

**Linking estuary rearing habitats to migration traits,
behaviour, and survival of juvenile coho salmon
(*Oncorhynchus kisutch*)**

by

Alexandra Claire Sawyer

B.Sc., University of Washington, 2018

B.A., University of Washington, 2011

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

in the
Department of Biological Sciences
Faculty of Science

© Alexandra Claire Sawyer 2022

SIMON FRASER UNIVERSITY

Spring 2022

Declaration of Committee

Name: Alexandra Claire Sawyer

Degree: Master of Science

Title: Linking estuary rearing habitats to migration traits, behaviour, and survival of juvenile coho salmon (*Oncorhynchus kisutch*)

Committee:

Chair: Nicholas Dulvy
Professor, Biological Sciences

Jonathan Moore
Supervisor
Professor, Biological Sciences

Isabelle Côté
Committee Member
Professor, Biological Sciences

Jason Toft
Examiner
Research Scientist, Aquatic and Fishery Sciences,
University of Washington

Ethics Statement

The author, whose name appears on the title page of this work, has obtained, for the research described in this work, either:

- a. human research ethics approval from the Simon Fraser University Office of Research Ethics

or

- b. advance approval of the animal care protocol from the University Animal Care Committee of Simon Fraser University

or has conducted the research

- c. as a co-investigator, collaborator, or research assistant in a research project approved in advance.

A copy of the approval letter has been filed with the Theses Office of the University Library at the time of submission of this thesis or project.

The original application for approval and letter of approval are filed with the relevant offices. Inquiries may be directed to those authorities.

Simon Fraser University Library
Burnaby, British Columbia, Canada

Update Spring 2016

Abstract

Estuaries are nursery habitats for juvenile Pacific salmon, yet quantifying estuary contributions to behaviour, adaptations, and fitness across the salmon life-cycle remains a challenge. Using data from 64 coho salmon populations ranging from California to Alaska, I first examined how juvenile migration traits covary with estuary and freshwater habitat characteristics. Populations from lower latitudes, and with access to more enclosed and complex estuaries, exhibited earlier and more protracted migrations. Second, I used a mark-recapture study to examine estuary residence, growth, and subsequent marine survival by juveniles from the Koeye River in British Columbia. Relative to larger individuals, small juveniles resided longer and grew more in the estuary before marine entry. Marine survival increased with juvenile body size and estuary growth improved survival prospects by 44-46%. This research reveals that juvenile salmon are locally adapted to estuary habitats, and that condition-dependent stopover can mitigate freshwater carryover effects and boost marine survival.

Keywords: estuary; Pacific salmon; migration; local adaptation; carryover effects; mark-recapture

Acknowledgements

This thesis has been an enriching journey—rewarding, challenging, and punctuated by many moments of wonder in wild places. I am grateful for the generosity and support of many people along the way. First and foremost, thank you to Jon Moore, who has been a great supervisor and mentor throughout my time at SFU. Thank you for consistently sharing not only your scientific expertise, but also your scientific ethos. I appreciate your support in navigating the twists and turns of graduate school, for giving me time and space to tackle diverse projects, and for pushing me to think critically and expansively. Importantly, you have shown me the value of situating meaningful science within a resonant story—a lesson I will carry with me. I am also grateful to Isabelle Côté, who has been such a warm and insightful member of my graduate committee. Your care and encouragement have buoyed me in times of need, and my research and writing have benefitted from your thought-provoking comments (and your unwavering commitment to precise language).

To the many folks in the Salmon Watersheds Lab at SFU, thank you. It has been such a joy to spend time with you smart, dedicated, and passionate people. I look forward to seeing where you end up, and what weird and wonderful things you do. Special thanks to Sam, for being a tireless source of guidance and support (both statistical and emotional). You have been over-the-top generous with your time, expertise, and connections, and never flinch when a one-hour meeting hits the three-hour mark. Special thanks also to Anna—I am so lucky that you’ve been there from day one. Whether we’re locked in a tiny room scribbling code on a whiteboard, or sitting on the floor transcribing big fishy thoughts onto paper bags, you’ve made this experience more fun, and way more funny. A big thank you also to Lauren, Mikayla, Tash, Sadika, and Emma for keeping the wheels on the bus.

