Margolis 1991).

Fraser River sockeye salmon populations exhibit substantial variation in inter-annual abundance (DFO 2014b), which can be used to test for density-dependent effects. Particularly large differences in Fraser River spawner abundance were observed in 2009 and 2010. Spawner abundance in 2009 was exceptionally low (approximately 1 million fish), compared to a record high of 13 million estimated spawners in 2010. Juvenile sockeye salmon produced from these years largely entered the ocean during 2011 and 2012 (from 2009 and 2010 spawning, respectively) and catch-per-unit-effort (CPUE) of juvenile sockeye salmon in the Strait was consequently anomalously high in 2012

(Neville and Sweeting 2013). Additionally, density-dependent interactions in the Strait may be magnified by the abundance of other pelagic fishes. Juvenile sockeye salmon in the Strait of Georgia co-occur with juvenile Fraser River pink salmon (*O. gorbuscha*) that compete for similar prey (Brodeur et al. 2007, Beamish et al. 2008, Beamish et al. 2010). Pink salmon have biennial life cycles and are effectively absent as juveniles from the Strait of Georgia in odd years and are highly abundant in even years (Beamish et al. 2010, Neville and Sweeting 2013). Species such as juvenile chum salmon (*O. keta*) and Pacific herring (*Clupea pallasi*) also exhibit interannual variability in abundance (Rensel et al. 2010, Beamish et al. 2012a), which may further moderate marine density-dependent interactions.

Although Fraser River sockeye salmon experience a common rearing environment in the Strait of Georgia, conditions during freshwater residence vary among populations within the watershed. Despite total spawner abundance in the Fraser River being extremely high in 2010, several populations experienced average or below average returns and low fry densities (DFO 2014). Therefore, although all Fraser River sockeye salmon populations experienced high competitor densities in the Strait of Georgia in 2012, freshwater density-dependent effects likely varied among nursery lakes.

The objectives of this study were to determine whether the body size, growth rate, and migratory phenology of juvenile sockeye salmon differed between 2011 and 2012, consistent with density-dependent effects during marine residence, while accounting for potential freshwater density-dependent effects. Although the conclusions that can be drawn with two years of data are necessarily limited, these particular cohorts represent abnormally large differences in sockeye salmon abundance that likely bracket the low and high densities that will be observed in this region. Preliminary analyses indicated juvenile sockeye salmon body size differed between 2011 and 2012 (Neville et al. 2013). Those results, coupled with the differences in spawner density between 2009 and 2010, provided some evidence for density-dependent growth; however, that preliminary analysis could not determine whether differences in body size were due to interactions occurring during freshwater or marine residence.

We predicted that size at capture (H1) and entry (H2) would be significantly greater and entry date significantly later (H3) in 2011 (low density) relative to 2012 (high density), particularly in lakes that had high densities of juveniles during freshwater residence. After accounting for these ocean entry effects, we hypothesized that growth rates for sockeye salmon would be greater in 2011 compared to 2012 (H4) due to density-dependent effects in the Strait of Georgia. Finally, as many species alter their movement patterns based on intra- or interspecific competitor density (Matthysen 2005, Chapman et al. 2012), we predicted that the mean migration speed of juvenile sockeye salmon would shift with increased competitor density (H5). Under conditions of reduced prey and limited potential growth that juvenile sockeye salmon may accelerate their migration speed within the Strait of Georgia to reach better feeding opportunities further north. Alternatively, as migration speed is correlated with body size (Freshwater et al. 2016b), density-dependent reductions in body size may result in a coincident decrease in migration speed.

5.3. Methods

5.3.1. Pelagic fish sampling and catch analysis

We captured juvenile salmon and other fishes throughout the Discovery Islands, Strait of Georgia, and lower Johnstone Strait (Fig. 5.1) in 2011 (18-31 May and 11-25 June) and 2012 (19 May – 1 June and 11-25 June), using a purse seine fished from the *F/V Ocean Venture*. The areas fished are described in detail in Neville et al. (2013). To increase population-specific sample sizes, we also incorporated 11 individuals collected during mid-water surface trawls by the *CCGS W.E. Ricker* in 2011 (June 24 – July 1). Sensitivity analyses indicated the inclusion of these samples did not change our conclusions (Appendix D). We randomly selected up to 30 juvenile sockeye salmon from each set to retain for sampling and the remaining individuals were identified to species, enumerated, and released. Immediately after capture, we recorded fork length, removed sagittal otoliths, and preserved tissue samples for genetic stock identification from all sampled fish. Individuals were assigned to spawning populations within the Fraser River using 14 microsatellite loci, with a 50% lower probability limit and an estimated 5% false assignment rate (Beacham et al. 2005). We restricted further analyses to populations that had at least 4 individuals captured in a sampling year. To meet this threshold, balance the dataset temporally, and to account for common density-dependent effects during freshwater rearing, we aggregated several spawning populations by their shared, primary nursery lake or lake-complex. Population specific sample sizes and their assignment to different nursery lakes are shown in Table A5.1.

We estimated the relative abundance of pelagic fishes that were captured during the purse seine surveys using catch-per-unit-effort (CPUE; number of individuals captured per set). For this study we restricted our analysis to species that were captured in at least 50 sampling sets across both years (183 and 194 sets completed in 2011 and 2012, respectively). We tested for differences between 2011 and 2012 in the total CPUE of all species, as well as the CPUE of individual species. A negative binomial generalized linear model (GLM) was used to test for differences in total CPUE because the summed catch data were over-dispersed. To test for species-specific differences in CPUE we used zero-inflated Poisson GLMs, which simultaneously estimate the probability of a non-zero response using a binomial distribution with a logit link function and estimate the probability of observing a specific count using a Poisson distribution with a log link function. We fit capture year as a fixed parameter and estimated its effect on mean catch size, as well as the proportion of zero catches (for species-specific CPUE). We estimated parameters relative to 2012, i.e. negative estimates indicate that the probability of observing a zero catch (for zero-inflated model component) or observing a larger catch (for the count model component) was lower in 2012. We adjusted our significance tests for multiple comparisons of fish abundance using a false discovery rate (Benjamini et al. 2006). We fit zero-inflated Poission GLMs in the *pscl* package (Zeileis et al. 2008) and conducted all statistical analyses using R version 3.2.2 (R Core Team 2017).

5.3.2. Sea surface temperature and zooplankton data

Interannual differences in environmental conditions, such as temperature and prey availability, may influence marine growth or migratory behavior, confounding tests of density-dependent effects. To address this possibility, we estimated interannual differences in sea surface temperature using data collected by lighthouses at Chrome and Entrance Island. We also estimated interannual differences in prey availability using zooplankton data sampled during Fisheries and Oceans Canada surveys that overlapped spatially and temporally (21 May – 25 June in 2011 and 2012; Fig. 5.1) with juvenile salmon sampling events. Zooplankton samples were collected by a 0.56 m diameter, vertical bongo net with 236 μm mesh towed at depths from 39-400 m. For this study, we used samples that had been aggregated into broad taxonomic groups (typically order; details in Mackas et al. 2013) and retained only taxa that have been commonly observed in juvenile sockeye salmon diets (Brodeur et al. 2007). We tested for interannual differences in seasonal increases in sea surface temperature with a linear model that included day of year, year, and their interaction as predictors. We tested for differences in the biomass of potential prey taxa between years using Mann-Whitney tests.

5.3.3. Abundance of effective female spawners

Estimates of juvenile sockeye salmon abundance within nursery lakes are unavailable for most Fraser River populations (DFO 2014b). Instead we assessed differences in freshwater density-dependent effects using estimates of spawner abundance in the parental generation as a proxy for juvenile sockeye salmon densities in nursery lakes. Spawner abundance estimates are collected by DFO using a variety of techniques including fence and tower counts, weir counts, and aerial and visual surveys (Grant et al. 2011; K. Benner, DFO, pers. comm.). These estimates are then converted to an estimate of effective female spawner (EFS) abundance using sex ratio and spawner success data collected during carcass surveys (Grant et al. 2011, DFO 2014b). We calculated EFS abundance in 2009 (parents of 2011 juveniles) and 2010 (parents of 2012 juveniles) relative to mean EFS abundance (1974-2010). However, these data were highly skewed and dominated by several outliers. Therefore, we treated freshwater density-dependent effects as a categorical variable and classified it as present if EFS abundance was greater than mean EFS abundance plus one standard deviation in 2010.

To estimate the effects of spawner density on competitive interactions between juveniles rearing in freshwater it was necessary to aggregate EFS abundance data within a nursery lake system. Typically, spawner abundance is estimated at the scale of conservation units (CUs). CUs are management units that consist of spawning populations with a common life history type, rearing environment, and run timing (Holtby and Ciruna 2007, Grant et al. 2011). Each group of spawning populations that we aggregated by nursery lake for the otolith microstructure analysis belongs to a single CU (Table A5.1), but may rear in a lake or lake complex in sympatry with CUs for which we do not have otolith samples. To provide an estimate of the maximum potential freshwater density-dependent effects juveniles may have encountered, we summed the spawner abundance for all CUs that are likely to contribute fry to the nursery lake or lake-complex used by spawning populations for which we have otolith data. We provide details on the relationship between spawning populations, nursery lakes, and CUs, as well as how these aggregates were grouped, in Table A5.1.

5.3.4. Otolith microstructure analyses

We used otolith microstructure techniques to estimate individual size at ocean entry, ocean entry date, and marine growth rates (see Freshwater et al. 2015 for validation and details on sample preparation). We used cellSens Imaging Software (Olympus Scientific Solutions America) to measure otolith radius, marine entry check radius, and the number of daily increments formed after marine entry. We made all measurements dorsal and perpendicular to the otolith’s anterior-posterior centerline and used the average of three sequential measurements, per otolith metric, for analysis. If an otolith was vateritic (an alternative crystalline structure that results in translucent and unreadable otoliths), damaged, if all measurements could not be completed, or if individual counts differed by more than 5 increments, that individual was excluded from subsequent analyses.

To estimate size at ocean entry, we used a linear regression (otolith radius vs. fork length) developed from a larger dataset of British Columbia sockeye salmon ranging in size from 66 to 209 mm and collected over six years. We estimated entry fork length from marine entry check radii with both scale (i.e. hard structure) proportional and body proportional methods (Francis 1990), then used the mean of both as an estimate of fork length at ocean entry. Briefly, these methods assume a single relationship between otolith length and fish length by estimating either fork length (FL) as a function of otolith radius (OR) (FL = 285.10 (±4.85 SE) X OR – 76.20 (±3.44 SE); $r^2 = 0.78$, $n = 920$; C. Freshwater, *unpublished data*) or vice versa (OR = 0.0027 (±0.0004 SE) X FL + 0.37 (±0.006 SE)). Estimates of previous body size are then corrected for each individual's deviation from the average otolith-body size relationship. By taking the mean of both methods, we partially account for the possibility that variation among individuals may be due to either their somatic growth or their otolith growth deviating from the mean relationship within the population (Francis 1990).

We estimated daily marine growth rates by subtracting estimated size at ocean entry from size at capture, then dividing by the number of daily increments. We calculated two estimates of migration speed (defined here as the rate at which individual fish moved away from their ocean entry point). For both, we first estimated migration distance as the linear distance (km) between the ocean entry point in the Fraser River estuary and capture location, after accounting for the Earth's curvature. We then divided the linear migration distance by the number of daily increments to estimate absolute migration speed. We converted migration speed in km day^{-1} to body lengths per second (bl sec^{-1}) using estimates of fork length at ocean entry. Since we were primarily interested in how individual migratory effort may shift with changes in density we focused on relative migration speed (i.e. bl sec^{-1}), but analyses estimating changes in migration speed in km day^{-1} are presented in Appendix D.

We used generalized linear mixed effects models to examine differences in individual characteristics between years of low and high juvenile salmon abundance during early marine rearing. Specifically we tested that 1) size at capture, 2) size at ocean entry, 3) ocean entry date, 4) marine growth rates, or 5) marine migration speed did not significantly differ between 2011 and 2012. We tested hypotheses 1-3 using linear mixed effects models in the *lme4* package (Bates et al. 2015), with sampling year and freshwater density-dependent effects (present or absent) as categorical fixed effects and random intercepts for each nursery lake to account for variation among rearing populations. To account for differences between years in ocean entry characteristics that may have been associated with freshwater rearing densities we included an interaction term between the two fixed effects.

Since ocean entry size and phenology can influence the early marine growth (Freshwater et al. 2016a) and migration rate (Freshwater et al. 2016b) of juvenile sockeye salmon, we constructed additional mixed effects models that included entry size and phenology as covariates to test hypotheses 4 and 5. We did not believe that freshwater density-dependence would have an effect on marine growth or migration speeds after accounting for entry traits, therefore we did not include this fixed effect or its interaction with capture year. Although we also estimated freshwater age using otolith annuli, only one age-2 individual was identified in the useable samples. As a result, freshwater age was not included as an additional covariate. To better interpret models that included covariates measured in different units, we centered and scaled entry size and entry date data (Schielzeth 2010) . To meet normality assumptions, we log transformed migration speed. We confirmed that explanatory variables were not collinear using variance inflation factors (the VIF of all explanatory variables was less < 2; VIF < 3 indicates minimal collinearity). We also checked for adequate model fit by examining quantile-quantile plots and the distribution of residuals.

5.4. Results

5.4.1. Pelagic fish abundance

The ten most abundant taxa collected in the purse seine survey included: five species of juvenile Pacific salmon (sockeye salmon, pink salmon, chum salmon, Chinook salmon *O. tshawytscha*, and coho salmon *O. kisutch*), Pacific herring, kelp greenling *Hexagrammos decagrammus* and rock greenling *H. lagocephalus* (CPUE for both species were pooled), Pacific sand lance *Ammodytes hexapterus,* northern anchovy *Engraulis mordax*, and three-spined stickleback *Gasterosteus aculeatus*. Total CPUE (i.e. catches of all zooplanktivorous fish species combined) was significantly greater in 2012 than 2011 (Table 5.1). This change in total abundance reflected increases in the abundance of nearly all the species we examined. The number of non-zero catches for juvenile sockeye salmon, pink salmon, and herring were significantly greater in 2012 than 2011 (Table 5.1, Fig. 5.2). After accounting for catches where no individuals were captured, CPUE for eight of the ten pelagic fishes (including all juvenile salmon species) was significantly greater in 2012 than 2011 (Table 5.1). Only Pacific sand lance and three-spined stickleback CPUE were significantly lower in 2012 than 2011 (Table 5.1).

5.4.2. Sea surface temperature and zooplankton abundance

Sea surface temperature (SST) increased over the migratory period in both years (Fig. A5.1). Seasonal increases in SST from the beginning of the migratory period through mid-July were similar in both years and the effect of year, as well as the interaction between year and Julian date, were not significant (β_{year} = -0.10±1.84, β_{int} = 0.00±0.01; DF = 194). A Mann-Whitney test indicated that the total biomass of potential prey items was not significantly different between 2011 and 2012 (Fig. A5.2). Similarly, there were no significant differences between years in the biomass of individual potential prey taxa (Fig. A5.2).

5.4.3. Juvenile salmon ocean entry characteristics, growth, and migration speed

Of the 204 juvenile sockeye salmon that were sampled for otoliths, 180 met the criteria required for inclusion in the analysis. Genetic stock identification indicated these individuals originated from seven nursery lake systems (Fig. 5.1; Table A5.1 summarizes the number of samples per population and nursery lake within a year). Based on estimates of effective female spawner (EFS) abundance in 2010 (the 2012 parental generation), we identified juveniles migrating from Chilko and Shuswap Lakes as having a high probability of experiencing freshwater density-dependent effects (EFS abundance in 2010 greater than long term mean plus one SD). EFS abundance in the five remaining lakes in 2010 and in all seven lakes in 2009 (2011 parental generation) was relatively low and individuals were unlikely to experience density-dependent effects (Table A5.2).

After accounting for variation among nursery lakes, juvenile salmon captured in the high abundance year (2012) were smaller than those collected in 2011 (mean FL_{2011} = 106.8 mm, mean FL_{2012} = 94.2 mm). However, the interaction between year and freshwater density was significant in the size at capture model (Table 5.2), indicating nursery lakes with high spawner abundance in 2010 had a greater difference in marine size between years (Table 5.2). Juvenile sockeye salmon out-migrating in the high abundance year were also approximately 10 mm smaller at ocean entry (equivalent to a 40-45% difference in mass) and exited the river almost one week earlier on average (Figs. 5.3, 5.4, Table A5.3). The interaction between year and freshwater density was significant in the entry size, but not the entry date, model. Therefore, differences in entry size between years were significantly greater in nursery lakes with large 2010 returns, while differences between years in entry date were relatively uniform among lakes (Table 5.2, Figs. 5.3, 5.4).

Smaller juveniles typically had faster mean growth rates than those that entered at a larger size, however this effect was not statistically significant (Table 5.2, Fig. 5.5a). Conversely, growth was significantly and positively correlated with ocean entry timing (Table 5.2). Individuals entering in the latter half of the season grew up to 0.5 mm/day more than those in the first (Table 5.2, Fig. 5.5b). After accounting for variation in entry size and entry date between years, there was no significant difference in marine growth rates between the low and high abundance years (Table 5.2, Fig. 5.8; mean $growth_{2011}$ = 0.81 mm day^{-1} ± 0.22 SD, mean $growth_{2012}$ = 0.80 mm day^{-1} ± 0.16 SD).

Migration speed (bl sec^{-1}) was correlated with both entry size and timing (Figure 6). Larger juveniles had a significantly greater migration speed than smaller individuals (Fig. 5.6a, Table 5.2) and juveniles that entered late in the year had a significantly greater migration speed that those entering early in the year (Fig. 5.6b, Table 5.2). After accounting for these relationships, individuals entering the ocean in the high abundance year had a significantly greater migration speed than juveniles entering when densities of fish competitors were low (Fig. 5.6, Table 5.2). After accounting for the effect of entry size and date, juveniles in 2012 had a mean migration speed 40% greater than those entering in 2011. Here we present parameter estimates from a model estimating changes in relative migration speed (i.e. bl sec^{-1}), however when we modeled absolute migration speed (km day^{-1}) as the response, all parameters remained significant and the patterns were qualitatively similar (Table A5.5, Fig. A5.3).

5.5. Discussion

Competition among and within Pacific salmon species during offshore residence is associated with decreased survival, growth, and size at maturity (Ruggerone et al. 2003, Ruggerone and Connors 2015, Debertin et al. 2017). In this study, we used two years characterized by large differences in the abundance of juvenile Pacific salmon and other pelagic species to test for density-dependent effects in sockeye salmon during the first weeks of marine residence. Juvenile sockeye salmon were significantly smaller at capture during the high abundance year (2012) and exhibited consistent differences in ocean entry characteristics. After accounting for variation among nursery lakes, juveniles sampled during the high abundance year were significantly smaller at ocean entry and outmigrated from freshwater earlier in the year. Differences between years in entry size were correlated with density-dependent effects during freshwater rearing (e.g., Martinson et al. 2008, Rich et al. 2009), while shifts in entry phenology were not. While we did not observe a significant difference in mean daily growth rate between high and low abundance years, juvenile sockeye salmon that entered when densities were high moved away from their ocean entry points at significantly greater rates.

Fraser River sockeye salmon entering the Strait of Georgia in 2012 experienced a considerably higher density of potential competitors than individuals entering the previous year. Mean catch-per-unit-effort (CPUE) of juvenile sockeye salmon increased more than six-fold between 2011 and 2012. We also observed large increases in the abundance of juvenile pink salmon and chum salmon – species with diets similar to that of sockeye salmon (Brodeur et al. 2007) and potential competitors (Ruggerone and Nielsen 2004, Beamish et al. 2010). Moreover, we found little evidence that the abundance of other zooplanktivorous species decreased to buffer the community from greater juvenile pink and sockeye salmon abundance. The CPUE of Pacific herring, the dominant pelagic forage fish in the Strait of Georgia (Orsi et al. 2007), was significantly greater in 2012 than 2011. Young-of-the-year herring CPUE also increased more than six-fold in 2012 (Boldt et al. 2015). Juvenile coho salmon and Chinook salmon CPUE were also significantly greater in 2012 than 2011. While estimates of Pacific sand lance and three-spined stickleback abundance showed an opposite pattern, it is unlikely that the lower CPUE of these species in 2012 compensated for increases in the abundance of the other eight given their low abundance relative to other pelagic fish species. We note, however, that our estimates only reflect the abundance of diurnal finfishes and do not account for potential differences between years in the abundance of jellyfish or taxa with diel vertical migrations. Jellyfish in particular may compete with zooplanktivorous fishes for common prey, resulting in lower salmon survival (Ruzicka et al. 2016).

Although the abundance of juvenile sockeye salmon competitors was high throughout the Strait of Georgia in 2012, density-dependent effects during freshwater residence likely varied among nursery lakes due to differences in the abundance of effective female spawners (EFS). We assumed individuals rearing in systems with exceptionally high EFS abundances (i.e. Chilko Lake and the Shuswap Lake complex) experienced density-dependent effects, while juveniles in other nursery lakes did not. We recognize that EFS abundance is an imperfect proxy for freshwater rearing densities, but feel previous studies justify its use here. The relationship between spawner and juvenile abundance has been modeled for Quesnel, Chilko and Shuswap Lakes (DFO 2014). In each lake a standard Ricker stock-recruit relationship between EFS and the abundance of sockeye salmon fry provides reasonably strong predictive power (r^2 = 0.4-0.8; DFO 2014). Although these models indicate per capita productivity is reduced when spawner abundance is high, there is still substantial variability in fry abundance (DFO 2014). Fry and smolt abundance estimates indicate that 2012 juvenile abundance in Chilko and Shuswap Lakes was the third highest and highest on record, respectively, while the abundance of Quesnel juveniles was below average (DFO 2014).