Time spent in the field grounds me as a scientist, and time spent in the field with good people makes all the difference. Special thanks to Will, for sharing your “adapt and thrive” mentality during peak week at the Koeye—it has proven useful in more ways than one. To Colin and Kyle, for valiant attempts to teach me to fly fish at the Keogh (and to Anna for showing that it really can be done, at least if you’re fishing for sculpin). To Julian, for demonstrating the proper way to caffeinate before a long day of estuary-tromping. And to Sara, for support on and off the water, and for showing that brains

matter more than brawn when it comes to a stuck seine net. In particular, it has been a special privilege to visit the lands and waters of many First Nations in the course of my field work. I am especially grateful for time at the Koeeye River in the Heiltsuk First Nation, and for eye-opening conversations and experiences while there.

Beyond my graduate school community, I am grateful to those that supported and inspired me along the way, and have continued to offer encouragement. To Kit Paulsen, for recognizing my enthusiasm and overlooking my inexperience, and offering me the job that set me on this path. To Daniel Schindler, for giving me the opportunity to get my feet wet in a truly spectacular setting, and for consistent support and straight-shooting feedback. And to Jason Toft, for being a great collaborator both above and under the water, and for coming full-circle as my defence examiner.

Finally, immense gratitude to my community back in Washington. To my dear friends, thank you for making me laugh through good times and hard times. I'm proud that many of you have grown into full-blown fish nerds in your own right. To my family, thank you for sharing your always strong opinions, providing your copy-editing services, and offering an endless fount of encouragement and patience along the way. And to my parents, in particular—thank you for always supporting my next big adventure.

Table of Contents

Declaration of Committee	ii
Ethics Statement.....	iii
Abstract.....	iv
Acknowledgements.....	v
Table of Contents.....	vii
List of Tables.....	ix
List of Figures	x
Chapter 1. Introduction	1
Chapter 2. Diverse juvenile salmon migration traits reflect latitudinal clines and estuary habitat variation	6
2.1. Abstract.....	6
2.2. Introduction	7
2.3. Methods	11
2.3.1. Juvenile coho salmon migration data.....	11
2.3.2. Estimation of migration trait parameters.....	13
2.3.3. Estuary habitat spatial data	14
2.3.4. Watershed covariate spatial data.....	16
2.3.5. Statistical analyses.....	20
2.4. Results.....	23
2.4.1. Trends in migration traits.....	23
2.4.2. Migration timing.....	25
2.4.3. Migration duration.....	27
2.4.4. Body size at migration	28
2.5. Discussion.....	31
2.6. Acknowledgements.....	38
Chapter 3. State-dependent estuary stopover boosts marine survival for juvenile salmon	40
3.1. Abstract.....	40
3.2. Introduction	41
3.3. Methods	44
3.3.1. Overview of methods.....	44
3.3.2. Data collection.....	45
3.3.3. Estuary residence analysis.....	47
3.3.4. Estuary growth analysis	49
3.3.5. Marine survival analysis	50
3.4. Results.....	52
3.4.1. Estuary residence.....	52
3.4.2. Estuary growth	53
3.4.3. Marine survival	55
3.5. Discussion.....	57

3.6. Acknowledgements.....	63
Chapter 4. General Discussion.....	64
References.....	72
Appendix A. Supplemental Material for Chapter 2	88
Appendix B. Supplemental Material for Chapter 3	93
Comparative methods for quantifying estuary residence.....	93
Results of comparative estuary residence analyses.....	95

List of Tables

Table 2.1.	Geographic details, trap coordinates, number of years sampled, and data holders associated with each juvenile coho salmon study population (n = 64).	17
Table 3.1.	Estimated effect sizes, 95% confidence intervals, and p-values for parameters included in the best-fit marine survival model.	56