We used differences in salmon abundance among years and nursery lakes to test for the presence of density-dependent effects during both freshwater and marine residence. As previously observed by Neville et al. (2013), juvenile sockeye salmon captured at sea were significantly smaller in 2012 relative to 2011. We determined that shifts in size were mirrored by differences in ocean entry traits. The mean size of individuals at ocean entry in 2012 was approximately 10 mm smaller those in 2011, while mean ocean entry date was approximately one week earlier. The interaction between high EFS abundance and capture year had a significant, negative effect on entry size, indicating that differences in ocean entry size were greatest in Chilko Lake and the Shuwap Lake complex. This evidence of freshwater density-dependent effects is supported by data suggesting below average early freshwater survival and juvenile salmon body mass preceding the 2012 outmigration in these two systems (DFO 2014b). Furthermore, similarly strong effects of competitor abundance on juvenile sockeye salmon growth and size have been documented in numerous Alaskan populations (Schindler et al. 2005, Rich et al. 2009)

Although ocean entry date was significantly advanced in the high abundance year (2012), the interaction between year and high EFS abundance was not significant, indicating this shift was relatively uniform across nursery lakes. Interannual variation in outmigration phenologies within sockeye salmon populations may be more strongly linked to regional environmental drivers, such as temperature or flow (Achord et al. 2007), than juvenile densities.

After accounting for the effect of entry size and date, sockeye salmon that outmigrated during the high abundance year (2012) did not grow at a significantly different rate from those captured in the low abundance year (2011). Evidence suggests competitive interactions among Chinook salmon are moderated by estuarine habitat quality (David et al. 2016). Since productivity in the Strait of Georgia appears to be predominantly regulated by bottom-up mechanisms (Preikshot et al. 2013), juvenile sockeye salmon may only experience density-dependent growth in years with poor environmental conditions. This result is also consistent with evidence from returning spawners that the effects of offshore competition outweigh interactions during the first ocean year (e.g., Ruggerone and Connors 2015).

Individual characteristics at ocean entry had mixed effects on growth. For instance, individuals that entered later in the year grew more rapidly than those entering earlier. Greater growth later in summer may be linked to increases in zooplankaton prey availability between May and July (Mackas et al. 2013), which occur one to two months after the initial spring phytoplankton bloom in early April (Allen and Wolfe 2013). Conversely, growth was weakly and negatively correlated with ocean entry size. Although this relationship was not significant, similar growth rates across size classes and between years indicate smaller bodied salmonids remain capable of growing quickly (reviewed in Marco-Rius et al. 2012), even when competitor densities are high.

Despite similar growth rates, we observed significant increases in migration speed in the high-density year. Consistent with previous observations (Freshwater et al. 2016b), the migration speed of juvenile sockeye salmon within a given year was strongly correlated with ocean entry characteristics – individuals that were larger or that entered later in the year migrated away from their ocean entry points at a significantly greater rate. After accounting for variation in entry timing and date, juvenile sockeye salmon that entered the ocean during the high abundance year migrated at a significantly greater rate than those in 2011 (~40% faster in bl sec^{-1}). Shifts in migration speed are consistent with previous evidence that juvenile salmon migratory patterns are influenced by local conditions. For example, the marine distribution of Columbia River Chinook salmon is linked to dynamic environmental conditions such as sea surface temperature and primary productivity that moderate geospatial cues (Burke et al. 2013). Both the spatial distribution of high CPUE sampling sites (Neville et al. 2013) and the probability of non-zero sockeye salmon catches were greater in 2012, suggesting increases in mean migration speed were linked to greater dispersal within the Strait of Georgia. However, given the data that can be collected from otoliths (i.e. mean linear distance travelled per day), we cannot exclude the possibility that individuals also migrated out of the Strait of Georgia more rapidly. Regardless, either greater dispersal to local habitats or a more rapid migration is consistent with individuals altering their movement patterns to reduce competitive interactions (Matthysen 2005, Chapman et al. 2012) and may have contributed to stable growth rates between years.

We recognize that our analysis would benefit from a greater number of sampling years, spanning a greater range of observed densities. However, we believe this study's broad conclusions remain valid. First, alternative time series of juvenile salmon abundance (Neville and Sweeting 2013), as well as the abundance of spawners in the parental generations (DFO 2014b), suggest that 2011 and 2012 represented anomalously low and high density years. Since these years likely represent reasonable lower and upper bounds of juvenile abundance in the Strait of Georgia, they should also provide a realistic threshold for density-dependent effects. A second issue is that differences between years in conditions unrelated to salmon abundance may have confounded our tests for density-dependent effects. While we cannot reject this possibility conclusively, both 2011 and 2012 exhibited comparable seasonal increases in sea surface temperature and were cooler than the long-term average (Masson 2013), conditions that are generally considered favorable for juvenile salmon survival in British Columbia (DFO 2014b). We also did not detect significant differences in the biomass of potential prey taxa between years. Although we were unable to complete a detailed examination of differences in prey quality between years, the Strait of Georgia zooplankton community does not periodically shift to lipid-poor species and species diversity remains fairly stable interannually (Mackas et al. 2013). The years we observed also did not exhibit anomalously high or low zooplankton biomass relative to previous long-term averages (Mackas et al. 2013), indicating foraging conditions throughout the Strait were probably fair.

Overall our findings indicate sockeye salmon outmigrating during a year of exceptionally high juvenile salmon and pelagic finfish abundance exhibited consistent differences in size associated with shifts in ocean entry characteristics, not differences in marine growth. Despite many million more juvenile salmon rearing in the Strait of Georgia, we did not observe lower growth rates in 2012. Conversely, juvenile sockeye salmon migrated from ocean entry points significantly more quickly in the high abundance year. Faster travel speeds or greater dispersal throughout the Strait of Georgia may buffer juvenile salmon from competitive interactions in nearshore environments and stabilize growth rates. We emphasize, however, that the conclusions that can be drawn with two years of survey data are limited, particularly given that 2011 and 2012 both appeared to be relatively optimal for Pacific salmon growth and survival. If rearing conditions are poor (e.g., high temperatures, mismatch between ocean entry and prey), density-dependent effects on early marine growth may become more severe (Levin et al. 2001, Connors et al. 2012). We also note that we predominantly relied on estimates of species abundance from diurnal surveys designed to target juvenile salmon and our ability to accurately characterize the pelagic community may be limited. To better understand potential density-dependent effects during marine rearing, future studies should examine years representing a greater range of environmental conditions and juvenile densities. Replicating investigations into growth during discrete stages of the migratory period and expanding surveys to sample a larger range of potential competitors will provide important information as to how different population and species assemblages may compete for shared prey resources.

Table 5.1 Mean catch-per-unit-effort (CPUE; individuals per purse seine set) during sampling surveys (n_{2011} = 183 sets; n_{2012} = 194 sets) and coefficients estimated from negative binomial (total CPUE) and zero-inflated (single species) Poisson regression models. P-values have been adjusted for multiple comparisons using a false discovery rate. Parameters were estimated relative to 2012, i.e. negative estimates indicate that the probability of observing a zero catch (for zero-inflated model component) or observing a larger catch (for the count model component) was lower in 2012. Species in which both model component coefficients were significant are bolded.

	Mean Catch ± SD		Zero-Inflated Model Coefficients		Count Model Coefficients	
Species	2011	2012	Estimate ± SE	p-value	Estimate ± SE	p-value
Total	1277 ± 7582	4454 ± 22005	NA	NA	1.25 ± 0.18	<0.005
Sockeye	**49 ± 239**	**323 ± 760**	**-1.09 ± 0.25**	**<0.005**	**1.61 ± 0.01**	**<0.005**
Pink	**10 ± 91**	**269 ± 707**	**-2.68 ± 0.26**	**<0.005**	**2.04 ± 0.02**	**<0.005**
Chum	73 ± 161	209 ± 451	-0.15 ± 0.29	0.622	1.03 ± 0.01	<0.005
Herring	**1013 ± 7572**	**3612 ± 22052**	**-0.73 ± 0.30**	**0.026**	**1.16 ± 0.01**	**<0.005**
Chinook	4 ± 9	6 ± 26	0.14 ± 0.21	0.566	0.54 ± 0.49	<0.005
Coho	7 ± 10	10 ± 27	0.20 ± 0.23	0.450	0.39 ± 0.04	<0.005

Anchovy	1 ± 3	3 ± 14	0.29 ± 0.29	0.381	1.41 ± 0.10	<0.005
Sand Lance	104 ± 611	5 ± 42	0.52 ± 0.29	0.099	-2.62 ± 0.03	<0.005
Stickleback	14 ± 76	11 ± 40	-0.33 ± 0.21	0.153	-0.43 ± 0.03	<0.005
Greenling	2 ± 8	8 ± 49	0.63 ± 0.31	0.062	1.95 ± 0.06	<0.005

Table 5.2 Estimated effect sizes of predictor variables from linear mixed models. Fixed effects include freshwater density-dependence (absent or present) and year (low marine densities in 2011 or high in 2012). Negative interactions indicate smaller size or earlier entry in 2012 in nursery lakes that also experienced freshwater density-dependent effects in that year. Continuous variables in growth and migration speed models were centered and scaled prior to fitting. Significant effect sizes (95% confidence intervals do not overlap with 0) are bolded.

Modeled Response	Predictor	Effect Size	95% Confidence Interval
Capture Size (mm)	Freshwater Density-Dependence	7.13	-1.44 – 16.33
	Year	0.26	-5.03 – 5.48
	Interaction	**-27.75**	**-35.96 – -19.40**
Entry Size (mm)	Freshwater Density-Dependence	-3.46	-17.54 – 10.01
	Year	-4.33	-8.73 – 0.14
	Interaction	**-18.48**	**-24.57 – -12.02**
Entry Date (Julian day)	Freshwater Density-Dependence	-0.85	-10.60 – 9.03
	Year	**-5.36**	**-8.55 – -1.96**
	Interaction	-0.57	-5.44 – 4.70

Growth (mm day^{-1})	Entry Size	-0.02	-0.06 – 0.01
	Entry Date	**0.06**	**0.03 – 0.09**
	Year	0.01	-0.05 – 0.08
Migration speed (log bl sec^{-1})	**Entry Size**	**0.14**	**0.04 – 0.25**
	Entry Date	**0.21**	**0.11 – 0.30**
	Year	**0.35**	**0.15 – 0.57**

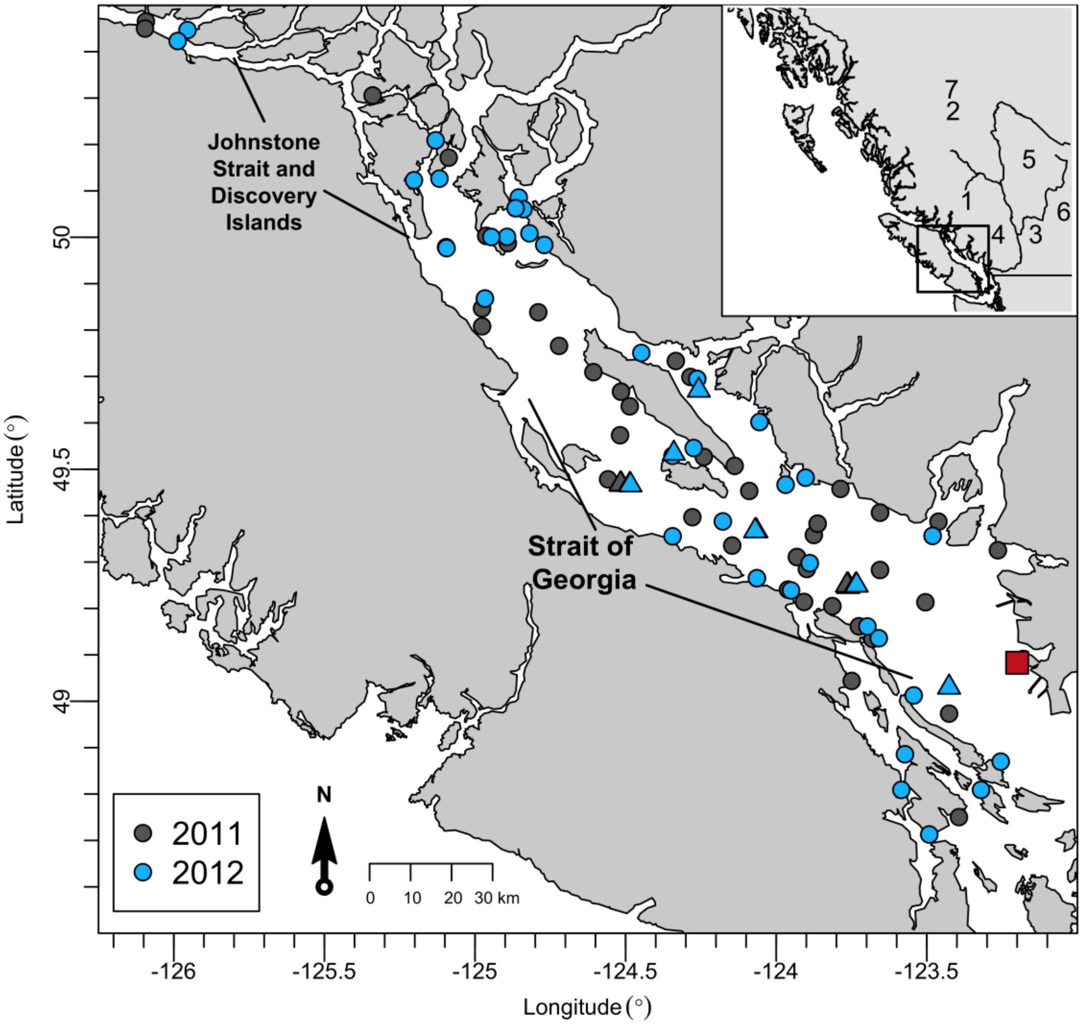

Figure 5.1 Map of study area, the Strait of Georgia and Johnstone Strait, with inset showing southern British Columbia and Fraser River watershed. Sampling sites where otoliths were collected are shown by filled circles and the approximate ocean entry location of Fraser River sockeye salmon by the red square. Juvenile fish and zooplankton sampling events shown as circles and triangles, respectively. Numbers in inset map represent approximate locations of lakes where sampled juveniles reared in freshwater: 1) Chilko, 2) Fraser, 3) Kamloops, 4) Lillooet, 5) Quesnel, 6) Shuswap and 7) Stuart.

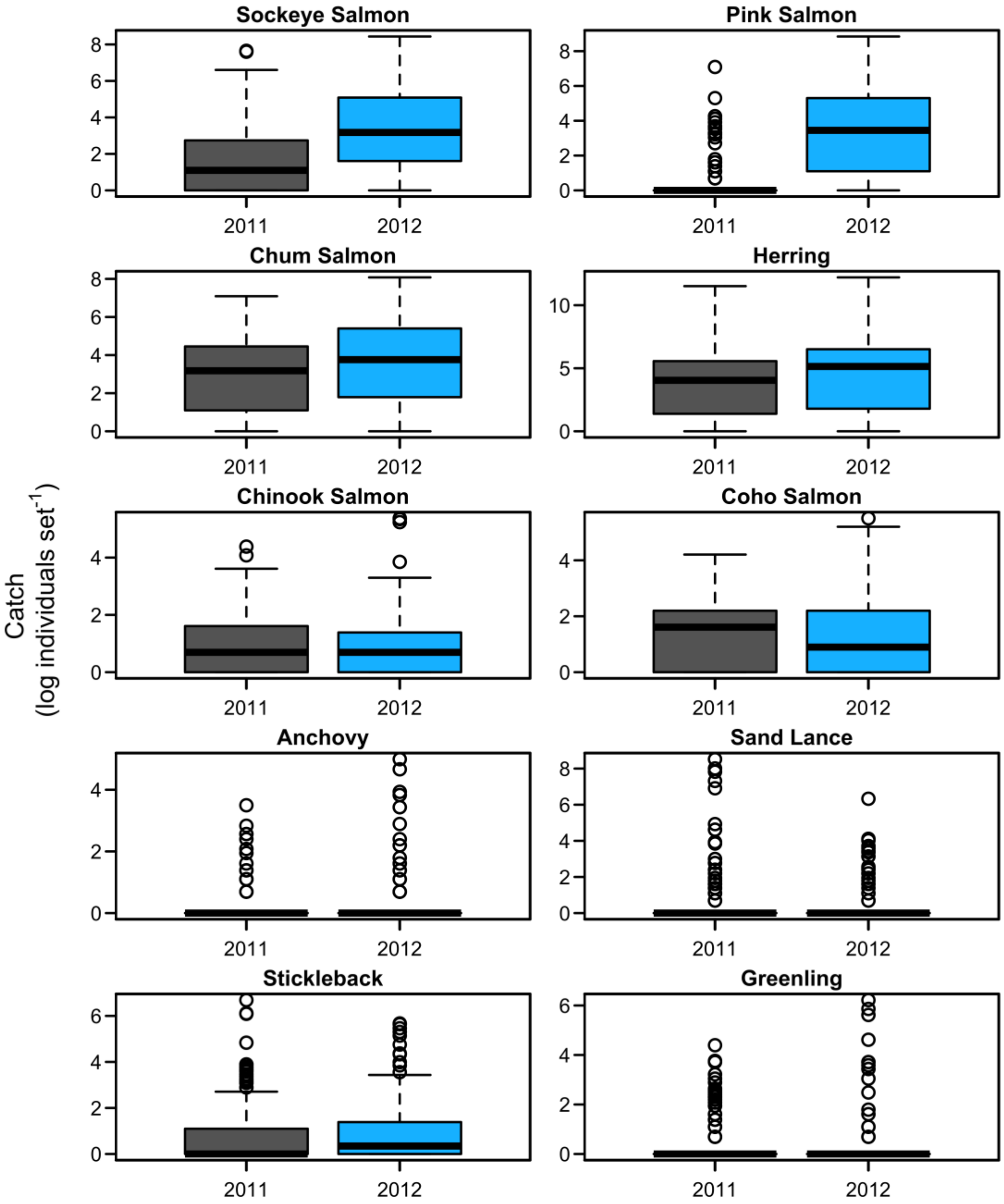

Figure 5.2 Catch-per-unit-effort (individuals per set, log transformed to improve readability) of pelagic fishes from Strait of Georgia purse seine surveys. There were 183 and 194 sampling sets in 2011 and 2012, respectively. Note that the scale of the y-axis changes between taxonomic groups. Box plots show the median as a center line, the interquartile range as whiskers, and all data outside that range as circles

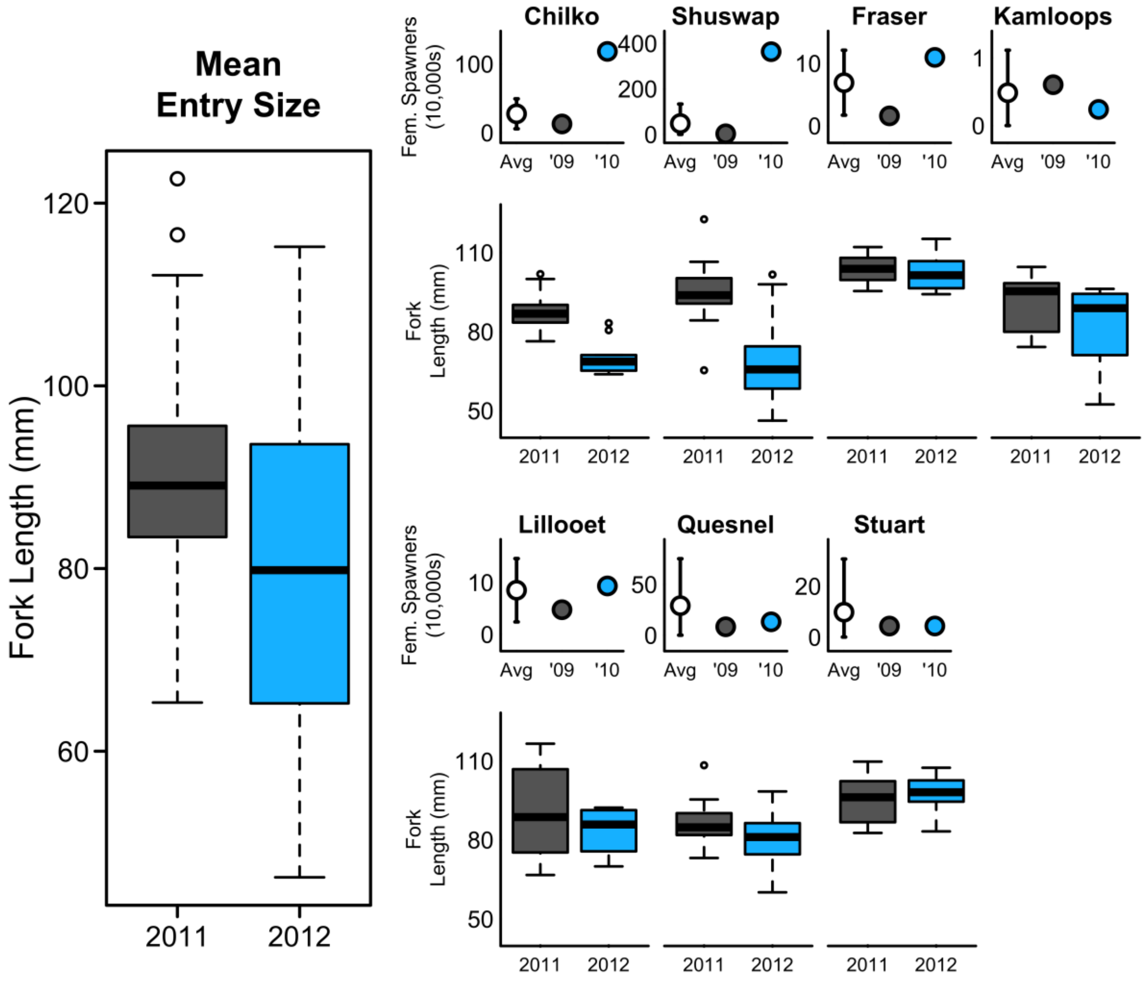

Figure 5.3 Estimates of ocean entry size from otolith microstructure for juvenile sockeye salmon captured in 2011 (grey) and 2012 (blue) and effective female spawner abundance in parental generations. Overall estimates of entry size are shown in leftmost panel and nursery lake-specific estimates are shown in the second and fourth rows. Dot plots represent effective female spawner abundance from 1973-2010 with 95% confidence interval (white), as well as in 2009 (grey) and 2010. Note that the y-axis scale for spawner abundance figures changes between lakes. Box plots show the median as a center line, the interquartile range as whiskers, and all data outside that range as circles.