List of Figures

Figure 2.1.	Geographic location of juvenile coho salmon trap sites (n = 64).....	12
Figure 2.2.	Correlation plot for all candidate predictor variables considered in partial least-squares regression models.	21
Figure 2.3.	Migration timing (peak and interquartile range; panel a) and body size at migration (mean and standard deviation; panel b) for each population included in the study.....	25
Figure 2.4.	Partial least-squares regression biplots and associated regression coefficients for a) early migration date (25th percentile), b) peak migration date, c) late migration date (75th percentile), and d) migration duration (interquartile range).	29
Figure 2.5.	Comparison of observed data and partial least-squares model predictions for a) peak migration date and b) migration duration.	30
Figure 3.1.	Map of the Koeye River estuary, indicating location of rotary screw trap (RST) and estuary sampling sites.	45
Figure 3.2.	Conceptual figure showing data used to determine size-selective marine survival relationships a) observed in the presence of estuary habitat and b) predicted in the absence of estuary habitat.	51
Figure 3.3.	Relationship between fork length at freshwater exit and estuary residence (with 95% CI), derived from GLM with a negative binomial error distribution.	53
Figure 3.4.	Mean daily estuary growth rates (with 95% CI about the mean) of juvenile coho salmon for each sampling year.....	54
Figure 3.5.	Density plots depicting observed size at freshwater exit (green) and predicted size at marine entry after estuary rearing (blue) for all juvenile coho salmon sampled at the RST in a) 2017, b) 2018, and c) 2019.	55
Figure 3.6.	Relationship between fork length at freshwater exit and marine survival of juvenile coho salmon.....	57

Chapter 1. Introduction

Animal migration, one of the great phenomena of the natural world, connects disparate habitats that vary in their inherent opportunities and constraints. Myriad species, ranging from monarch butterflies to gray whales, undertake predictable, directional journeys from one habitat to another to maximize fitness amidst a seasonally shifting resource landscape (Alerstam et al. 2003, Dingle and Drake 2007). Simultaneously, migratory animals must balance resource opportunities with costs associated with the time, energy, and risk inherent to reaching and surviving in a given habitat (Werner and Gilliam 1984, Alerstam et al. 2003). In addition to suitable conditions in current and future habitats, migratory animals rely on connectivity between habitats to complete their migrations (Runge et al. 2014). As such, conditions encountered during migration—including along migratory corridors and in migratory stopover habitats—are important determinants of migration success. Situated along migratory routes, stopover habitats offer resources (e.g., food, water) and environmental conditions (e.g., low predation rates) that allow migrants to rest and refuel prior to resuming passage (Moore et al. 1995). Although typically occupied for a short period of time—ranging from several hours to several days—stopover habitats can be crucial for migrants to sustain energy reserves required to complete long-distance migrations (Moore et al. 1995, Weber et al. 1999, Runge et al. 2014). However, migratory connectivity is increasingly fragmented by human activity (Runge et al. 2014), and the ability of migratory species to adapt to changing conditions remains to be seen (Moore et al. 1995, Bowlin et al. 2010, Reed et al. 2011)

Migratory life-histories—the migratory traits and behaviours exhibited by a given species or population—represent “solutions” to the problem of navigating dynamic opportunities and constraints across habitats (Alerstam et al. 2003, Dingle and Drake 2007). An animal’s life-history is the suite of attributes that affects its fitness, and integrates both genetic variation and phenotypic plasticity expressed throughout the life-cycle (Stearns 2000, Waples et al. 2001). Traits and behaviours such as the timing of migration, the size and age at which animals migrate, and the number of migrations undertaken in the course of a lifetime are key components in the life-histories of migratory animals (Alerstam et al. 2003). Natural selection acts on these differential traits to shape optimal migratory life-history strategies (Dingle and Drake 2007, Bowlin et