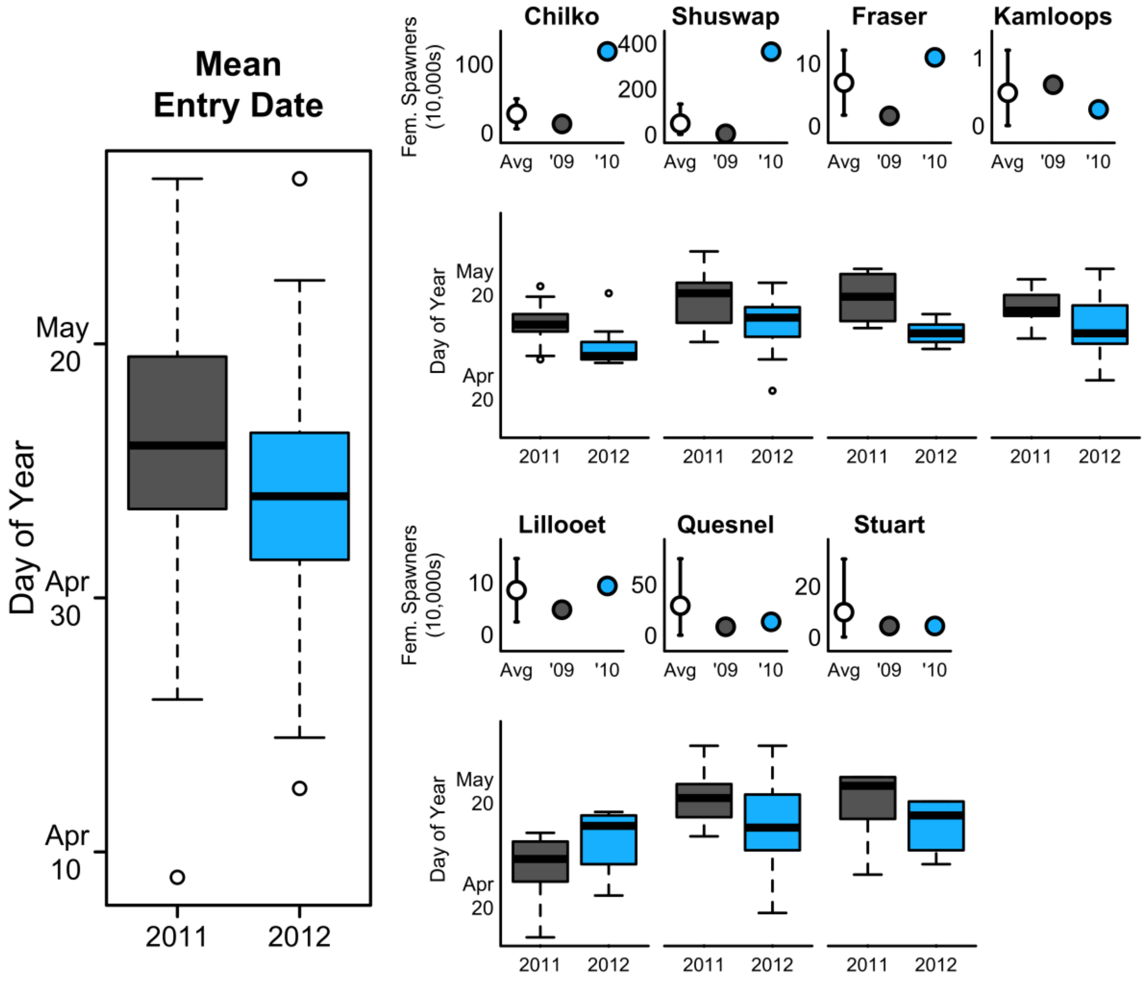

Figure 5.4 Estimates of ocean entry date from otolith microstructure for juvenile sockeye salmon captured in 2011 (grey) and 2012 (blue) and effective female spawner abundance in parental generations. Overall estimates of entry size are shown in leftmost panel and nursery lake-specific estimates are shown in the second and fourth rows. Dot plots represent effective female spawner abundance from 1973-2010 with 95% confidence interval (white), as well as in 2009 (grey) and 2010. Note that the y-axis scale for spawner abundance figures changes between lakes. Box plots show the median as a center line, the interquartile range as whiskers, and all data outside that range as circles.

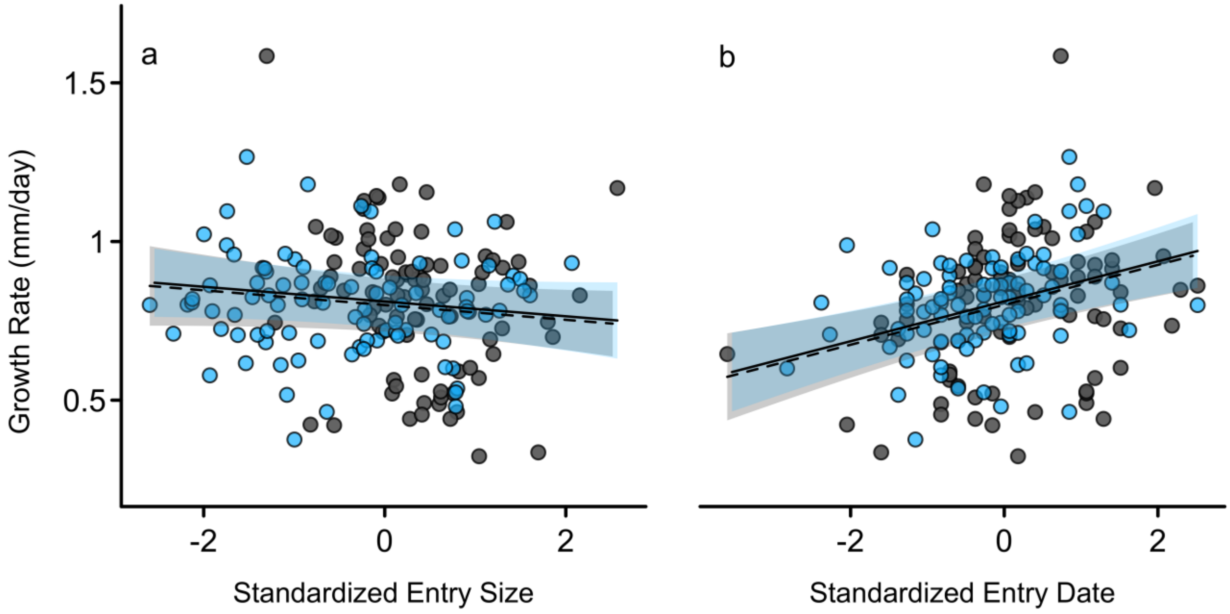

Figure 5.5 Estimated mean daily growth rate of juvenile sockeye salmon as a function of entry size (a) and date (b) showing data from a low (grey) and high (blue) abundance year. Shaded regions represent the 95% prediction intervals of the linear mixed effects model for each year (low-density, blue; high-density, grey). Prediction intervals incorporate variation among nursery lakes and are calculated holding model covariates at their mean value. Note that x-axis values have been centered and scaled.

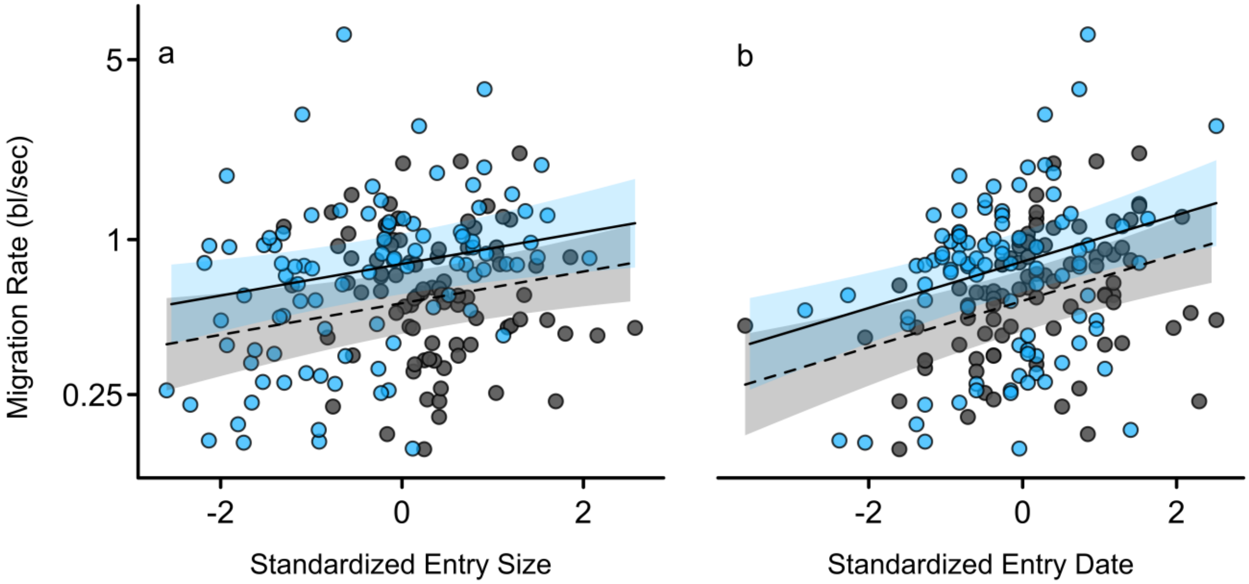

Figure 5.6 Estimated mean migration speed of juvenile sockeye salmon as a function of entry size (a) and date (b) showing data from a low (grey) and high (blue) abundance year. Shaded regions represent the 95% prediction intervals of the linear mixed effects model for each year (low-density, blue; high-density, grey). Prediction intervals incorporate variation among nursery lakes and are calculated holding model covariates at their mean value. Note that x-axis values have been centered and scaled and that the y-axis has been log-transformed.

Chapter 6 - Individual variation, population-specific strategies, and stochastic processes shape marine migration phenologies

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6.1. Abstract

The phenology of long distance migrations can influence individual fitness, moderate population dynamics, and regulate the availability of ecosystem services to other trophic levels. Phenology varies within and among populations, and can be influenced by the conditions individuals experience prior to departure, as well as those encountered en route. Yet tracking large numbers of mobile individuals from multiple populations is logistically challenging, limiting our knowledge of how intrinsic and extrinsic factors influence variation in phenologies across ecological scales. In this study, we used two natural tags, DNA and otolith microstructure analysis, to estimate the relative influence of individual traits (life history strategy, body size at departure, and growth during migration), population-specific strategies, and interannual variability on the phenology of marine migrations in juvenile sockeye salmon (*Oncorhynchus nerka*). We show that the timing and duration of juvenile sockeye salmon migrations were correlated with both life history strategy and body size, while migration duration was also associated with differences in departure timing and growth during migration. Furthermore, after accounting for the effect of individual traits, several populations exhibited differences in migration phenology that may be consistent with local adaptation. Finally, we observed substantial interannual and residual variation, suggesting stochastic environmental conditions moderate the influence of carry-over effects that develop prior to departure, as well as population-specific strategies. Migratory phenologies are shaped by complex interactions between drivers acting at multiple ecological and temporal scales. Given evidence that intraspecific diversity can stabilize ecological systems, conservation efforts should seek to maintain migratory variation within populations, which allows

them to respond to environmental stochasticity, as well as variation among populations, to preserve locally adapted phenotypes.

6.2. Introduction

Long-distance migrations are taxonomically widespread and have profound ecological impacts by linking distinct communities or habitats (Bauer and Hoye 2014). However long distance movements can also result in high fitness costs due to increased energy expenditure, harsh environmental conditions, and greater predation risk. As a result, mortality rates during migrations are often high, with a disproportionately large effect on population dynamics (Pearcy 1992, Sillett and Holmes 2002, Newton 2006). Since mechanisms of mortality are rarely static in time or space, variation in the phenology of migrations may alter individual fitness costs and shape population dynamics (Cooke et al. 2004, Newton 2006).

Processes occurring at multiple ecological scales may influence migration phenology. If migratory traits are strongly heritable, local selective pressures may lead to population-specific strategies that minimize travel costs. For example, sockeye salmon (*Oncorhynchus nerka*) populations exhibit distinct adult spawning phenologies associated with thermal regimes in freshwater habitats (Hilborn et al. 2003). Similarly, black-tailed godwit (*Limosa limosa*) migrations reflect population-specific differences in overwintering habitat quality (Gunnarsson et al. 2006). Yet individuals also exhibit considerable variation in phenology, often due to strong carry-over effects from earlier life history stages (Norris and Taylor 2006). Physical condition (Marra et al. 1998) and body size (Freshwater et al. 2016b), as well as age (McKinnon et al. 2014, Tibblin et al. 2015), can influence the timing or duration of migrations. Additionally, severe environmental conditions or other local stochastic processes can alter individual migration schedules (Schaub et al. 2004, Senner et al. 2015). Ultimately, both carry-over effects and stochastic events may reduce apparent differences among co-migrating populations by increasing variation among individuals.

The extent and scale of phenological variation within metapopulations may have distinct ecological implications. Greater diversity in the timing or duration of migrations can increase the availability of the ecosystem services that mobile populations provide, for example, by increasing higher trophic levels' access to prey (Schindler et al. 2010, Kovach et al. 2013, Deacy et al. 2016). Phenological diversity may also improve the likelihood that migratory species persist, by decreasing a metapopulation's exposure to poor environmental conditions and the risk of mass mortality events (Morris et al. 2007). Such portfolio effects may become increasingly valuable in the face of future environmental change (Anderson et al. 2015). In such a scenario, whether variation is predominantly expressed within or between populations may determine if management actions focus on maintaining specific component populations or diversity within the aggregate as a whole. Furthermore, as migration phenologies advance and become more compressed (Kovach et al. 2013), the likelihood of management intervention increases, creating an additional incentive to quantify baseline intraspecific diversity.

Despite their ecological consequences, our understanding of how phenologies vary across scales is limited by the logistical challenges associated with estimating traits among and within co-migrating populations. Many common techniques, such as surveys of species abundance during migratory periods, confound sympatric populations and provide little data on individual traits that may influence variation in phenology (Forrest and Miller-Rushing 2010). Marking a large number of individuals with low cost tags (e.g., passive integrated transponder tags) can counteract some of these issues (Zabel and Achord 2004); however, individual data can often only be collected at the time of tagging and these efforts are limited to specific habitats (e.g., riverine systems with hydropower development). A second option is to use larger tags with greater transmission frequency and data storage capacity, which can provide precise movement data on an individual scale (Furey et al. 2016). Yet because these systems have high costs per sampling unit, they are infrequently used to directly compare multiple populations simultaneously. As an alternative to artificial tags, natural markers such as DNA, parasites, stable isotopes, or calcareous structures can provide migration or connectivity data at individual scales (Gillanders 2010).

In this study, we used two natural markers, DNA and otolith microstructure, to identify co-migrating conservation units (CUs) of juvenile Fraser River sockeye salmon and estimate a suite of individual characteristics, including the timing and duration of early marine migrations within a proposed critical habitat (Beamish et al. 2012a). We first used hierarchical clustering techniques to identify groups of CUs with similar early marine characteristics in each sampling year. Next, we constructed hierarchical models to examine how diversity in the phenology (timing and duration) of marine migrations varied across ecological scales. Specifically we explored whether 1) the timing and duration of nearshore migrations were influenced by individual traits (life history strategy, body size, and growth); 2) whether CUs exhibited consistent differences in migratory phenology after accounting for these individual traits; and 3) if the relationships between individual traits and phenology differed among CUs and between years.

6.3. Methods

6.3.1. Field sampling

We sampled juvenile salmon in the Discovery Islands and Johnstone Strait (Fig. 6.1) weekly, throughout the peak migratory period of Fraser River sockeye salmon (late May to mid July) in 2014, 2015 and 2016. Fish were collected with a modified purse seine with a small mesh bunt (300 m by 20 m with 0.6-cm mesh bunt), fished from the *F/V Nordic Queen* during daylight hours. We randomly selected up to 30 juvenile sockeye salmon per set to retain for sampling, which were then euthanized with an overdose of MS-222. Immediately after capture, we recorded fork lengths and preserved tissue samples for genetic stock identification. Individuals were assigned to spawning populations within the Fraser River using 14 microsatellite loci, with a 50% lower probability limit and an estimated 5% false assignment rate (Beacham et al. 2005). Although individuals were assigned to spawning populations, we chose to aggregate samples at the level of conservation units (CUs), typically the focal unit for management, to ensure sufficient year-specific sample sizes. CUs consist of spawning populations with a common life history type, nursery lake rearing environment, and adult migration timing (Holtby and Ciruna 2007, Grant et al. 2011). A CU’s name refers to the lake(s) where the majority of juveniles rear and is followed by an abbreviation of the CU’s run timing: early summer (ES), summer (S), or late summer (L).

6.3.2. Otolith microstructure analysis

For each year of sampling we selected CUs with at least five individuals for further analyses. For each selected CU, otoliths were removed from up to 60 individuals spanning that year's sampling period. We used otolith microstructure techniques to estimate age at outmigration, size at ocean entry, ocean entry date, duration of residence in the Strait of Georgia (i.e. number of daily increments), and marine growth rates (see Freshwater et al. 2015 for validation and details on sample preparation). We made all measurements dorsal and perpendicular to the otolith's anterior-posterior centerline and used the average of three sequential measurements, per otolith metric, for analysis. If an otolith was vateritic, damaged, if all measurements could not be completed, or if individual counts differed by more than five increments, that individual was excluded from subsequent analyses.

The relationship between otolith and somatic growth can vary during development, rendering estimates based on simple regressions inaccurate (Campana 1990). Therefore, to estimate fork length at ocean entry we used a biological intercept model following Campana (1990)

$$FL_{e,i} = FL_{c,i} + ((OR_{e,i} - OR_{c,i}) * (FL_{c,i} - FL_h) * (OR_{c,i} - OR_h)^{-1}) \qquad \text{Eq. 6.1}$$

where FL is fork length and OR otolith radius for individual i at ocean entry e, at capture c, or at hatch h (the biological intercept). We assumed FL_h was 19.8 mm, the mean value for intermediate temperature treatments from a published, lab-based study on multiple Fraser River sockeye salmon populations (Beacham and Murray 1988). We also used a mean value calculated from a subset of otoliths (0.226 mm ± 0.019 SD, n =31) for the

OR_h parameter because this metric could not be estimated for all samples. We note that the accuracy of biological intercept models are robust to normal variation around the intercept because the values are small relative to variance in later life stages (Campana 1990).

We estimated marine growth rates as

$$G_i = \left(FL_{c,i} - FL_{e,i}\right) * D_i^{-1} \qquad \text{Eq. 6.2}$$

where G is the mean daily growth rate for individual i and D is the number of daily increments formed between marine entry and the otolith edge.

6.3.3. Statistical analyses

We used a hierarchical cluster analysis to explore variation in overall migratory patterns among Fraser River sockeye salmon CUs within each sampling year. We calculated a pairwise Mahalanobis distance matrix using individual estimates of ocean entry size, ocean entry date, duration of residence, and mean growth rate, grouped by CU. Since the sampled CUs and the distributions of individual traits varied among years we calculated a unique distance matrix for each year. We then used hierarchical clustering with complete linkages to identify CUs with similar migratory characteristics.

We next constructed two sets of hierarchical, linear models to estimate individual variation in phenological traits: the start date of marine migrations (i.e. ocean entry date) and the duration of the initial marine migration (i.e. number of days resident in the Strait of Georgia and Johnstone Strait). In the ocean entry date models we included size at ocean entry as an explanatory variable, while in the migration duration models we also included ocean entry date and marine growth rate as covariates. Initial models fit poorly because sea-type juveniles appeared to exhibit distinct migratory phenologies, even after accounting for differences in body size. Since there is evidence that sea-type sockeye salmon exhibit unique migratory behaviours (Tucker et al. 2009, Beamish et al. 2016), we included life history type as a binary, categorical effect. Before fitting models we confirmed that explanatory variables were not collinear using variance inflation factors (the VIF of all explanatory variables was less < 2; VIF < 3 indicates minimal collinearity). We centered and scaled continuous predictor variables to better compare models that included covariates measured in different units (Schielzeth 2010).

To account for non-independence and estimate variation at different ecological scales, we fit CU, nested within year, as random effects. We included both random intercepts and random slopes to account for CU- and year-specific deviations in mean values, as well as relationships between explanatory and response variables. To assess the importance of different predictor variables, we compared models with varying numbers of fixed effects, however the life history type dummy variable was always retained. We compared competing models using differences in the Widely Applicable Information Criterion, ΔWAIC, an alternative to AIC when comparing models with non-flat priors (McElreath 2016). Details of model structure are provided in Table 6.1.

6.3.4. Parameter estimation

We fit models within a Bayesian framework using weakly informative priors (Table 6.1). We sampled from the posterior distribution using Markov chain Monte Carlo (MCMC) techniques implemented in Stan using the *rethinking* package (McElreath 2016) in the program R (R Core Team 2017). We ran three MCMC chains of 7000 iterations each, with a warm-up of 1500 iterations. To confirm the models converged appropriately, we inspected chain coherence and stability with trace plots, ensured an adequate number of effective samples were produced, and examined each parameter’s Gelman-Rubin convergence diagnostic.

6.4. Results

We collected otolith data from 621 juvenile salmon belonging to nine CUs during three years of sampling (Table A6.1). CUs exhibited consistent differences in a suite of early marine traits (entry size, entry date, growth rate, and duration of residence), which resulted in groupings that were relatively stable across years (Fig. 6.2). Typically Lillooet-Harrison, Nadina-Francois, and Francois-Fraser CUs clustered together, with the remaining CUs forming a second group.

We observed substantial variability among individuals in both the timing and duration of their nearshore migration. Within a given year sockeye salmon entered the Strait of Georgia over a 40-50 day period and resided in the Strait between six and 69 days (Figs. 6.3, 6.4). We also observed consistent differences in migration phenology among CUs and sampling years (Figs. 6.3, 6.4). For example, individuals from the Nadina-Francois-ES CU consistently entered the marine environment later in the summer (Fig. 6.3) and migrated through the Strait more quickly than other CUs (Fig. 6.4).

Hierarchical linear models further resolved how variation in migratory phenology was partitioned among individuals, CUs, and sampling years. Model selection indicated strong support for including life history type and entry size as predictors of entry date; similarly, life history type, entry size, entry date, and marine growth rates were supported as predictors of migration duration (for both response variables the top model had >0.99 of model weight and the ΔWAIC of the next best model >20; Table A6.2, A6.3). Yet even after accounting for the effect of these individual traits, there were considerable differences among years and CUs in migration timing and duration (Fig. 6.5), which generally mirrored the patterns described above. Posterior estimates of migration timing variance were smaller than estimates of duration variance (Fig. 6.6), while estimates of interannual and residual variance were greater than variation among CUs (Fig. 6.6).

Life history type, represented by freshwater age, had a strong effect on the timing and duration of migration. Although we did not sample the Fraser River's most abundant sea-type CU in this analysis, in 2015 we observed sea-type migrants (i.e. freshwater age-0) in two CUs that are typically dominated by lake-type individuals. Sea-type individuals made up a relatively small fraction of the total catch (1.5% across all years); however these juveniles consistently entered the marine environment later in the year ($\beta_{\text{entry date}}$ = 23.1 days (10.9-36.4 90% HPDI)) and migrated through the Strait more slowly ($\beta_{\text{entry date}}$ = 29.9 days (15.8-45.1 90% HPDI)) than individuals that had reared in nursery lakes for one or two years.

Model selection indicated strong support for including all individual traits as fixed covariates; however, the overall mean effect of entry size, entry date, and marine growth on migratory phenology was weakened by interannual differences in the magnitude, and even direction, of effect sizes (Figs. 6.7, 6.8). Body size was generally positively correlated with entry date and negatively correlated with number of days spent migrating (i.e. larger individuals entered later in the year and migrated more quickly on average), however these patterns reversed in certain years (Figs. 6.7, 6.8b). Entry date and marine growth had more consistent effects on migration duration – individuals that entered late in the year and grew quickly moved through the Strait in a shorter period of time (Figs. 6.8c, 6.8d). Although there was considerable interannual variability in the effect size of individual covariates, the posterior means of CU-specific estimates were nearly always centered on zero (Fig. A6.1), suggesting the effect of individual traits on migration timing and duration is stable among CUs.

6.5. Discussion

The phenology of long distance migrations can influence individual fitness (Kokko 1999, Dickerson et al. 2005), as well as the availability of ecosystem services provided by migratory populations (Schindler et al. 2010). Consequently, how phenology varies among and within populations can shape the dynamics both of migratory species (Cooke et al. 2004, Newton 2006) and higher trophic levels (Ruff et al. 2011, Schindler et al. 2013, Deacy et al. 2016). We used hierarchical models to examine how variation in the timing and duration of juvenile sockeye salmon marine migrations was partitioned among individuals, conservation units (groupings of evolutionarily distinct populations), and sampling years. Migration phenology was correlated with a suite of individual characteristics, suggesting carry-over effects from conditions experienced during freshwater residence impact behavior. Even after accounting for these individual effects, however, several CUs exhibited distinct migratory strategies. Furthermore, we observed considerable interannual variation in migration phenology, likely due to environmental stochasticity. Years differed not only in mean migration timing and duration, but also in the relationship between individual traits and migration phenology. Our results provide evidence that migratory diversity within a metapopulation is shaped by interactions between individual characteristics, population-specific behaviours, and stochastic processes occurring at multiple temporal scales.

Individuals can exhibit considerable variation in traits such as body size or condition that moderate migratory performance (Marra et al. 1998, Gunnarsson et al. 2006). Previous evidence indicated body size and ocean entry timing contribute to the broad spatial distribution of juvenile sockeye salmon along a migratory corridor (Tucker et al. 2009, Beacham et al. 2014a, Freshwater et al. 2016b). The present study clarifies that individual traits shape the timing and duration of migration at finer scales (across multiple CUs rather than aggregates of CUs and within individual years) and earlier in the migratory period than these previous studies. Interestingly these findings mirror recent work demonstrating substantial individual-level variation in estuarine residence across numerous Pacific salmon species (Moore et al. 2016).

Life history type, represented by freshwater age, had a particularly strong influence on the timing and duration of marine migrations. On average, sea-type individuals (i.e. freshwater age-0) entered the marine environment more than three weeks later and remained in the Strait for approximately a month longer than lake-type individuals. The sea-type juveniles observed in this study originated from lake-type CUs, a scenario that is relatively rare in sockeye salmon in this region (Burgner 1991). However their phenology resembled that of the Harrison River CU, the most abundant sea-type population in the Fraser River, which also enters the ocean relatively late in the year and resides in the Strait of Georgia longer than other CUs (Tucker et al. 2009, Beamish et al. 2016). Harrison River has experienced high levels of productivity in recent years relative to other CUs in the metapopulation (Peterman and Dorner 2012, Freshwater et al. *accepted*). Therefore, while we can only speculate as to why age-0 fish from lake-type CUs were observed here, it is possible that sea-type individuals experience relatively greater fitness under current environmental conditions and may become proportionally more abundant.

Migrants often moderate their behavior based on the interaction between food availability, energy deposition rate, and departure timing (Jenni and Schaub 2003). In this study, entry date was negatively correlated with the duration of migration, indicating juveniles that entered late in the year migrated out of the region relatively quickly. Seasonal increases in movement rates may reflect changes in zooplankton prey abundance within the Strait, which typically peaks in early summer (Mackas et al. 2013). The duration of migration was also positively correlated with growth rates, suggesting individuals that were growing more rapidly, remained in the Strait for longer. Together these effects indicate migrating juvenile salmon may alter their migratory behavior based on environmental conditions. Consistent with this hypothesis, the migratory rate of juvenile Chinook salmon is correlated with estimates of primary productivity and zooplankton biomass (Tomaro et al. 2012, Burke et al. 2013), and juvenile sockeye salmon may increase travel speeds when competitor density is high (Freshwater et al. 2017).

Although body size was positively correlated with entry date, its effect on migratory duration varied across years. This variability contrasted with previous studies where size was consistently and positively correlated with travel speeds (Freshwater et al. 2016a, b, 2017). Size effects may have been weakened here by the strong influence of entry date (although VIF did not indicate significant collinearity between entry size and date, the two are moderately correlated). Furthermore, the effect of size on migration duration reversed in 2015, a year in which body size was both smaller on average and much less variable, which may have limited the potential for clear size effects.

Sockeye salmon populations exhibit distinct spatial distributions (Tucker et al. 2009, Beacham et al. 2014a) and physical traits (e.g., body size; Beacham et al. 2014b) during migrations. However, it is not immediately clear how variation within populations interacts with population-specific strategies to shape migratory characteristics. In this study we first identified groupings of CUs based on four early marine traits: body size, marine growth rate, entry date, and migration duration. These groupings were consistent between years, suggesting local selective pressures may lead to a specific suite of characteristics. CU groupings were not clearly associated with ecological characteristics such as adult migration timing or a CU’s location in the watershed. However, it is possible that groupings are the result of similar selective pressures in lakes that are independent of geographic location (e.g., predator or prey communities).

Based on posterior estimates from hierarchical models, CUs exhibited consistent differences in the timing and duration of migration, after accounting for variation in individual characteristics. Therefore, CU-specific phenologies are not solely an artifact of differences in body size. For instance, two CUs from interior tributaries (Francois-Fraser-S and Nadina-Francois-ES) began their marine migrations late in the year and moved relatively rapidly through the Strait of Georgia. These trends in migration timing are consistent with observations in the Fraser (Neville et al. 2016) and Columbia Rivers (Weitkamp et al. 2015), where interior populations tend to migrate later than those located further downriver. Such a pattern may be linked to differences among populations in migration distance (Weitkamp et al. 2015), latitudinal differences in cues that initiate migration, such as flow or temperature (Achord et al. 2007), or genetic isolation (Beacham et al. 2005). Until now, however, it was unclear whether population-specific ocean entry phenologies had carry-over effects on nearshore migration schedules.

Notably, the relationships between individual traits and migration phenology were consistent among CUs. This stability suggests that individual variation has consistent effects within a given sampling year and provides additional evidence that CU-specific phenologies are the result of traits that were not incorporated into our models.

Given that both biotic (e.g., prey availability) and abiotic (e.g., inclement weather) drivers can lead to interannual variation in animal migrations (Jenni and Schaub 2003), it was unsurprising that sockeye salmon phenologies varied across sampling years. Too few years were sampled here to reliably test specific hypotheses; however, abiotic factors such as temperature (Jonsson and Jonsson 2014), river flow velocity (Connor et al. 2013), and current strength (Burke et al. 2014) have been shown to constrain juvenile migrations in salmon populations. The effect of these physical factors on the timing and speed of migrations may also be moderated by biological variables such as zooplankton biomass (Tomaro et al. 2012), primary productivity (Burke et al. 2013), or density-dependent increases in migration rate (Freshwater et al. 2017). As a result of above average snowpack, Fraser River flows in 2014 were high and peaked early (Allen and Latornell 2015), potentially contributing to the early and compressed distribution of ocean entry dates in this year. Meanwhile the slow migration out of the Strait in 2014 could have been related to conditions broadly favorable for growth, including relatively cool temperatures (Chandler 2015), low juvenile sockeye salmon densities (Neville 2015), and a relatively late phytoplankton bloom (Allen and Latornell 2015).

The relatively large posterior estimate of residual variance indicates migration phenology within a given CU and year is heterogeneous, even after accounting for variation in traits such as body size. Juvenile salmon marine migrations appear to be influenced by hydrographic features within large river plumes (Burke et al. 2014), as well as wind-induced surface currents (Davidsen et al. 2009). Given the relatively small size of juvenile sockeye salmon, they may be particularly vulnerable to such stochastic processes. Indeed variance in the duration of migration was consistently greater than variance in entry date, suggesting that individuals moving downriver in high densities become more dispersed as they migrate through marine habitats. Acoustic tagging studies of Chilko Lake juvenile sockeye salmon also indicate migration rates are more variable in marine environments than freshwater (Clark et al. 2016), supporting this hypothesis.

The variation in migration phenologies that we observed may be used to inform management strategies in several ways. First, our findings appear to support the use of the Chilko CU as an indicator stock for the watershed as a whole. Although several interior CUs exhibited divergent migratory phenologies, the majority, including Chilko, exhibited relatively similar behaviors. If these sampling years are representative, Chilko individuals may serve as a reasonably proxy for CUs that are more rarely sampled. The Nadina-Francois and Francois-Fraser CUs that did exhibit unique migration phenologies, migrated late in the year and moved through the Strait of Georgia relatively rapidly. They may be relatively less vulnerable to nearshore stressors (e.g., low prey biomass, harmful algal blooms) as a result. Second, certain individual traits appear to have consistent, predictable impacts and are relatively easily observed at the population level. For instance, when ocean entry occurs earlier in the year, juvenile salmon appear to utilize nearshore habitats for longer periods. If nearshore residence co-occurs with adverse conditions, then certain year classes may be more likely to exhibit poor early marine survival. More broadly, the benefits of intraspecific diversity to ecological resilience are increasingly recognized (Schindler et al. 2010). If preserving variation in juvenile migration strategies becomes a priority, our results indicate that managers should seek to conserve diversity both within and between sockeye salmon CUs.

Catch data provide a snapshot of the spatial distribution of migrating fishes and, as a result, it is possible that our estimates of migration duration were biased. Individuals that move more rapidly through a given sampling location are less likely to be collected, which may lead to overestimates of mean residence. Conversely, removing individuals via sampling may prematurely terminate their residence, resulting in an opposite bias. Although it is impossible to accurately quantify these errors, several characteristics of this sampling design increase our confidence in our results. First, juvenile sockeye salmon were scarce or absent during sampling events at the beginning and end of each year's survey (e.g. Neville et al. 2016), which suggests that our protocol captured the bulk of the migration and missed few abnormally rapid or slow migrants. Second, tagging data suggest juvenile sockeye salmon migrate through our sampling region quickly relative to the Strait of Georgia (Clark et al. 2016), likely because Johnstone Strait appears to be a particularly poor location for juvenile salmon growth (McKinnell et al. 2014, Journey et al. *in press*). As a result individuals would have likely remained within the sampling region for a relatively brief period if they were not captured. Nevertheless, until these biases are better quantified, our estimates of migration duration are best considered an index.

This study clarifies how processes acting across multiple ecological scales, and both before and after departure, moderate migration phenology. We observed evidence of substantial carry-over effects from freshwater residence on the timing and duration of juvenile sockeye salmon migrations. Furthermore, conditions experienced en route, appeared to alter migratory behavior via changes to growth rates. Yet these individual traits do not fully account for variation in phenology among populations, suggesting local adaptation can constrain individual migratory variation. Finally, stochastic processes at interannual and finer scales introduced additional variability and moderated the effect of traits such as body size. The cumulative effect of these drivers is to increase the duration over which migratory populations are present in specific habitats. Such increases in phenological diversity may act to stabilize the productivity of population aggregates, while simultaneously increasing the availability of the ecosystem services provided by migrants (Schindler et al. 2010, Ruff et al. 2011, Schindler et al. 2013).

Table 6.1 Model for duration of migration through the Strait of Georgia of individual sockeye salmon *i* belonging to conservation unit *c* in year *t*. Migration timing (i.e. ocean entry date) model was identical except that entry date and marine growth were not included as covariates.

Data model	$y_{tci} \sim \text{Normal}(\mu_{tc}, \sigma)$
Process model	$\mu_{tc} = A_{tc} + B_{date,tc} + B_{growth,tc} + B_{size,tc} + B_{age,tc}$ $A_{tc} = \alpha + \alpha_c + \alpha_t$ $B_{date,tc} = \beta_{date} + \beta_{date,c} + \beta_{date,t}$ $B_{growth,tc} = \beta_{growth} + \beta_{growth,c} + \beta_{growth,t}$ $B_{size,tc} = \beta_{size} + \beta_{size,c} + \beta_{size,t}$ $B_{age,tc} = \beta_{age} + \beta_{age,c} + \beta_{age,t}$
Multivariate Priors	$\begin{bmatrix} \alpha_c \\ \beta_{date,c} \\ \beta_{growth,c} \\ \beta_{size,c} \\ \beta_{age,c} \end{bmatrix} = \text{MVN}(0, \boldsymbol{S_c})$ $\begin{bmatrix} \alpha_t \\ \beta_{date,t} \\ \beta_{growth,t} \\ \beta_{size,t} \\ \beta_{age,t} \end{bmatrix} = \text{MVN}(0, \boldsymbol{S_t})$
Adaptive Priors	$S_{x,t} = \begin{pmatrix} \sigma_{\alpha_t} & 0 \\ 0 & \sigma_{\beta_{x,t}} \end{pmatrix} \mathbf{R} \begin{pmatrix} \sigma_{\alpha_t} & 0 \\ 0 & \sigma_{\beta_{x,t}} \end{pmatrix}$ $S_{x,c} = \begin{pmatrix} \sigma_{\alpha_c} & 0 \\ 0 & \sigma_{\beta_{x,c}} \end{pmatrix} \mathbf{R} \begin{pmatrix} \sigma_{\alpha_c} & 0 \\ 0 & \sigma_{\beta_{x,c}} \end{pmatrix}$

	where x is the explanatory covariate: date, growth, size, or life history
Fixed Priors	$\alpha \sim \text{Normal}(15,30)$ $\beta_{age} \sim \text{Normal}(0,30)$ $(\beta_{date}, \beta_{growth}, \beta_{size}) \sim \text{Normal}(0,3)$ $(\sigma, \sigma_c, \sigma_t) \sim \text{Cauchy}(0,2)$ **R** ~ LKJcorr(4)

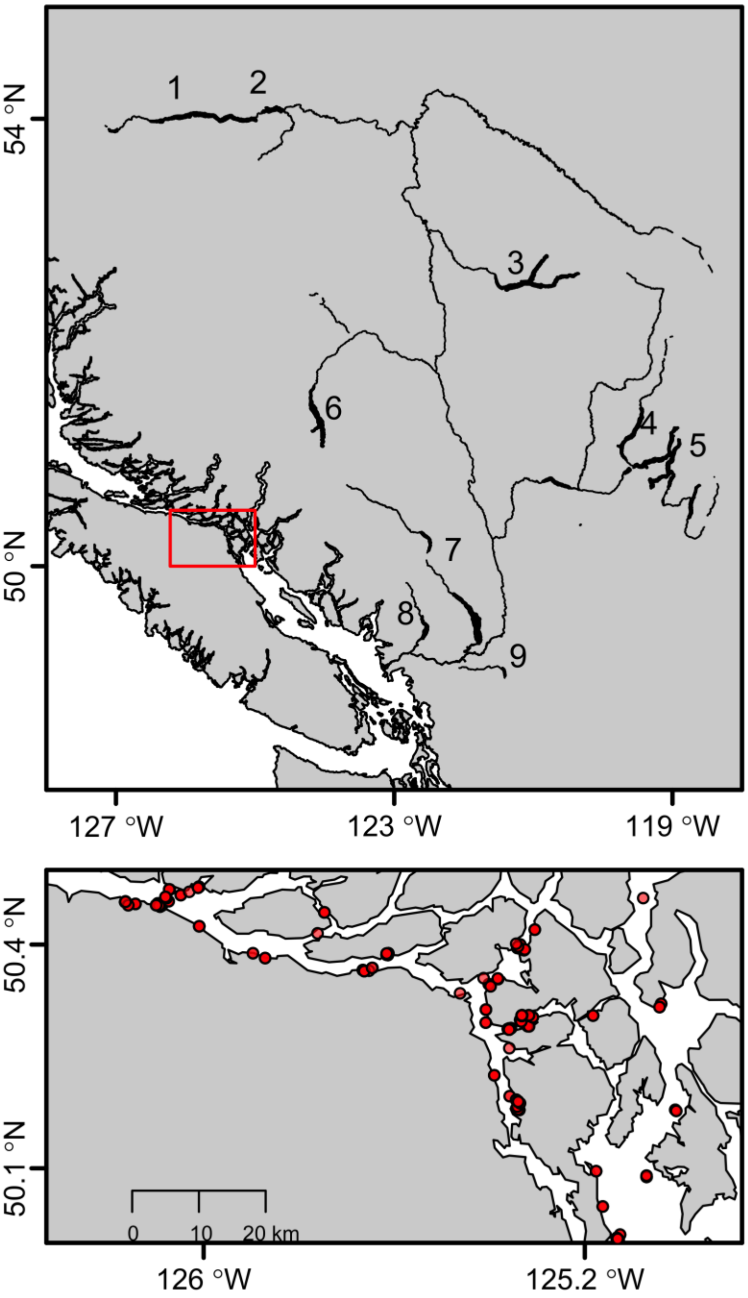

Figure 6.1 Location of nursery lakes for Fraser River CUs examined in this study (top panel) and sampling locations for individual fish within Johnstone Strait and the Discovery Islands (bottom panel). Numbers in top panel correspond to nursery lakes of following CUs: 1) Nadina-Francois, 2) Francois-Fraser, 3) Quesnel, 4) Shuswap-ES, 5) Shuswap-L, 6) Chilko, 7) Lillooet-Harrison, 8) Pitt, and 9) Chilliwack.