al. 2010). As the seasonal conditions in a particular habitat become more or less favourable, natural selection rewards those migrants that display traits advantageous for survival and reproduction (Dingle and Drake 2007). Successful migratory life-histories therefore integrate a suite of developmental, physiological, and behavioural traits—adaptations that enable migratory animals to “solve the problem” of spatiotemporal resource variation (Bowlin et al. 2010). Certain aspects of migratory life-histories can be further influenced by carryover effects, whereby the experience of a migratory animal in one habitat influences its performance and behaviour in subsequent habitats (Norris 2005, O’Connor et al. 2014). Carryover effects reflect an individual’s ability to access and utilize resources, and commonly manifest in differences in biological condition (e.g., body size, lipid storage, hormone levels; Harrison et al. 2011). Although carryover effects directly influence individual fitness, in aggregate they can scale up to affect survival and reproduction at the population level (Norris 2005, Harrison 2011). Thus both ecological and evolutionary forces, linked across a continuum of habitats, interact to shape the life-histories and fitness of migratory species.

Pacific salmon (*Oncorhynchus* spp.) are a striking exemplar of long-distance migration, with complex anadromous life-cycles that span freshwater, estuarine, coastal, and oceanic habitats. Pacific salmon are born in freshwaters, and rear from a period of months to years in natal habitats before migrating downstream to the sea (Quinn 2018). Their seaward migration coincides with smoltification, the physiological transition that enables these heretofore freshwater fishes to survive and thrive in saltwater environments (Hoar 1974). Upon entering the ocean, salmon generally move from nearshore to offshore habitats where they feed and mature, ultimately gaining more than 90% of their total body mass. Ocean residence patterns vary within and between species, lasting from a few months for “jack” individuals to several years for the oldest-maturing species (Quinn 2018). Eventually, adults initiate a return migration from the ocean back to natal freshwaters, where they spawn and subsequently die. Migrating adult salmon are the target of commercial and subsistence fisheries, as well as an important prey resource for aquatic and terrestrial predators alike. Accordingly, the adult migration phase has been the subject of intense research, shedding light on extensive adult trait diversity and how local adaptations support both population stability and long-term persistence (e.g., Hilborn et al. 2003, Schindler et al. 2010). Though less studied, evidence suggests that juvenile life-history traits can have similarly weighty

consequences for population productivity and resilience to shifting environmental conditions (Freshwater et al. 2018, Sturrock et al. 2020, Cordoleani et al. 2021, Jones et al. 2021, Wilson et al. 2021).

Situated at the nexus of freshwaters and the ocean, estuaries can function as important rearing habitats for juvenile Pacific salmon (Thorpe 1994, Weitkamp et al. 2014). Beyond enabling gradual acclimatization to saline conditions, estuaries are considered juvenile salmon nurseries for their enhanced capacity to provision prey and offer predator refuge (Simenstad et al. 1982). Estuaries feature an abundance of energy-dense zooplanktonic and macroinvertebrate prey preferred by juvenile salmon (Arbeider et al. 2019, Woo et al. 2019), and juveniles rearing and foraging in these habitats can experience high growth rates (Hayes et al. 2008, Goertler et al. 2016, Chalde and Fernández 2017) and reduced levels of density-induced competition (David et al. 2016). In addition, many estuaries contain structurally complex microhabitats that serve as refugia from predators and other environmental stressors (Simenstad and Cordell 2000, Chalifour et al. 2019, Sharpe et al. 2019, Seitz et al. 2020). Access to high-quality estuary habitat has been associated with higher rates of survival to adulthood (Magnusson and Hilborn 2003, Meador 2014). In addition to their nursery role, estuaries may serve as stopover habitats in the course of seaward migration, offering juvenile salmon advantageous conditions for growth and bolstering of energy reserves prior to facing novel challenges in the ocean (Moore et al. 2016). Broadly, observed patterns of estuary use vary both within and across populations, and with the types of estuary habitats available (reviewed in Levings 2016). However, despite its importance, the estuary rearing phase is often overlooked in Pacific salmon life-cycle analyses. Rather, “freshwater exit” and “marine entry” are commonly conflated in space and time—a false equivalence which fails to account for growth and mortality processes specific to the estuary stage of juvenile salmon life-histories (Jones et al. 2021).