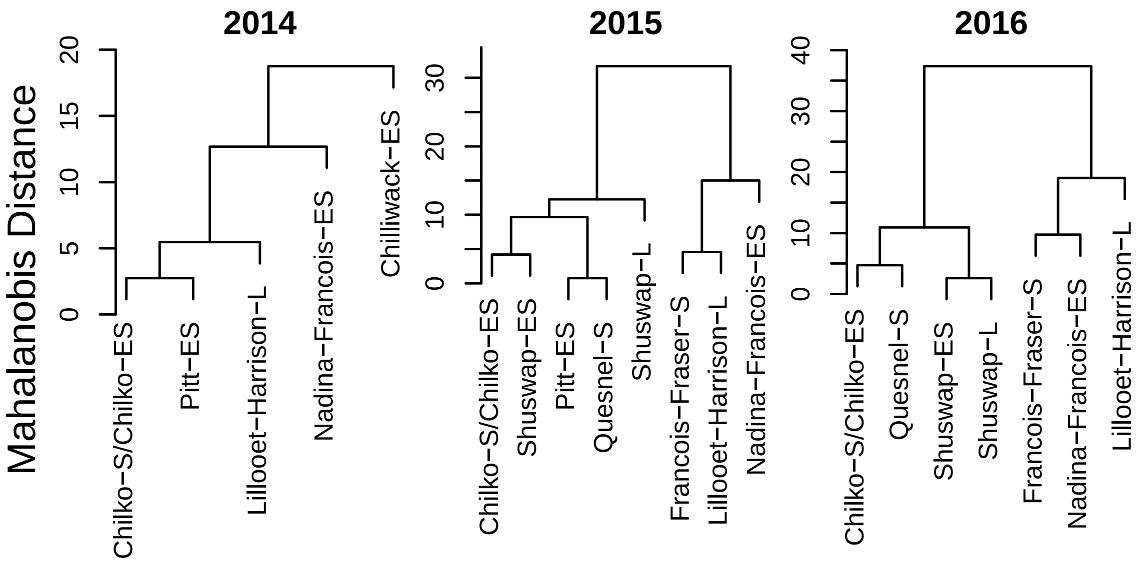

Figure 6.2 Groupings of sockeye salmon conservation units based on individual migratory traits: entry size, marine growth rate, duration of residence in the Strait of Georgia, and midday of residence. The hyphenated letters in CU names refer to adult run timings: ES-early summer, S-summer, and L-late.

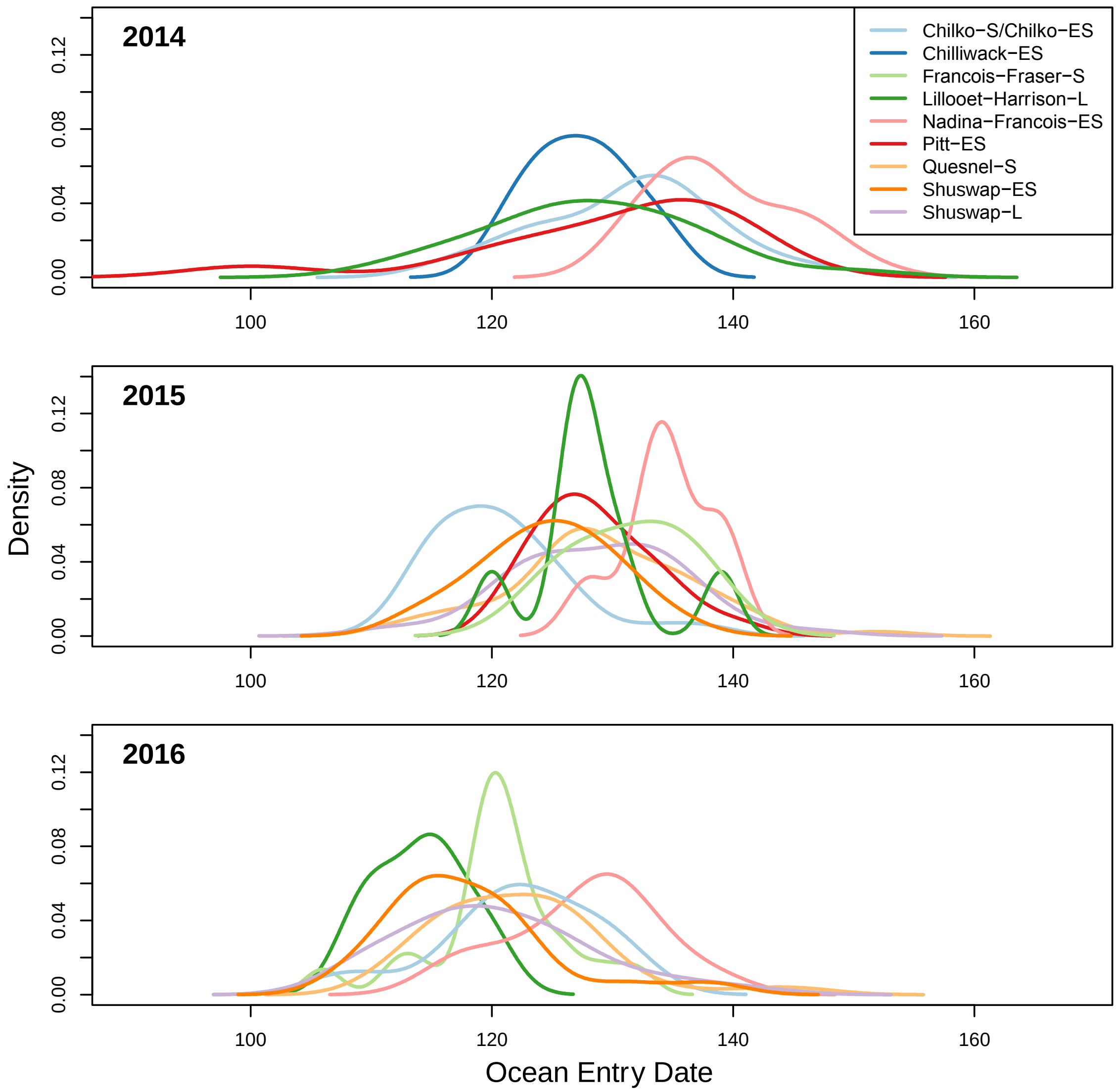

Figure 6.3 Date of entry into Strait of Georgia (Julian day) grouped by CU and year.

Data were smoothed using a kernel density estimator.

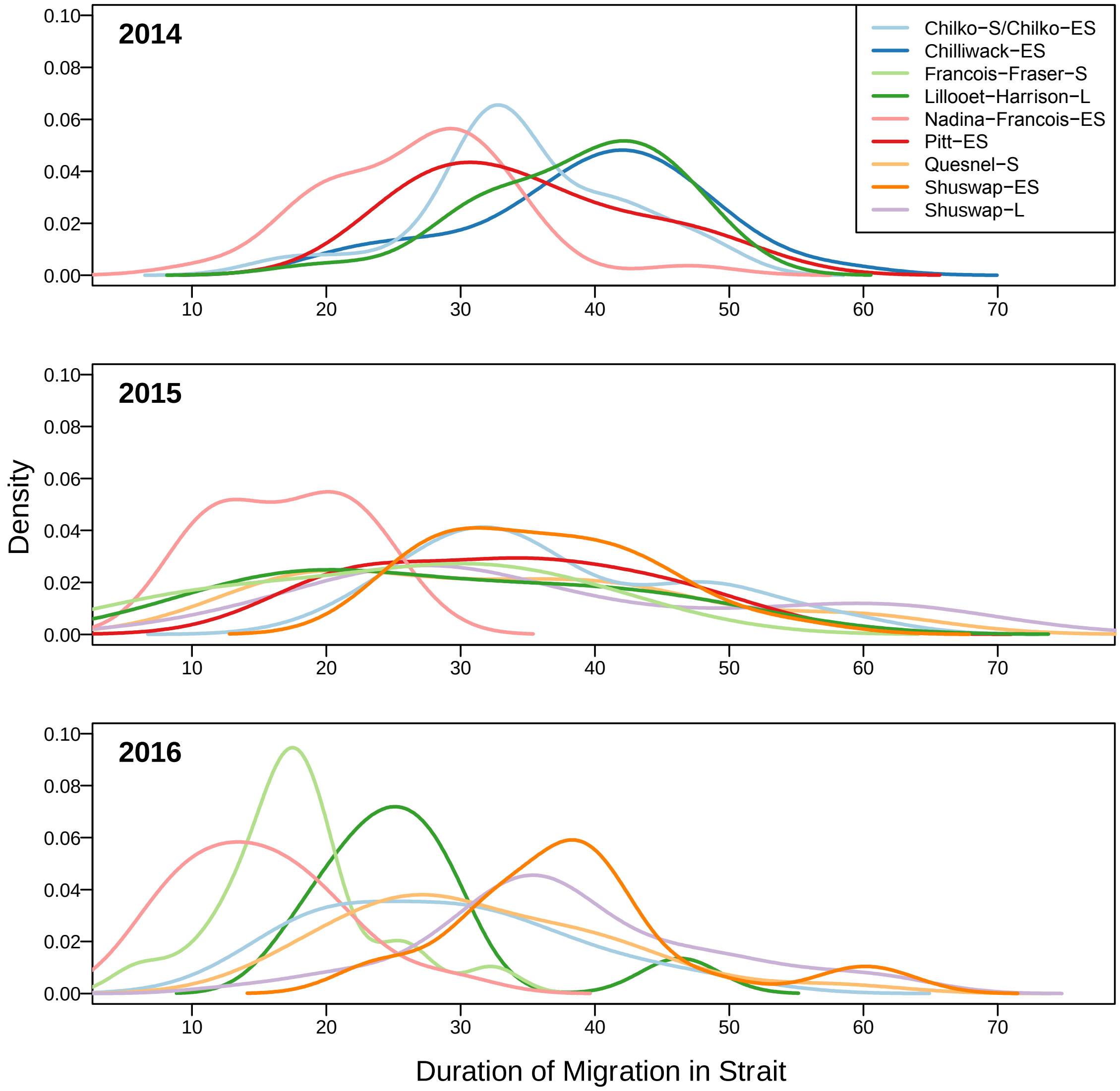

Figure 6.4 Duration of migration through the Strait of Georgia (number of days between ocean entry and capture) data grouped by CU and year. Data were smoothed using a kernel density estimator.

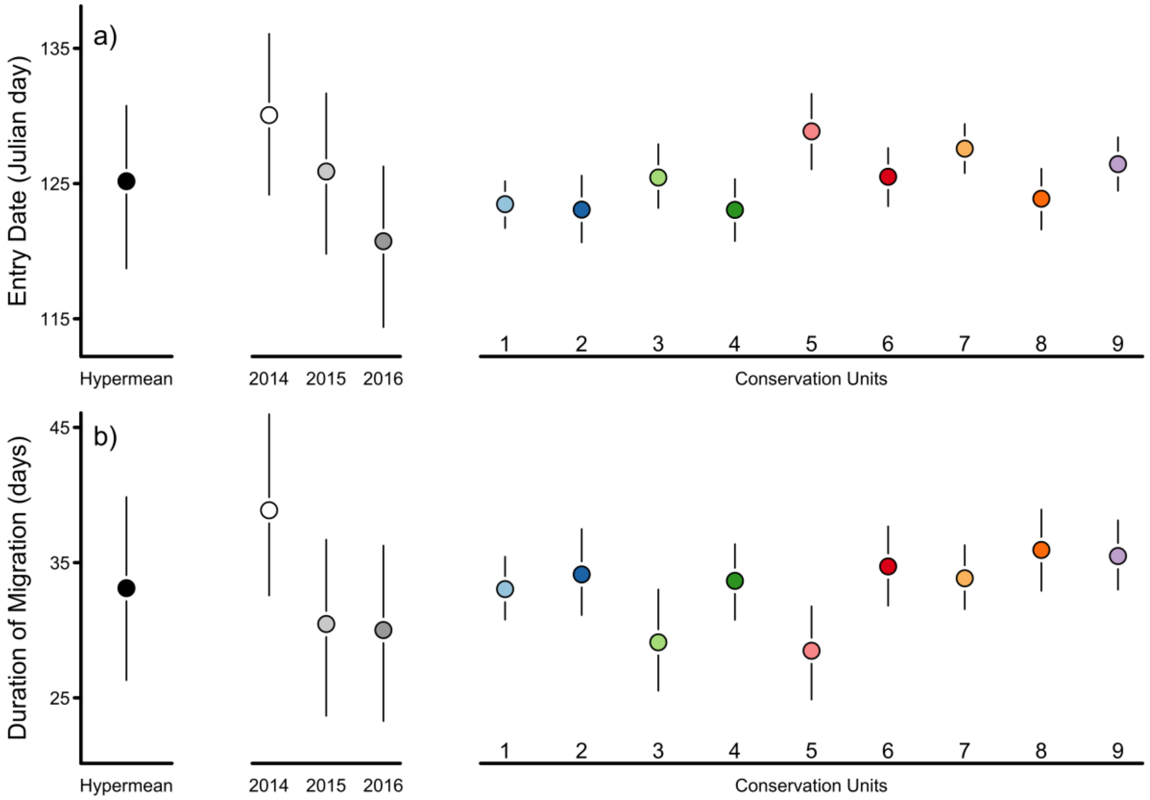

Figure 6.5 Posterior estimates of overall mean entry date (a) and duration of migration (b), as well as year- and CU-specific deviations from the hypermean. Whiskers represent 90% highest posterior density interval (HPDI) estimates. CUs: 1) Chilko-S/Chilko-ES, 2) Chilliwack-ES, 3) Francois-Fraser-S, 4) Lillooet-Harrison-L, 5) Nadina-Francois-ES, 6) Pitt-ES, 7) Quesnel-S, 8) Shuswap-ES, 9) Shuswap-L.

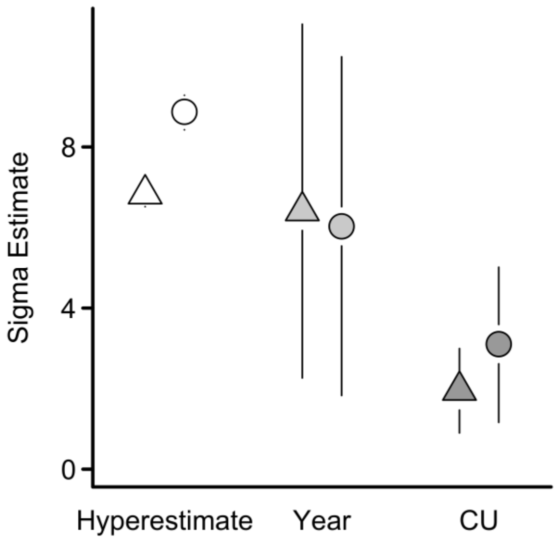

Figure 6.6 Posterior estimates of variance parameters (σ) across ecological scales for the entry date model (triangles) and duration of migration model (circles). Whiskers represent 90% highest posterior density interval (HPDI) estimates.

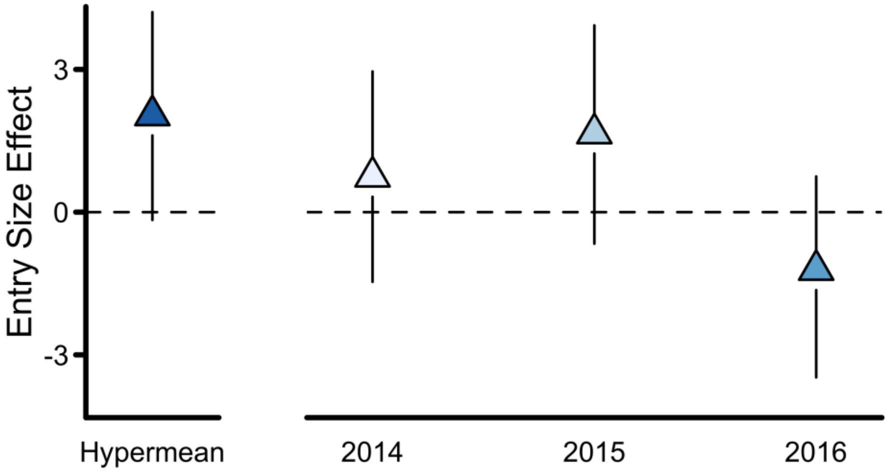

Figure 6.7 Posterior mean estimates of entry size effects (hypermean and year-specific) on ocean entry date. Whiskers represent 90% highest posterior density interval (HPDI) estimates.

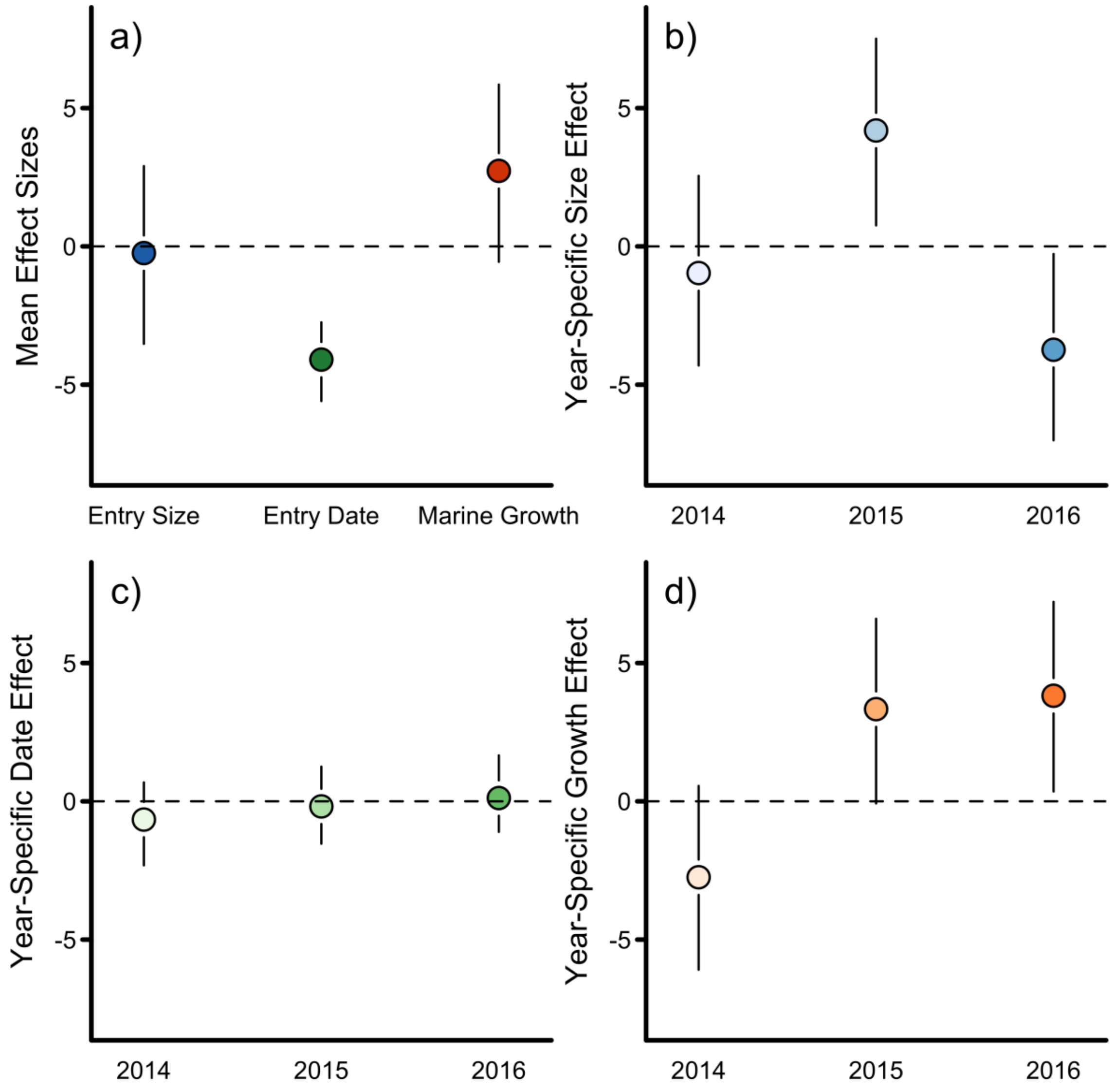

Figure 6.8 Posterior hyper- (a) and year-specific (c-d) mean effect sizes for explanatory covariates in the duration of migration model. Whiskers represent 90% highest posterior density interval (HPDI) estimates.

Chapter 7 - Discussion

Knowledge of how physical condition and phenology vary among migrating individuals, as well as populations, is necessary to assess their vulnerability to natural and anthropogenic stressors. In the case of Pacific salmon populations, variation in early marine migratory characteristics may be particularly critical because this period appears to regulate spawner recruitment (Pearcy 1992). Sockeye salmon exhibit substantial variation in traits, such as body size (Tucker et al. 2009, Beacham et al. 2014b) and spatial distribution (Tucker et al. 2009, Beacham et al. 2014a), that may result in differential survival among stocks; however, it is currently unclear how ecological mechanisms occurring across spatial and temporal scales interact to shape this heterogeneity.

In this dissertation, I used natural markers to explore intraspecific diversity within migrating juvenile sockeye salmon. By examining variation at finer scales than previous investigations, I was able to clarify how rearing conditions in both freshwater and marine habitats (i.e. prior to and during juvenile migrations) contribute to migratory diversity. Consistent differences among populations and years demonstrate that individual behaviors are constrained by local adaptation and environmental stochasticity. Simultaneously, however, the strong effect of ocean entry traits on individual condition and behavior during migration suggests freshwater residence plays an integral role in shaping the early marine life history juvenile salmon.

7.1. Effect of individual traits

Juvenile salmon exhibit variation in downstream migration timing (Furey et al. 2016) and their use of estuarine stopover habitats (Moore et al. 2016). Furthermore, within a given population, Pacific salmon are broadly distributed along the continental shelf during their juvenile marine migrations (Tucker et al. 2009), which indicates that either migration speed or phenology must vary among individuals. In this dissertation, I provide evidence that individual characteristics present at ocean entry were correlated with migratory variability at sea, suggesting conditions experienced during freshwater residence have considerable carry-over effects on juvenile migrations. For example, individuals that were larger at ocean entry maintained their size advantage during migration (Fig. 3.5) and typically migrated more rapidly (Figs. 4.4a, 6.8b). It is possible that faster swimming speeds are a direct result of larger body size (Ware 1978, Trudel and Welch 2005). Alternatively, correlations between differences in foraging (Mittelbach 1981) or risk-taking (Werner et al. 1983) behaviours that are mediated by body size, could increase migratory efficiency.

Ocean entry date was often an even stronger predictor of migratory behavior than entry size. Juveniles that entered later in the year moved north more quickly (Figs. 4.4b, 5.6b, 6.8c), suggesting that the relative benefits of remaining nearshore, presumably to maximize growth prior to migration, may decline through the summer. Juvenile salmon that fail to overlap with adequate marine prey resources may experience reduced survival (Cushing 1990, Tomaro et al. 2012). Given that ocean entry phenology is heritable (Manhard et al. 2017), individuals constrained to enter relatively late in the year may improve their likelihood of survival by migrating north as rapidly as possible.

Entry size and timing are predicted to influence interannual variation in the recruitment of salmon populations (Henderson and Cass 1991, Tomaro et al. 2012, Miller et al. 2013); however the ecological mechanisms leading to altered mortality rates remain unclear. This dissertation clarifies that entry size and phenology are correlated with the duration of nearshore residence, which, in turn, may regulate arrival timing on offshore foraging grounds. Consequently, variation in entry characteristics may moderate the degree to which individuals overlap in space and time both with nearshore stressors (e.g., predators, pollutants), as well as seasonal peaks in zooplankton biomass of offshore foraging grounds (Coyle and Pinchuk 2003). In certain instances the effect of ocean entry traits was quite strong. Juveniles that entered very late in the year and at small sizes were more likely to remain on the continental shelf into the late fall (Fig. 4.6). Although there are no survival data available for fall-migrating individuals specifically, populations with similar distributions (e.g., Rivers Inlet; Tucker et al. 2009) have exhibited poor marine survival in recent decades (McKinnell et al. 2001). Thus, variation in entry size and phenology may lead to differential survival rates, even in the absence of processes such as gape-limited predation.

Freshwater age was another strong predictor of individual variation in migratory traits. On average, age-2 fish migrated more rapidly than younger individuals (Fig. 4.3c), however at the coastwide scale this effect was difficult to disentangle from the influence of body size. Within the Strait of Georgia the effects of age on migration phenology were associated with life history strategy. Age-0 individuals (i.e. sea-type or underyearling migrants) entered late in the year and moved out of the Strait more slowly, even after accounting for entry size effects. These age-0 individuals were particularly unusual because they originated from lake-type CUs (Quesnel and Shuswap) and were highly abundant during in-river surveys in one sampling year (C. Neville, *unpublished data*). It is unclear why a sea-type life history has become abundant in these CUs. However the productivity of the Harrison River CU, a population dominated by sea-type individuals that have a similarly delayed ocean entry phenology (Beamish et al. 2016), has increased in recent years (Peterman and Dorner 2012, Freshwater et al. *accepted*). Thus it seems possible that selection may be favoring a sea-type life history and that age-0 individuals could become proportionally more abundant in the future.

Migratory rate was also correlated with individual traits that developed during marine residence, specifically average growth rates. In two of three years, juveniles with faster growth migrated through the Strait of Georgia more slowly (Fig. 6.8d). It is unclear whether this correlation is due to individuals reducing travel rates when they encounter conditions that are favorable for growth or whether individuals grow rapidly as a result of migrating slowly. However juvenile Chinook salmon migratory rates have been correlated with both copepod biomass (Tomaro et al. 2012) and primary productivity (Burke et al. 2013), suggesting salmon may moderate their migratory behavior based on the conditions they encounter. Density-dependent effects on migratory rate (described in further detail below) also point to this possibility.

7.2. Population-specific strategies

All anadromous sockeye salmon populations appear to mature in offshore pelagic habitats (Burgner 1991). Yet during freshwater residence, these same populations span a large latitudinal gradient and occupy diverse freshwater environments, ranging from coastal systems influenced by tidal forces to high altitude lakes located thousands of kilometers inland (Burgner 1991). Furthermore, sockeye salmon exhibit stock-specific spatial and temporal distributions during their first months of ocean residence (Tucker et al. 2009, Beacham et al. 2014a), which suggests this heterogeneity has a lasting impact. By examining migrations at a smaller scale and accounting for variation among individuals, I was able to provide a more nuanced understanding of differences among population groups.

First, migratory rate was correlated within regional aggregates, and therefore associated with ocean entry location, at coastwide scales. Populations migrating through the Strait of Georgia moved more rapidly than those migrating along Vancouver Island's west coast (Fig. 4.5), suggesting travel speeds vary with migratory route. Stark oceanographic differences between inside and coastal waters in southern BC (Mackas et al. 2007, Mackas et al. 2013, McKinnell et al. 2014) may contribute to differences between these specific migratory corridors.

Second, I observed substantial variation among Fraser River CUs in both the timing and duration of their migration through the Strait of Georgia (Figs. 6.3, 6.4). After accounting for entry size effects, estimates of CU-specific deviations from the overall mean were moderate (Fig. 6.5) and the effect of individual traits on migration phenology was consistent across CUs (Fig. A6.1). Thus, some of the heterogeneity in raw observations appears to be linked to variation in body size (Beacham et al. 2014b). Two interior CUs (Nadina-Francois-ES and Francois-Fraser-S), however, were clear exceptions, entering the Strait late in the year and migrating quickly (Fig. 6.5). Interior populations of Columbia River Chinook salmon exhibit a similar pattern as juveniles, suggesting marine migrations are influenced by geographic location and, potentially, the difficulty of in-river migrations (Weitkamp et al. 2015). Additionally, the Nadina-Francois-ES and Francois-Fraser-S CUs are two of the most derived population groups within the Fraser River watershed (Beacham et al. 2005). Sample sizes for other interior CUs (i.e. populations rearing in Takla, Trembleur, and Stuart lakes) were too low to include in this analysis, but data collected in-river suggests that at least the Early Stuart CU also migrates late in the year (Neville et al. 2016). The location of these populations at the head of the Fraser River may reduce the likelihood of individuals from more heterogeneous, downriver CUs straying and successfully spawning, thereby increasing the potential for local adaptation.

7.3. Environmental drivers of variability

Aquatic organisms inhabit an environment where movement is energetically costly and prey is patchily distributed in space and time. Consequently, the ecologies of small-bodied marine species are strongly shaped by environmental variability (Bakun 1996). In the case of Pacific salmon, the distribution and growth of early marine life history stages can be regulated by biological processes, such as prey availability, as well as directly by physical processes, such as temperature or the strength of hydrographic structures (Quinn 2005). In particular, recent associations between high pink salmon abundance and reduced sockeye salmon growth and survival suggest that competition during marine residence can limit population productivity (Ruggerone et al. 2003, Connors et al. 2012, Ruggerone and Connors 2015). Previous studies of interspecific competition have focused on offshore interactions at large scales (i.e. growth effects integrated across a given year and the entire Gulf of Alaska), however it is predicted that similar density-dependent effects may occur during nearshore residence (Beamish et al. 2010).

I used two survey years (2011 and 2012) to test for density-dependent effects on a suite of early marine traits. These years were characterized by dramatic changes in the abundance of con- and heterospecific competitors, while differences in environmental metrics (temperature, zooplankton prey biomass) were moderate. High sockeye salmon densities during freshwater residence were correlated with smaller body size at ocean entry (Fig. 5.3), consistent with density-dependent growth in constrained habitats generally (Sinclair 1989), and in salmon specifically (Foerster 1944, Schindler et al. 2005). Conversely, downstream migration timing did not covary with juvenile abundance (Fig. 5.4) and may be more strongly influenced by differences in flow or stream temperature (Achord et al. 2007, Kovach et al. 2013). Despite large increases in the abundance of juvenile sockeye salmon, as well as three other common pelagic zooplanktivores, juvenile sockeye salmon growth rates in the Strait of Georgia did not vary between years (Fig. 5.5). Juveniles did, however, migrate at significantly faster rates in the high abundance year, even after accounting for differences in entry characteristics (Fig. 5.6), consistent with evidence from other species that migratory behavior may be moderated by the abundance of competitors (Dierschke and Delingat 2001, Chapman et al. 2012)

Unfortunately it was beyond the scope of this dissertation to closely explore how additional environmental variables might influence migratory diversity. Yet, the broader migratory ecology literature provides several plausible hypotheses. Of these, differences in prey availability are particularly pertinent given the effects of density-dependence I observed. Migrants with sufficient energy stores may accelerate their movements when foraging opportunities encountered en route are poor (Jenni and Schaub 2003). In southern British Columbia, the biomass, community composition, and phenology of zooplankton prey vary between years (Mackas et al. 2006, Mackas et al. 2013). While sockeye salmon stomach fullness is less variable (Beamish et al. 2010), presumably low prey availability could reduce growth and advance migration phenologies if juveniles are not constrained by other factors. Changes in migratory characteristics could also be associated with shifts in temperature (Welch et al. 1998) or stress events such as harmful algal blooms (Rensel et al. 2010), which may limit growth and increase the costs of delaying northward migration.

A second category of drivers includes physical processes that may directly influence the distribution or energy expenditure of migrating individuals. The timing and duration of bird migrations can be strongly influenced by severe weather events (Senner et al. 2015) or even moderately unfavorable wind speeds (Schaub et al. 2004). Similarly, in aquatic species changes in river flow (Quinn et al. 1999, Connor et al. 2013), temperature (Achord et al. 2007, Kovach et al. 2013), or the strength of oceanic currents (Mork et al. 2012, Burke et al. 2014) can influence migration phenology. Given that hydrographic processes vary within, as well as between years, changes in current strength or wind speed may act to increase variability in the distribution of nearshore migrants.

7.4. Caveats and limitations

As with all ecological studies dependent on field-collected data, the conclusions presented here were limited by the resources available. Although I incorporated data collected across seven field seasons, differences between years in the timing and location of sampling events, the gear types that were used, and the populations that were targeted prevented the three surveys from being pooled. Longer time series would have been valuable to more rigorously test hypotheses regarding environmental effects (e.g., density dependence) and identify freshwater drivers of variation in ocean entry traits. Furthermore, multi-decadal estimates of migratory diversity could be used to test whether variation in migratory traits is correlated with trends in the productivity of sockeye salmon populations.

It was also necessary to make several assumptions about data quality that may have influenced my results. First, growth rates estimated from otolith microstructure may be imprecise over short temporal scales (Neilson and Geen 1985, Pepin et al. 2001). To minimize these effects, I estimated mean daily growth rates over the entire marine period in Chapters 5 and 6. Since back-calculated estimates of entry size are relatively robust in juvenile salmon (Claiborne and Campbell 2016), I am confident that these are reasonably accurate indicators of growth. While I did use mean increment spacing over one week intervals in Chapter 3 as a proxy for growth at shorter temporal scales, sensitivity analyses indicated that the results were robust when using estimates of mean growth rate over the entire period. Nevertheless, it is possible that the results could vary if proxies that integrate growth over shorter scales (e.g., insulin growth factor) were used (Ferriss et al. 2014).

Second, there is uncertainty associated with estimates of ocean entry dates from otolith microstructure. While Chapter 2 validated the formation of a marine entry check in Vancouver Island juveniles, visual estimates were overestimated relative to chemical by approximately one week (Fig. 2.3). Interestingly, subsequent microchemical analyses indicated that ~25% of Fraser River juveniles (*n* = 15) had an opposite bias, with visual entry checks *underestimated* relative to chemical checks by 6-21 days (L. Godbout, DFO, *pers. comm.*). Visual and chemical estimates are likely formed by distinct physiological processes, and differences between estimates may vary across river systems. Since visual entry checks are likely correlated with the beginning of rapid summer growth (Neilson et al. 1985, Zhang and Beamish 2000), they are likely reasonable proxies for downstream movements into more productive estuarine waters, rather than changes in salinity directly.

Finally, most of the conclusions regarding population-specific migratory strategies in this dissertation are based upon data aggregated at the scale of CUs. CUs are the focal unit for most management actions and can contain multiple distinct spawning populations with common nursery habitats, ecological characteristics, and genetic history (Holtby and Ciruna 2007). I aggregated data at this level to increase sample sizes for specific analyses and because certain “treatments” (e.g., freshwater density-dependent effects) could be assigned to CUs, but not individual populations. However, component populations within a CU have variable levels of interbreeding and ecological diversity (Holtby and Ciruna 2007). Therefore, it is possible that pooling samples obscured population-specific traits that are ecologically relevant.

7.5. Future Directions

Despite recent advances, several key dimensions of migratory ecology remain understudied. First, migratory research is often dominated by studies on a single life stage (e.g., breeding vs. wintering habitats; Runge et al. 2014), which can hamper efforts to identify drivers of population declines. This issue is relevant to many species, but is particularly pertinent for salmon where research has largely focused on migrations in freshwater and, more recently, nearshore environments (Quinn et al. 2005). Yet the vast majority of individual growth occurs offshore (Groot and Margolis 1991) and large-scale marine environmental conditions regulate the productivity of many salmon populations (Beamish and Bouillon 1993, Mantua et al. 1997). Thus, it is concerning that our understanding of how individuals, populations, and even species are distributed in offshore habitats is limited and often based on high seas tagging data collected decades ago (Quinn 2005). Without knowledge of stock-specific distributions it is impossible to gauge the influence of offshore competitive interactions (e.g., Ruggerone and Nielsen 2004) or alternative migratory strategies (e.g., Beamish et al. 2016) on differential survival. Sustained offshore sampling efforts, paired with comprehensive genetic stock identification, would be the most direct way to collect these data, however such methods may be prohibitively costly. Alternatively, isotopic signatures derived from hard structures could be compared between species or populations to test for evidence of differential use of marine habitats (Welch and Parsons 1993, Hanson et al. 2013), assuming sufficient environmental variation is present.

Second, migration ecology would benefit from robust, quantitative tests of how migratory diversity affects management and conservation outcomes. Greater diversity clearly increases the aggregate availability of the ecosystem services provided by salmon (Schindler et al. 2010, Deacy et al. 2016) and migratory strategies have been proposed as a driver of differential survival among populations (Cooke et al. 2004, Tucker et al. 2009, Beamish et al. 2016). Yet mechanistic links between migratory diversity, survival, and divergent population dynamics have not been clearly established. A detailed understanding of offshore distributions, described above, plays one key role by clarifying how populations overlap with prey resources, environmental stressors, and competitors. Additional efforts should be directed at determining whether variation among individuals in early marine traits influences offshore distributions and survival (e.g., expanding the investigation into lingering migrants in Chapter 4). These data could be used to estimate stage-specific survival rates, identify mechanisms of mortality, and parameterize simulation models that are used to inform managers. Given the interest in linkages between ecological diversity and the stability of ecosystem services (i.e. portfolio effects, Schindler et al. 2010), the hypothesis that migratory diversity is correlated with decreased variability in Pacific salmon productivity could also be explicitly tested.

7.6. Conclusions

Migrations fundamentally represents a tradeoff between the costs of long-distance movements and the fitness benefits associated with occupying unique habitats across seasons or ontogeny (Dingle 1996). Optimal migratory behaviors will vary with individual condition relative to the environment encountered during migrations (Jenni and Schaub 2003). Furthermore, migratory traits, such as body size and phenology, are both phenotypically plastic and constrained by genetics. Thus individual rearing histories (i.e. carry-over effects) and population identity can act synergistically to moderate migratory diversity (Marra et al. 1998, Gunnarsson et al. 2006). Since migratory environments are dynamic, temporal and spatial variability will further regulate how migrating individuals are distributed relative to one another (Jenni and Schaub 2003). This thesis clarifies how processes occurring at each of these ecological scales interact to produce variation in juvenile sockeye salmon marine migrations. As a result, we gain a clearer understanding of migrations broadly, as well as the specific factors that shape sockeye salmon's life history during a period critical to individual survival and population productivity.

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Appendices

Appendix A: Supplemental information for Chapter 2

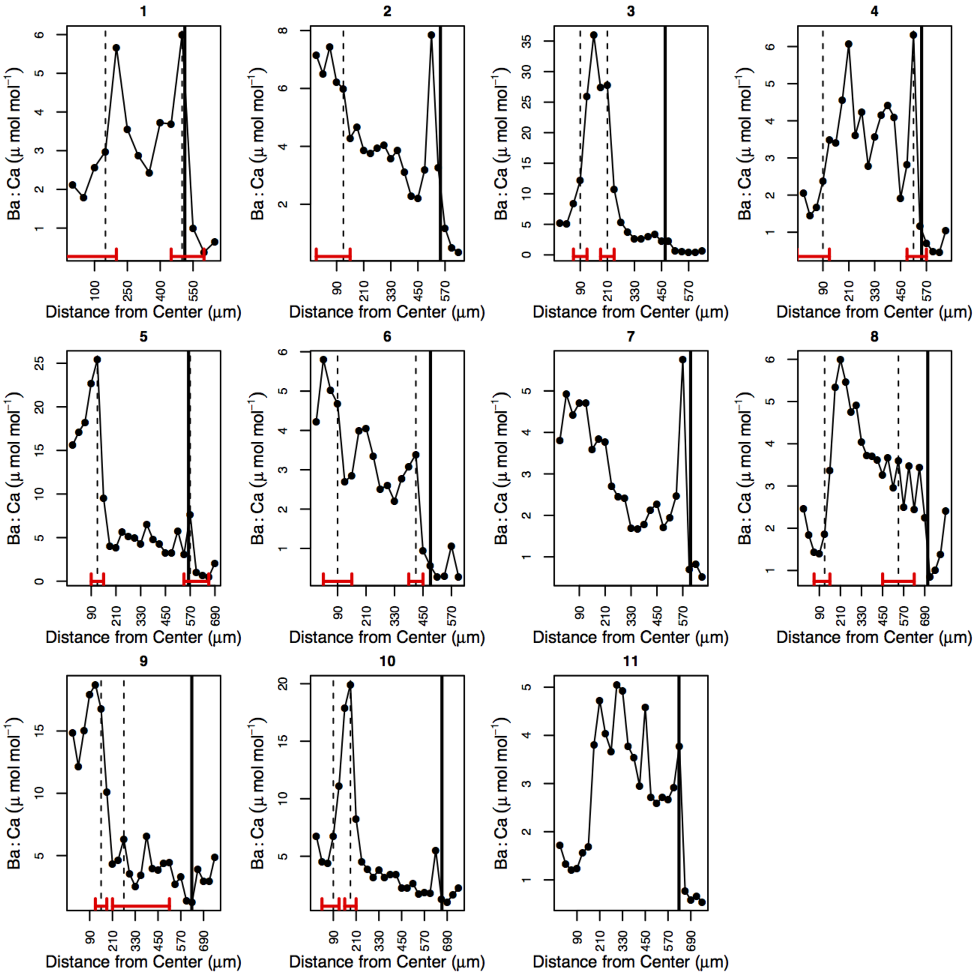


Figure A2.1 Ba:Ca concentrations of ICP-MS laser transects. Transects run from otolith primordia to dorsal periphery The zone representing transition to saltwater is characterized by an increase in Sr:Ca. Visual marine entry check estimates are represented by solid black vertical lines. Breakpoint estimates and 95% C.I. are represented by dashed vertical and horizontal red lines respectively. Note Sample 11 has two breakpoint estimates since the model failed to converge when restricted to one.

Appendix B: Supplemental information for Chapter 3

Table A3.1 Number of individuals per population captured in each sampling region and included in latitudinal gradient analysis. Regions are shown in Fig. 3.1. Note that population-region-year combinations with fewer than 20 individuals were excluded from SSM analysis.

Year	Population	Strait of Georgia	South Vancouver Island	North Vancouver Island	Triangle Island	Hecate Strait	Haida Gwaii	Northern BC
2007	Great Central		109	78	2	36	4	1
	Sproat		33	34	1	64	27	8
2008	Great Central		65	32	5	10	3	7
	Sproat		27	41	19	33	26	19
	Chilko	36	1	0	22	28	18	6
	Lower Adams	171	1	0	12	12	19	1

Table A3.2 Theoretical justifications for pathways included in *a priori* structural equation models.

Explanatory Variable	**Response Variable**	**Justification**	**Reference**
Population	Freshwater age Days at sea Entry radius	Minimal inter-breeding and diverse freshwater spawning/rearing habitats have resulted in strong population specific characteristics in salmonids. Freshwater foraging and temperature conditions, as well as heredity appear to be correlated with age at emigration, body size, and phenology.	Koenings & Burkett 1987; Burgner 1991; Hutchings & Jones 1998; Obedzinski & Letcher 2004; Quinn 2005; Trudel *et al.* 2009; Trudel *et al.* 2011; Tucker *et al.* 2009; Beacham *et al.* 2014a,b
	Early growth Late growth	Direct effects on marine growth may occur due to population specific differences in near-shore residency, migratory route, and foraging behavior.	
	Capture size	A direct effect of population on capture size was not initially included, but necessary for adequate model fit. This suggests residual variation in body size is present that is correlated with population identity, but that cannot be attributed to the mediating variables.	
Year	Freshwater age Days at sea Entry radius	Freshwater outmigration age, size and timing appear to be relatively flexible traits that are influenced by freshwater foraging conditions. Therefore, inter-annual variability in productivity or temperature may result in delayed or advanced migration at different sizes.	Burgner 1991; Peterman 1984; Welch, Ishida & Nagasawa 1998; Quinn 2005; Cross *et al.* 2009; Bi et al. 2011; Tomaro et al. 2012; Connor et al. 2013
	Early growth	Marine growth in Pacific salmon varies inter-annually with the abundance and timing of primary productivity, extent of density dependent competition, and temperature.	
	Late growth		
	Capture size	As above, a direct effect of year on capture size was not initially included, but necessary for adequate model fit. This suggests residual variation in body size is present that is	

		correlated with sampling, but that cannot be attributed to the mediating variables.	
Freshwater age	Days at sea Entry radius	Age-2 Sockeye Salmon juveniles tend to be consistently larger than age-1 juveniles and may out-migrate from rearing lakes earlier in the year.	Burgner 1991; Bugayev 2000; Welch et al. 2011
Entry radius	Days at sea Early growth Capture size	The mean size of individuals captured during juvenile out-migration periods appears to peak early in the year, suggesting larger post-smolts emigrate first. Larger size at ocean entry and greater freshwater growth have also been correlated with greater growth at sea, likely due to improved swimming performance, increased gape size and size-dependent differences in spatial distribution. Finally, since initial size influences subsequent size, fish that are larger at ocean entry may retain that size advantage.	Irvine & Ward 1989; Huss, Persson & Bystrom 2007; Ruggerone, Nielsen & Agler 2009; Malick *et al.* 2011; Weitkamp, Bentley & Litz 2012
Days at sea	Early growth	The number of days at sea reflects ocean entry phenology, which may drive variation in salmonid growth rates via match-mismatch dynamics. Since individuals that enter during periods of peak prey availability should grow best, rather than those that enter earliest in the year, days at sea will not necessarily be positively correlated with initial growth rate.	Burgner 1991; Borcherding *et al.* 2010; Tomaro *et al.* 2012
	Capture size	Days at sea should have a direct effect on capture size because salmonid growth rates generally accelerate after ocean entry. Individuals who have been at sea for longest, will have the greatest opportunity for growth.	
Early growth	Late growth	Rapid initial growth can predict future growth rates, particularly if individuals are gape limited and rely on body size to increase their niche breadth. Modeling exercises have indicated that fish populations often transition from size- to growth-dependent mortality suggesting that variation in growth can have cascading effects on individual fitness	Post 2003; Borcherding *et al.* 2010; Thanassekos, Robert & Fortier 2012

Late growth	Final capture size	Since the majority of growth in salmonids occurs at sea, marine growth rates are likely the primary driver of size variation after initial differences in fork length disappear. Growth immediately prior to capture will also reflect spatial variability in foraging conditions along the migratory corridor that is predicted to influence migrating salmon survival. Finally, marine growth is often a better predictor of marine survival than initial size or juvenile abundance.	Burgner 1991; Mackas, Thomson & Galbraith 2001; Ferriss, Trudel & Beckman 2014; McKinnell *et al.* 2014; Miller *et al.* 2014

Table A3.3 Rankings of latitudinal gradient in ship fork length models.