In the study of Pacific salmon and their habitats, quantifying estuary contributions to behaviour, adaptations, and fitness remains a persistent challenge. In this thesis, I examine linkages between estuary rearing habitats and juvenile coho salmon (*O. kisutch*) migration traits, migratory stopover behaviour, and marine survival. My first data chapter (Chapter 2) explores how juvenile coho salmon migration traits covary with estuary and freshwater habitat characteristics across populations spanning more than 20 degrees of latitude. My second data chapter (Chapter 3) examines estuary residence,

growth, and subsequent marine survival by juvenile coho salmon from the Koeye River in British Columbia. Collectively, these chapters offer insight into estuary influence on the migratory life-histories of Pacific salmon, and the role of estuary habitats in mitigating upstream carryover effects and improving downstream survival prospects.

In Chapter 2, I investigated diversity in juvenile coho salmon migration traits across populations and potential linkages with rearing habitat characteristics. Migration traits can reflect local adaptations to habitat conditions experienced across the life-cycle, from juvenile rearing grounds (e.g., Beechie et al. 2006) to adult migration corridors (e.g., Hodgson and Quinn 2002). I compiled data from 64 coho salmon populations, ranging from Central California to Southeast Alaska, to examine the extent to which juvenile migration timing and body size at migration were correlated with estuary habitat extent, configuration, and quality, in addition to natal watershed characteristics such as latitude, elevation, lake influence, and catchment area. Analyses revealed considerable diversity across populations with respect to both migration timing and body size. Migration timing and duration were significantly correlated with latitudinal clines and with metrics of estuary habitat configuration, including shoreline complexity and degree of enclosure. Broadly, these findings showcase underappreciated dimensions of local adaptation, suggesting that juvenile salmon migratory life-histories reflect adaptation not only to proximate freshwater habitats, but also to future estuarine habitats.

In Chapter 3, I focused on a single coho salmon population from the Koeye River watershed to describe patterns of estuary stopover by juveniles *en route* to the ocean, and explore implications of this stopover period for marine survival. Studies of both migratory birds (Loria and Moore 1990) and fishes (Bond et al. 2008, Satterthwaite et al. 2012) suggest that use of stopover habitats may be state-dependent, whereby low-condition individuals exhibit longer stopovers as a means of improving their energy stores—and therefore survival prospects—prior to resuming migration (Moore et al. 1995, Runge et al. 2014). I used a mark-recapture study to quantify estuary residence and growth by juvenile coho salmon migrants from three successive cohorts. Analyses revealed that smaller juveniles resided for a longer period in the estuary, and that estuary growth substantially improved marine survival prospects. Together, these findings suggest that estuary stopover behaviour can mitigate freshwater carryover effects for juvenile coho salmon, with the potential to boost watershed-level productive capacity and buffer size-selective survival in the ocean.

In my concluding chapter (Chapter 4), I discuss the key findings and broad implications of my thesis research and suggest areas for future investigation. Collectively, my research suggests that the migratory life-histories of coho salmon are locally adapted to estuary habitat characteristics, and showcases the potential benefits of estuary stopover for individual survival to adulthood.

Chapter 2. Diverse juvenile salmon migration traits reflect latitudinal clines and estuary habitat variation