Dataset	Model Name	Explanatory Variables	DF	AIC	ΔAIC
VI	lm0	None	2	-360.63	1010.16
VI	lm.Lat	Latitude	3	-962.13	408.66
VI	lm.Stock	Stock	4	-1024.31	346.47
VI	lm.Year	Year	4	-1337.03	33.75
VI	lm.SY	Stock + Year	4	-679.79	691.00
VI	lm.LY	Latitude + Year	4	-1337.03	33.75
VI	lm.LS	Latitude + Stock	4	-1024.31	346.47
VI	lmFull	Stock + Year + Lat	5	-1370.79	0.00
FR	lm0	None	2	-536.60	186.63
FR	lm.Lat	Latitude	3	-718.73	4.50
FR	lm.Stock	Stock	3	-581.40	141.83
FR	lm.Full	Latitude + Stock	4	-723.23	0.00

Table A3.4 Scores of VI and FR SEMs, with standardized variables, across various goodness-of-fit indices.

Index	VI Model	FR Model	Threshold	Model Fit	Reference
NFI	0.990	0.990	> 0.95	Excellent fit	Bentler & Bonnett 1980
NNFI	0.987	1.052	> 0.95	Excellent fit	Hu & Bentler 1998
RMSEA	0.034	0.000	0 – 0.08	Good fit	MacCallum, Browne & Sugawara 1996
CFI	0.998	1.000	Close to 1	Excellent fit	Bentler 1990

Table A3.5 Total number of individuals retained from each sampling region for otolith analysis. The number of age-2 individuals, if any, is shown in parentheses. Regions are shown in Figure 1 of main text.

Year	Population	Strait of Georgia	South Vancouver Island	North Vancouver Island	Triangle Island	Hecate Strait	Haida Gwaii	Northern BC
2007	Great Central		15	15 (2)	0	16 (2)	0	0
	Sproat		11	15	0	18	16 (1)	7 (1)
2008	Great Central		28 (2)	14 (2)	0	10 (8)	0	7 (5)
	Sproat		12	15	12	18	16 (2)	17 (4)
	Chilko	0			14 (1)	11	18	4 (1)
	Lower Adams	16			12	11	18	

Table A3.6 Rankings of size selective mortality metric models.

SSM Metric	Model Name	Explanatory Variables	K	AICc	ΔAICc	AICc Wt	LL	Cum. Wt
Variance	mod1	None	2	180.87	0.00	0.45	-88.01	0.45
Variance	mod3	Year	3	181.90	1.03	0.27	-87.03	0.73
Variance	mod2	Latitude	3	182.90	2.03	0.17	-87.53	0.89
Variance	mod6	Latitude+Year	4	183.93	3.05	0.10	-86.30	0.99
Variance	mod4	Stock	5	189.86	8.99	0.01	-87.20	1.00
Variance	mod7	Year+Stock	6	190.64	9.76	0.00	-85.12	1.00
Variance	mod5	Latitude+Stock	6	194.33	13.46	0.00	-86.96	1.00
Variance	mod8	Latitude+Stock+Year	7	195.43	14.56	0.00	-84.49	1.00
Skewness	mod1	None	2	14.13	0.00	0.65	-4.64	0.65
Skewness	mod3	Year	3	16.92	2.79	0.16	-4.54	0.81
Skewness	mod2	Latitude	3	16.99	2.86	0.15	-4.57	0.96
Skewness	mod6	Latitude+Year	4	20.31	6.18	0.03	-4.49	0.99
Skewness	mod4	Stock	5	22.59	8.46	0.01	-3.57	1.00

Skewness	mod5	Latitude+Stock	6	27.34	13.21	0.00	-3.47	1.00
Skewness	mod7	Year+Stock	6	27.49	13.36	0.00	-3.54	1.00
Skewness	mod8	Latitude+Stock+Year	7	33.36	19.23	0.00	-3.46	1.00
Kurtosis	mod1	None	2	48.98	0.00	0.37	-22.06	0.37
Kurtosis	mod2	Latitude	3	49.51	0.54	0.29	-20.83	0.66
Kurtosis	mod3	Year	3	50.17	1.19	0.21	-21.16	0.87
Kurtosis	mod6	Latitude+Year	4	51.40	2.42	0.11	-20.03	0.98
Kurtosis	mod5	Latitude+Stock	6	55.80	6.82	0.01	-17.70	0.99
Kurtosis	mod4	Stock	5	56.36	7.39	0.01	-20.45	1.00
Kurtosis	mod7	Year+Stock	6	60.62	11.64	0.00	-20.11	1.00
Kurtosis	mod8	Latitude+Stock+Year	7	61.47	12.49	0.00	-17.51	1.00

Table A3.7 Relative performance of models predicting size at capture as a function of different growth estimates (measured in µm). All models include population and sampling year as fixed effects.

Growth Variable	**df**	**ΔAIC**	$\boldsymbol{r^2}$
Average Daily Growth Rate	7	0	0.375
First Week's Growth	7	2.09	0.372
Last Week's Growth	7	22.81	0.335
First and Last Weeks' Growth	8	2.10	0.373

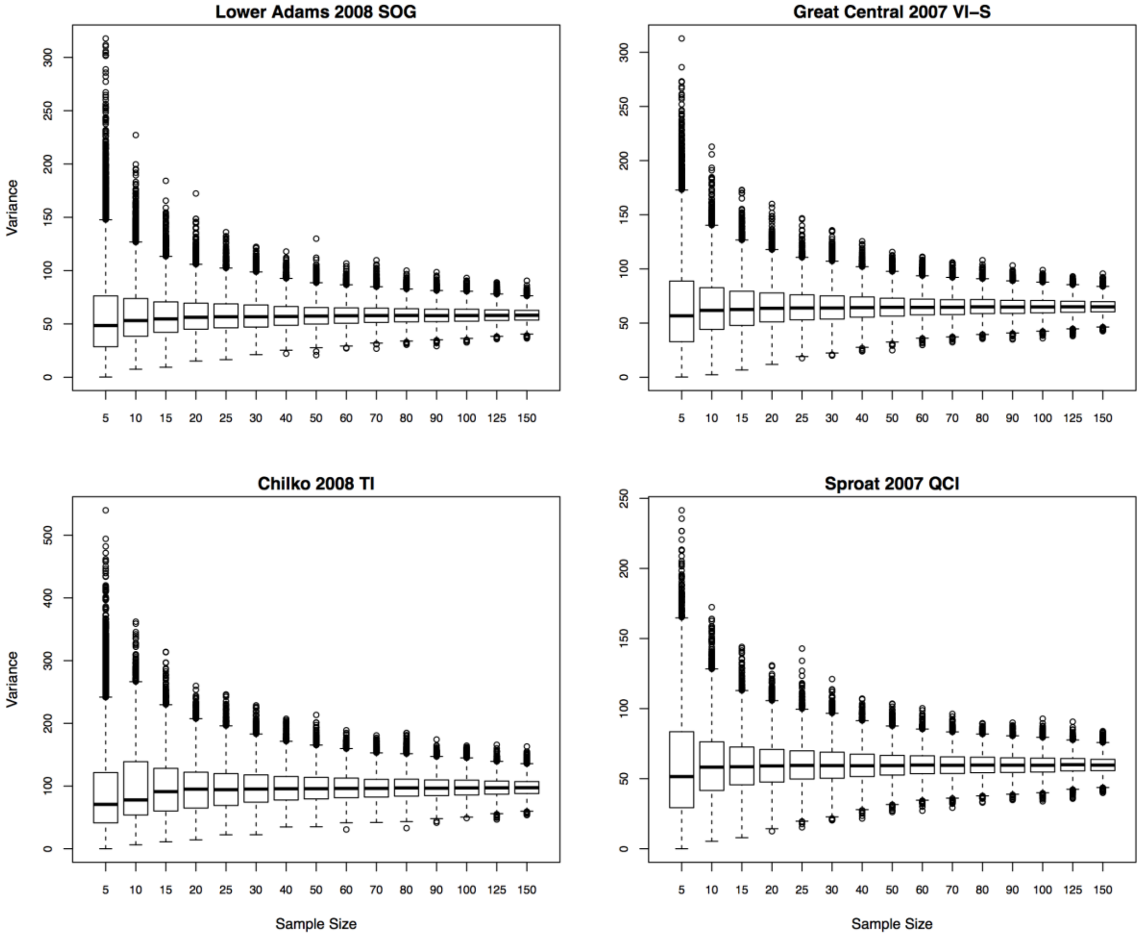


Figure A3.1 Changes in estimates of variance with sample size. Estimates were calculated by sampling, with replacement, 5 to 150 times from a given subpopulation (i.e. a unique combination of stock, capture region, and year) and repeating 10,000 times for a given sample size. Plot labels refer to the subpopulations. Original sample sizes of the subpopulations were: $n_{\text{LA08-SG}} = 171$, $n_{\text{GC07-VIS}} = 109$, $n_{\text{CH08-TI}} = 22$, and $n_{\text{SP07-QCI}} = 27$. Box and whiskers represent interquartile range with medians and dots represent outliers (e.g., third quartile + 1.5 * the interquartile range).

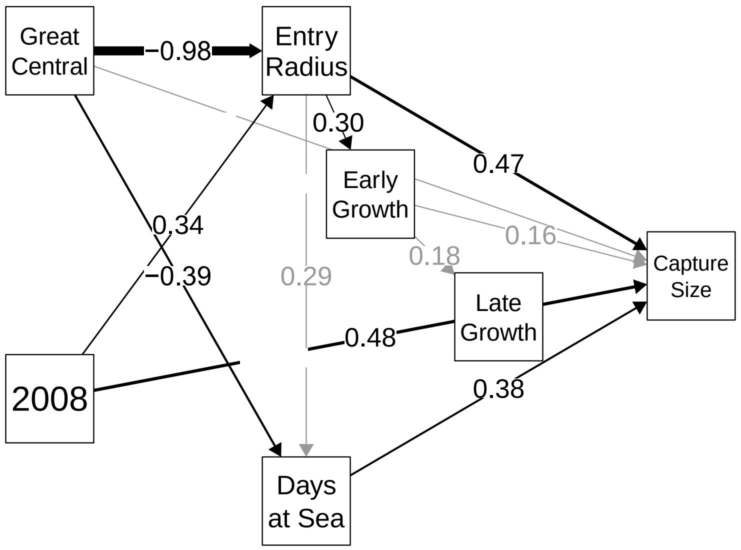


Figure A3.2 Structural equation model examining the direct and indirect effects of population identity, year of capture, and early marine characteristics on size during migration of juvenile Sockeye Salmon originating from Vancouver Island, excluding all age-2 post-smolts. Chi-square goodness of fit tests indicated adequate fit ($\chi^2 = 1.35$, DF = 2, $P = 0.51$). Non-significant predictor variables and paths are not shown to improve readability. Population identity and year were coded as dummy binary variables. Therefore estimates in are relative to Sproat Lake individuals captured in 2007. Path coefficients reflect standardized variables. Grey and black lines represent significant relationships with standardized effect sizes ≤0.3 and >0.3, respectively; line width reflects the relative strength of the correlation.

Appendix C: Supplemental information for Chapter 4

Table A4.1 AICc rankings for top migratory rate (km/day) models (Δ AICc < 7). Explanatory variables include: ocean entry characteristics, capture region (north or south), population aggregate (i.e. Vancouver Island or Fraser River), and year of capture. Interactions are between listed variable and capture regions. Plus (+) symbols indicate a variable is retained in the model and empty cells that it is not. Top ranked model is bolded.

Entry Date	Entry FL	Pop. Group	Capture Region	Year	Date Int.	FL Int.	Pop. Int.	Year Int.	DF	logLik	AICc	ΔAICc	Weight	r^2
+	**+**	**+**	**+**	**+**	**+**		**+**	**+**	**10**	**-318.77**	**658.16**	**0.00**	**0.59**	**0.907**
+	+	+	+	+	+	+	+	+	11	-318.30	659.34	1.18	0.33	0.907
+	+	+	+	+	+	+	+		10	-321.54	663.69	5.53	0.04	0.906
+	+	+	+	+	+			+	9	-322.69	663.88	5.72	0.03	0.906

Table A4.2 AIC rankings for binomial GLMs describing probability of juvenile sockeye salmon being captured in summer (0) or fall (1) surveys. Plus (+) symbols indicate a variable is retained in the model and empty cells that it is not. Top ranked model is bolded.

Entry Date	Entry FL	Population	df	AICc	ΔAICc
+	**+**		**2**	**-114.4**	**0**
+			1	-106.6	7.8
+	+	+	4	-106.5	8
+		+	3	-99.3	15.1
	+		1	-77.9	36.5
	+	+	3	-77.5	37
		+	2	-5.8	93.5

Table A4.3 Traits estimated from otolith microstructure (mean ±1 SD) across population aggregates, years, and sampling regions. Southern-fall captures are not shown due to small sample size.

		2007	2008			
		Summer	Summer		Fall	
		VI	VI	Fraser	VI	Fraser
Northern	Capture date (Julian)	182 ± 2	180 ± 2	180 ± 3	290 ± 5	287 ± 5
	Entry FL (mm)	89 ± 14	111 ± 14	86 ± 12	65 ± 7	73 ± 8
	Entry date (Julian)	120 ± 7	119 ± 8	133 ± 5	156 ± 8	157 ± 7
	Migratory rate (bl sec^{-1})	10.8 ± 2.6	11.5 ± 2.6	13.5 ± 2.9	5.3 ± 0.7	5.8 ± 0.9
Southern	Capture date (Julian)	175 ± 1	174 ± 1	180 ± 1	NA	NA
	Entry FL (mm)	68 ± 7	82 ± 14	74 ± 9	NA	NA
	Entry date (Julian)	121 ± 7	122 ± 7	133 ± 7	NA	NA
	Migratory rate (bl sec^{-1})	3.9 ± 1.3	2.7 ± 1.3	2.6 ± 0.5	NA	NA

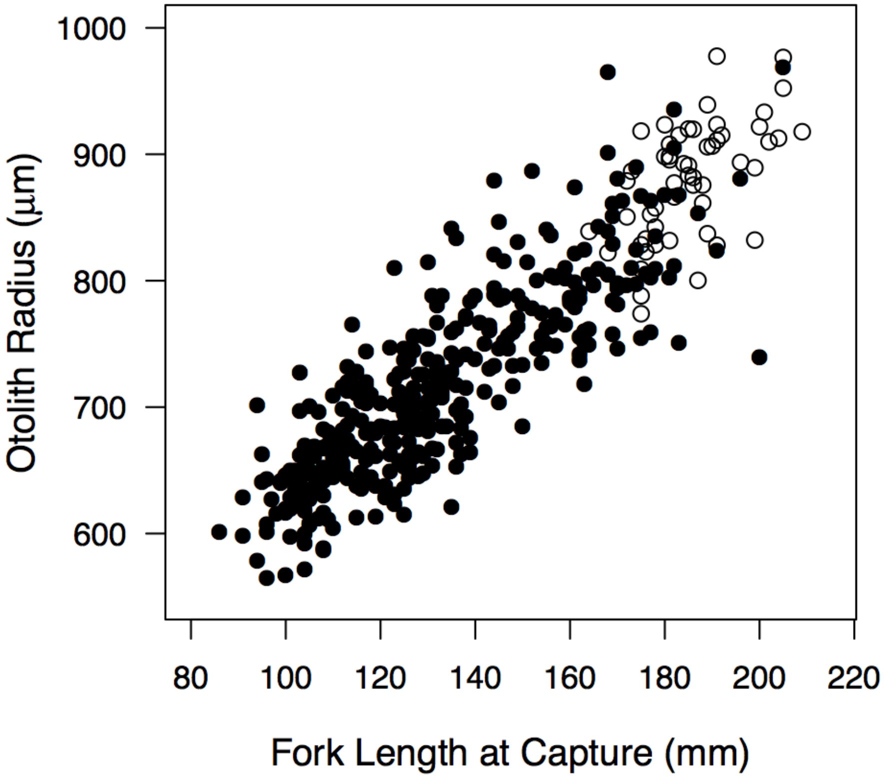


Figure A4.1 **Relationship between juvenile sockeye salmon fork length at capture (mm) and otolith radius (µm).** Filled and open symbols represent individuals captured during summer and fall surveys, respectively.

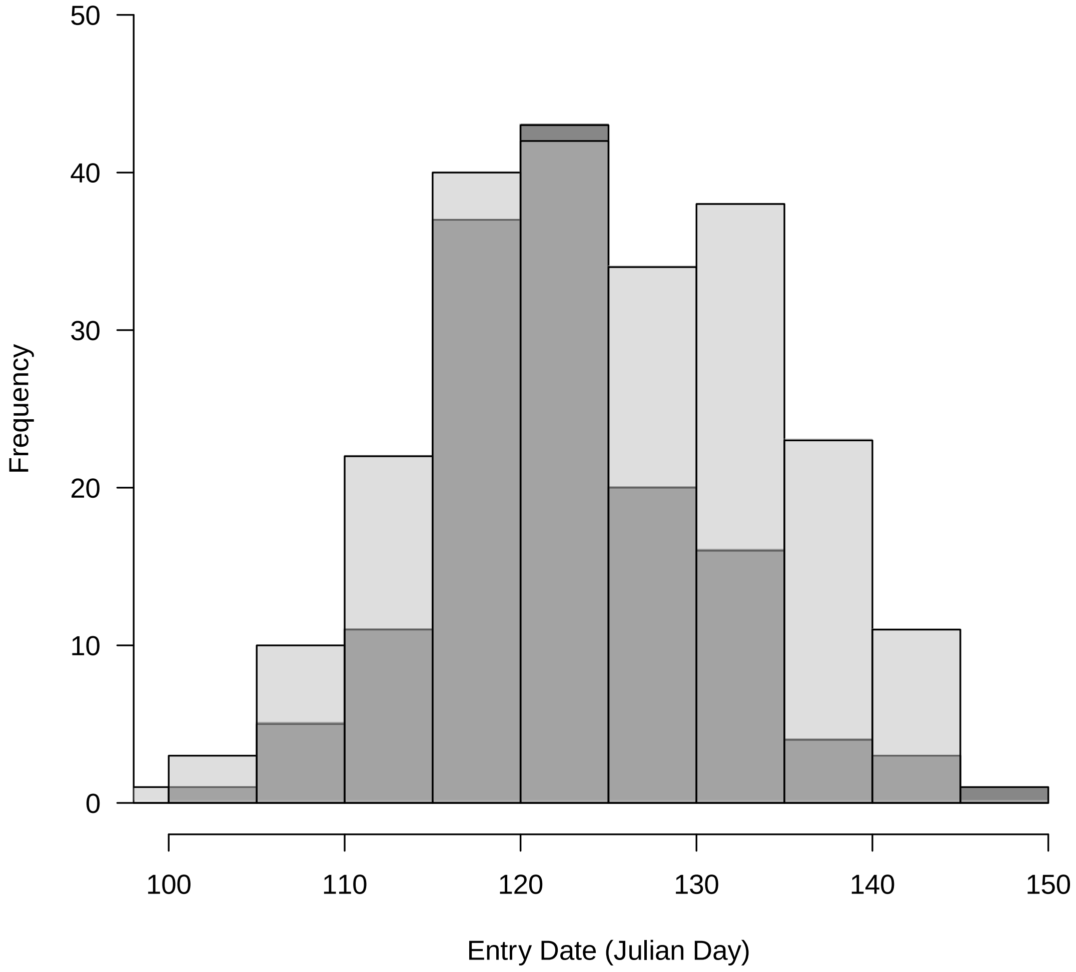


Figure A4.2 Back-calculated ocean entry date of Vancouver Island (*n* = 261) and Fraser River (*n* = 104) juvenile sockeye salmon captured during summer surveys. Dark grey and light grey bars represent individuals caught in southern and northern sampling region respectively

Appendix D: Supplemental information for Chapter 5

Sensitivity of results to removal individuals captured in Ricker trawl survey

To increase the number of individuals representing different nursery lakes in our analysis, we included samples collected during a June trawl survey ($n = 11$) conducted by DFO. To ensure that including these samples did not bias our results we excluded them and re-estimated all model parameters. Although individual parameter estimates varied, the direction and significance of each term was consistent regardless of whether these individuals were excluded (Table A5.4).

Sensitivity of results to migratory rate units

To ensure our conclusions were not biased by examining differences in relative migratory rate (bl sec^{-1}), we repeated our analysis with models that used migratory rate in km day^{-1} as the response. The effects of entry size, entry date, and sampling year on absolute migratory rate (km day^{-1}; Table A5.5, Fig. A5.3) were approximately equivalent to their effect on relative migratory rate presented in the main text (bl sec^{-1}).

Table A5.1 Population composition, sample size, and conservation units rearing sockeye salmon nursery lakes. Abundance estimates from CUs with a high likelihood of overlap were summed when estimating effective female spawner abundance in a given nursery lake.

Spawning Populations	Conservation Unit	Nursery Lake	2011 *n*	2012 *n*	Potentially Overlapping CUs	Likelihood of Overlap
Chilko Lake	Chilko-S/Chilko-ES	Chilko Lake	27	9	None	NA
Stellako River	Francois-Fraser-S	Fraser Lake	4	10	Nadina-Francois-ES	Low
North Thompson River	Kamloops-ES	Kamloops Lake	8	8	None	NA
Birkenhead River	Lillooet-Harrison	Lillooet Lake	8	4	Harrison (U/S)-L	High
Mitchell River	Quesnel-S	Quesnel Lake	9	10	None	NA
Horsefly River	Quesnel-S	Quesnel Lake	10	5	None	NA
Quesnel/Mitchell	Quesnel-S	Quesnel Lake	0	3	None	NA
Lower Adams River	Shuswap-L	Shuswap Lake-Main Arm	8	8	Shuswap-ES	High
Lower Shuswap	Shuswap-L	Mara Lake	0	9	Shuswap-ES	High
Scotch Creek	Shuswap-ES	Shuswap Lake-Main Arm	0	9	Shuswap-L	High
Seymour River	Shuswap-ES	Shuswap Lake-Seymour Arm	7	9	Shuswap-L	High
Tachie River	Takla-Trembleur-Stuart-S	Stuart Lake	6	9	Takla-Trembleur-Estu	Low

Table A5.2 Effective female spawner abundance in sockeye salmon CUs.

	EFS Abundance (100,000s)		
Nursery Lake	2009	2011	Mean
Chilko Lake	12.73	118.15	27.49 ± 21.77
Fraser Lake	1.58	10.93	6.89 ± 5.19
Kamloops Lake	0.6	0.24	0.49 ± 0.63
Lillooet Lake	4.74	9.31	8.48 ± 6.09
Quesnel Lake	8.28	13.16	29.06 ± 46.23
Shuswap Lake	2.6	363.47	47.71 ± 85.59
Stuart Lake	4.32	4.34	9.77 ± 20.90

Table A5.3 Year-specific mean characteristics (with SD) of juvenile sockeye salmon captured during 2011 and 2012 purse seine surveys.

	Capture Size (mm)		Entry Size (mm)		Entry Date (Julian day)		Growth Rate (mm/day)		Migratory Rate (bl/sec)	
Nursery Lake	2011	2012	2011	2012	2011	2012	2011	2012	2011	2012
Chilko Lake	110 ± 15.6	87 ± 11.2	87 ± 6.3	70 ± 7.1	128 ± 5.2	122 ± 6.4	0.89 ± 0.20	0.74 ± 0.14	0.64 ± 0.25	0.65 ± 0.28
Fraser Lake	109 ± 7.7	115 ± 10.1	104 ± 6.8	102 ± 6.8	136 ± 8.1	126 ± 3.1	0.78 ± 0.10	0.79 ± 0.15	1.17 ± 0.72	1.12 ± 0.34
Kamloops Lake	98 ± 10.7	100 ± 11.1	91 ± 11.3	82 ± 17.0	133 ± 5.3	127 ± 9.8	0.76 ± 0.27	0.76 ± 0.15	1.05 ± 0.46	0.83 ± 0.42
Lillooet Lake	109 ± 16.4	97 ± 13.8	91 ± 18.1	84 ± 10.2	118 ± 10.0	126 ± 11.0	0.73 ± 0.15	0.84 ± 0.12	0.44 ± 0.16	1.02 ± 0.54
Quesnel Lake	101 ± 16.1	98 ± 9.8	86 ± 8.2	80 ± 9.8	138 ± 7.5	131 ± 11.4	0.83 ± 0.20	0.81 ± 0.14	0.69 ± 0.44	0.89 ± 0.65
Shuswap Lake	112 ± 16.6	83 ± 12.7	94 ± 12.3	68 ± 12.6	135 ± 8.2	129 ± 6.9	0.81 ± 0.31	0.80 ± 0.18	0.33 ± 0.81	1.10 ± 0.80
Stuart Lake	102 ± 10.3	110 ± 10.5	96 ± 10.0	97 ± 7.9	137 ± 11.0	130 ± 7.1	0.68 ± 0.23	0.83 ± 0.15	0.52 ± 0.68	1.07 ± 0.83

Table A5.4 Estimated effect sizes of predictor variables from linear mixed models after removing individuals collected in trawl survey. Fixed effects include freshwater density-dependence (absent or present) and year (low marine densities in 2011 or high in 2012). Negative interactions indicate smaller size or earlier entry in 2012 in nursery lakes with freshwater density-dependent effects (i.e. Chilko and Shuswap). Continuous variables in growth and migration speed models were centered and scaled prior to fitting. Significant effect sizes (95% confidence intervals do not overlap with 0) are bolded.

Modeled Response	Predictor	Effect Size	95% Confidence Interval
Capture Size (mm)	Freshwater Density-Dependence	8.27	-4.44 – 19.20
	Year	4.20	-0.92 – 9.82
	Interaction	**-29.08**	**-36.78 – -20.78**
Entry Size (mm)	Freshwater Density-Dependence	-3.87	-15.69 – 7.99
	Year	-3.61	-8.40 – 0.88
	Interaction	**-17.86**	**-24.41 – -10.36**
Entry Date (Julian day)	Freshwater Density-Dependence	-0.01	-8.41 – 7.91
	Year	**-3.63**	**-7.23 – -0.66**
	Interaction	-1.59	-6.84 – 3.56

Growth (mm day^{-1})	Entry Size	-0.03	-0.06 – 0.01
	Entry Date	**0.06**	**0.03 – 0.10**
	Year	0.01	-0.05 – 0.07
Migration speed (log bl sec^{-1})	**Entry Size**	**0.19**	**0.09 – 0.28**
	Entry Date	**0.27**	**0.17 – 0.36**
	Year	**0.29**	**0.08 – 0.50**

Table A5.5 Estimated effect sizes of predictor variables from linear mixed model with absolute migratory rate as response. Significant effect sizes (95% confidence intervals do not overlap with 0) are bolded.

Modeled Response	Predictor	Effect Size	95% Confidence Interval
Migratory Rate (log km day^{-1})	**Entry Size**	**0.33**	**0.21 – 0.42**
	Entry Date	**0.21**	**0.11 – 0.31**
	Year	**0.35**	**0.15 – 0.55**

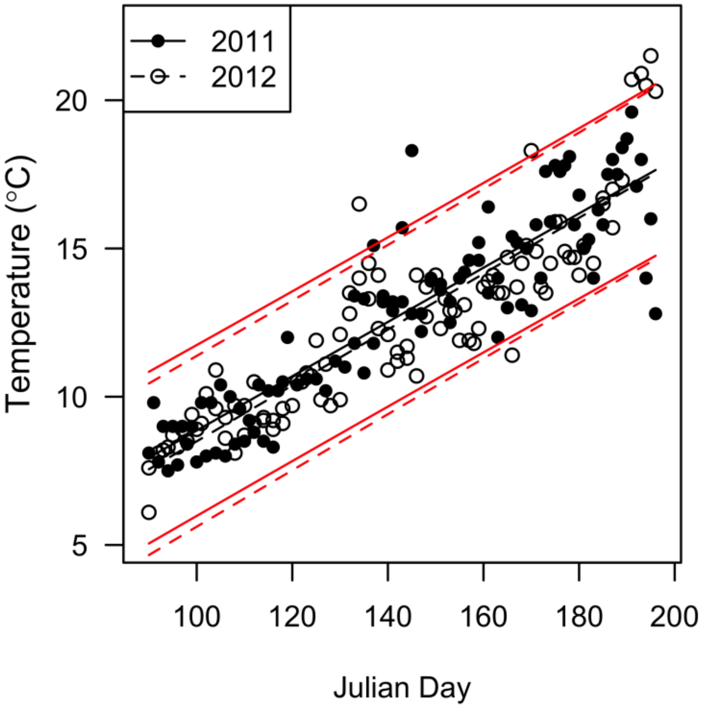


Figure A5.1. Seasonal changes in sea surface temperature in the Strait of Georgia over the migratory period of juvenile sockeye salmon. Red lines represent 95% prediction intervals for linear model.

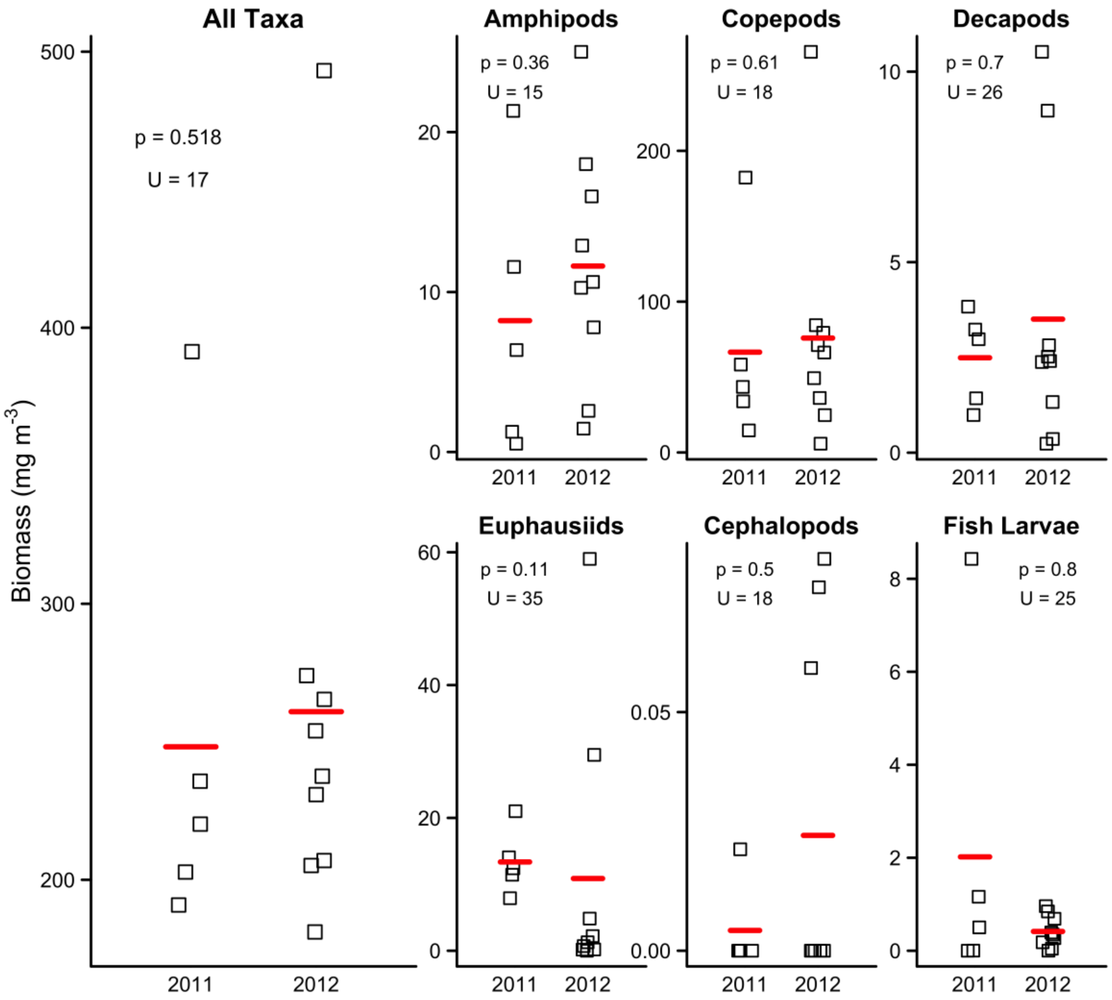


Figure A5.2 Observed biomass of potential juvenile Pacific salmon prey taxa from vertical plankton tows. Black squares represent values from individual sampling stations and red lines represent taxon-specific mean values across stations within a sampling year. Total biomass includes only the listed taxonomic groups and excludes groups that are not likely to be targeted by juvenile salmon. P-values and U statistics from overall and taxon-specific Mann-Whitney tests are shown within each panel. Note that the scale of the y-axis changes between taxonomic groups.

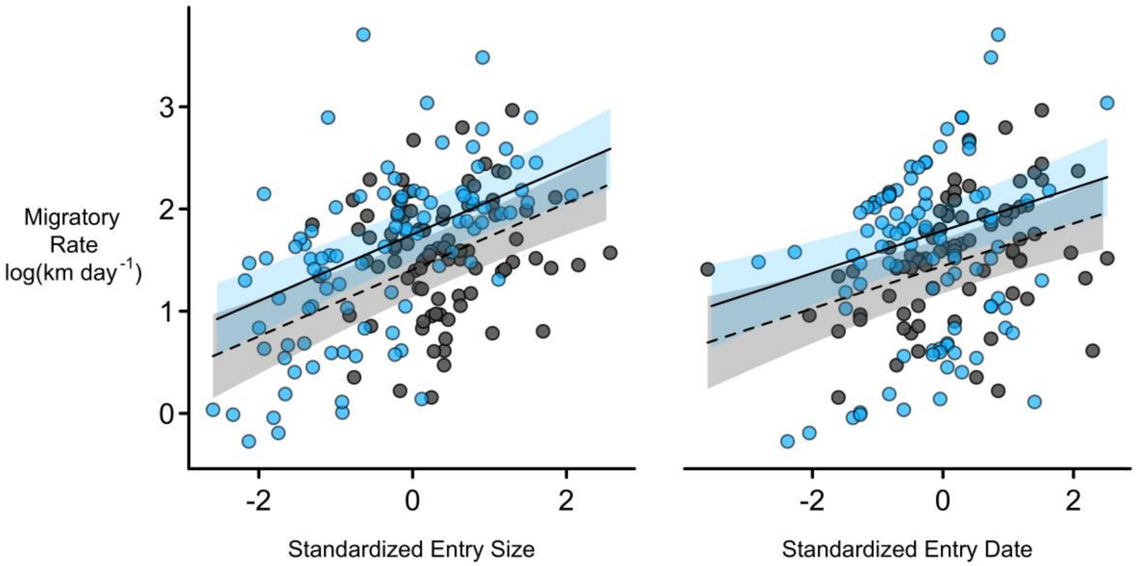


Figure A5.3 Estimated mean migratory rate as a function of entry size (left) and date (right) showing data from a low (grey) and high (blue) abundance year. Shaded regions represent the 95% prediction intervals of the linear mixed effects model for each year (low density, blue; high density, grey). Prediction intervals incorporate variation among nursery lakes and are calculated holding model covariates at their mean value. Note that x-axis values have been centered and scaled.

Appendix E: Supplemental information for Chapter 6

Table A6.1 Population-specific sample sizes for otolith analyses.

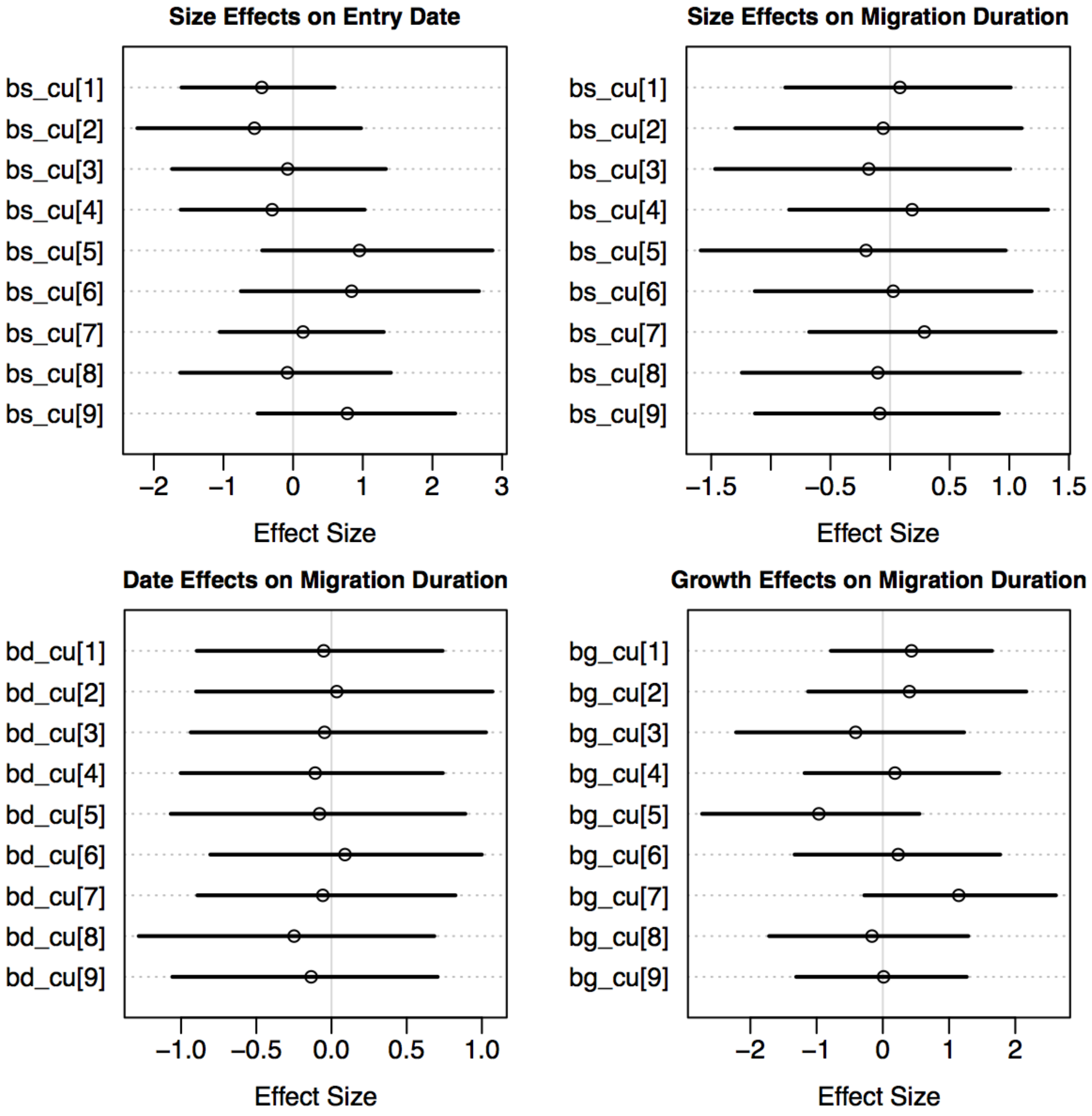
Conservation Unit	Population	2014	2015	2016
Chilko	Chilko Main	54	52	28
Chilko	Chilko South	0	7	0
Chilliwack-ES	Dolly Varden	31	0	0
Francois-Fraser-S	Stellako	0	5	19
Lillooet-Harrison-L	Birkenhead	24	8	10
Nadina-Francois-ES	Nadina	31	7	17
Pitt-ES	Pitt	12	20	0
Quesnel-S	Quesnel_Deception	0	22	0
Quesnel-S	Quesnel_Mitchell	0	1	14
Quesnel-S	Mitchell	0	46	12
Quesnel-S	Upper Horsefly	0	43	24
Shuswap-ES	Seymour	0	19	21
Shuswap-L	Lower Adams	0	49	20
Shuswap-L	Lower Shuswap	0	0	10
Shuswap-L	Middle Shuswap	0	0	15

Table A6.2 Full model rankings from entry date models. All models contain life history type as a dummy variable and random intercepts and slopes for CU and year.

Model Name	Fixed Covariates	Life History	Entry Size	WAIC	Effective Parameters	ΔWAIC	WAIC Weight
m3.s1	2	X	X	4174.5	18.9	0	1
m3	1	X		4198.6	11.6	24	0

Table A6.3 Full model rankings from migration duration models. All models contain life history type as a dummy variable and random intercepts and slopes for CU and year.

Model Name	Fixed Covariates	Life History	Entry Date	Growth	Entry Size	WAIC	Effective Parameters	ΔWAIC	WAIC Weight
m1.dgs1	4	X	X	X	X	4497.9	22.2	0	1
m1.dg1	3	X	X	X		4529.4	15.4	31.5	0
m1.gs1	3	X		X	X	4578.2	19.6	80.3	0
m1.g1	2	X		X		4600.6	13.6	102.7	0
m1.ds1	3	X	X		X	4651	16.7	153.2	0
m1.d1	2	X	X			4669.4	12.1	171.5	0
m1.s1	2	X			X	4692	12.7	194.1	0
m1	1	X				4705.1	10.1	207.2	0


Size Effects on Entry Date

Size Effects on Migration Duration

Date Effects on Migration Duration

Growth Effects on Migration Duration

Figure A6.1 CU-specific estimates of individual effects on entry date and migration duration.