2.1. Abstract

The seaward migration of juvenile Pacific salmon (*Oncorhynchus* spp.) is a critical life-history transition, and the timing and size at which juveniles migrate can influence both individual survival and population productivity. Migration between freshwater, estuarine, and marine environments reflects trade-offs between growth opportunities and mortality risks in each habitat. Estuaries can offer favourable growth conditions and serve as predator refugia, and many juvenile salmon species exhibit a distinct estuary rearing phase. However, relative to marine and freshwater processes, little is known about the potential role of estuary habitats in shaping migration traits. Here, we demonstrate that juvenile coho salmon (*O. kisutch*) exhibit diverse migration traits which vary along latitudinal gradients and with estuary habitat configuration. Using data from 64 populations ranging from California to Alaska, we analysed the extent to which juvenile migration timing and body size at migration were correlated with characteristics of estuarine and freshwater rearing habitats. We found considerable diversity in migration timing traits across populations: peak migration date ranged from early-April to mid-June, and duration of the migration window ranged from 7 to 65 days. Partial least-squares regression revealed that populations at more southerly latitudes, and with access to more complex and enclosed estuaries, exhibited earlier and more protracted migrations. For coho salmon populations with access to maximally enclosed and complex estuaries, the juvenile migration window was predicted to last more than two weeks longer, and peak two weeks earlier, relative to populations with access to comparatively open and simple estuaries. Although there was also substantial variation in population-specific body size at migration, we did not find correlations between size-related traits and estuary or watershed characteristics. Broadly, our findings suggest that the migratory life-histories of coho salmon reflect adaptation to estuary habitat characteristics, in addition to latitudinal clines in marine and freshwater processes. Our study highlights underappreciated dimensions of local adaptation across wide-ranging salmon populations, and underscores the need to conserve and restore the mosaic of rearing habitats that sustain population-level diversity.

2.2. Introduction

Pacific salmon (*Oncorhynchus* spp.) exhibit remarkable trait diversity, illustrated by wide-ranging phenotypic differences in the timing, size, and age at which major life-history events unfold. Distinct migratory life-histories can reflect local adaptations to habitat conditions experienced across the life-cycle, from juvenile rearing grounds (e.g., Beechie et al. 2006) to adult migration corridors (e.g., Hodgson and Quinn 2002). Understanding the distribution of life-history traits, and linkages between trait diversity and key habitats and processes, can shed light on how salmon populations might respond to contemporary environmental change. For example, disproportionate loss of particular habitats—such as high-elevation headwater streams and low-lying coastal estuaries—can alter selective regimes responsible for generating and maintaining trait diversity both within and across populations, potentially eroding future adaptive capacity (McClure et al. 2008, Williams et al. 2008). To date, much research has focused on traits of adult salmon spawners, and how local adaptations can shape success and response diversity across habitats (Hilborn et al. 2003) and contribute to portfolio effects and stability within and across populations (Greene et al. 2010, Schindler et al. 2010, Moore et al. 2014). There is arguably less understanding of the diversity and geographic distribution of juvenile life-history traits, even though these traits can strongly influence population productivity and resilience (Freshwater et al. 2018, Sturrock et al. 2020, Cordoleani et al. 2021, Jones et al. 2021, Wilson et al. 2021).

For juvenile Pacific salmon, migration from natal freshwaters to the sea is a critical life-history transition and reflects local adaptation to seasonal opportunities and constraints across marine and freshwater ecosystems (Gross et al. 1988, Quinn et al. 2009). Broadly, evidence suggests that juvenile salmon migrations are locally adapted to match temporally limited marine “windows of opportunity” in the nearshore coastal zone coincident with the productivity regimes of their prey (e.g., zooplankton; Holtby et al. 1990; McCormick et al. 1998; Spence and Hall 2010). Key migration traits—including timing and duration of the migration window and size and age at outmigration—can have important consequences for individual survival and population productivity. For example, there is some evidence that juvenile salmon survive at higher rates when ocean entry timing matches peak spring zooplankton abundance along the North American continental shelf (Ryding and Skalski 1999; Chittenden et al. 2010; Satterthwaite et al.

2014; Wilson et al. 2021; but see Scheuerell et al. 2009). At the individual level, juveniles that enter marine waters with a larger body size tend to have higher rates of survival to adulthood (Ward et al. 1989; Henderson and Cass 1991; Koenings et al. 1993; but see Ulaski et al. 2020), which may reflect a greater ability to withstand novel challenges (e.g., capture of marine prey, evasion of marine predators) and accumulate sufficient energy stores to avoid overwinter starvation (Sogard 1997, Beamish and Mahnken 2001, Duffy and Beauchamp 2011). As the timing of peak prey abundance can vary interannually, so will optimal outmigration timing (Wilson et al. 2021). Thus, juvenile salmon migration traits presumably reflect natural selection for both long-term mean optima and their degree of historic variability (McCormick et al. 1998, Quinn et al. 2009).

Despite evidence that juvenile salmon migration traits are subject to selection by long-term marine “windows of opportunity,” widespread variation persists both within and across populations. Some of this variation can be linked to phenotypic plasticity and norms of reaction associated with the freshwater life stage (Waples et al. 2001, Hutchings 2004). For example, juvenile body size at the time of seaward migration may be strongly influenced by freshwater rearing conditions, including water temperature, productivity, competition, and density dependence (Quinn 2018). Further, because juvenile salmon are generally unable to sample marine conditions prior to migration, they may rely on proximate freshwater signals (e.g., stream discharge, thermal experience) that have historically covaried with optimal growth and survival conditions in the ocean to cue migration decisions (McCormick et al. 1998, Sykes et al. 2009, Spence and Hall 2010, Spence and Dick 2014). For example, at northern latitudes peak primary productivity—and the subsequent peak in zooplankton productivity—tends to occur later in the calendar year and over a more predictable range of dates. Simultaneously, proximate migration cues such as lengthening photoperiod, spring freshet, and warming water temperatures tend to occur later at northern latitudes, constrained by factors such as the timing of ice breakup. Coincident with these processes, salmon populations hailing from higher-latitude watersheds generally exhibit later and more constricted migrations than those from lower latitudes (Quinn et al. 2009, Spence and Hall 2010). Additional population-level variation in rearing elevation and migration distance to the ocean may add to latitudinal clines, such that migration timing is relatively later for higher-elevation and longer-migrating populations (Spence and Hall 2010, Carr-Harris et al. 2018). While the freshwater habitat processes that cue and constrain juvenile

migrations are increasingly well-characterized, to this point the potential role of estuary habitats in shaping migration traits has not been extensively considered.

Many Pacific salmon species exhibit a distinct estuary rearing phase prior to ocean entry (Thorpe 1994, Weitkamp et al. 2014, Moore et al. 2016), and there is increasing evidence that estuarine habitat use can influence juvenile migratory strategies and lifetime fitness (Jones et al. 2021; Chapter 3). Complex vegetated habitats at the estuary-terrestrial interface, such as emergent salt marsh and rockweed and eelgrass beds, commonly support higher densities of juvenile salmon relative to simpler habitats, such as sand flats and armored shorelines (Heerhartz and Toft 2015, Chalifour et al. 2019, Sharpe et al. 2019, Seitz et al. 2020). These habitats can be productive foraging grounds, featuring an abundance of energy-dense planktonic and macroinvertebrate prey such as copepods, mysids, and larval and adult insects (Simenstad et al. 1982, Arbeider et al. 2019, Woo et al. 2019). Indeed, juvenile salmon have been observed feeding and growing at higher rates in estuaries relative to upstream freshwaters (Hayes et al. 2008, Hoem Neher et al. 2013, Weitkamp et al. 2015, Goertler et al. 2016, Chalde and Fernández 2017). Early migration to the estuary and prolonged estuary rearing may reflect an adaptive strategy by which juvenile salmon increase their body size prior to entering the size-selective marine environment. Indeed, small juvenile salmon have been observed making extended estuary stopovers *en route* to the ocean, and resultant growth could boost chances of survival to adulthood (Bond et al. 2008; Egorova 2016; Chapter 3). Estuary habitat quality may further mediate juvenile salmon survival rates, with populations that rear in more pristine estuaries exhibiting higher rates of survival to adulthood (Magnusson and Hilborn 2003, Meador 2014).

While estuaries are increasingly recognized for their role in supporting a diversity of migratory life-histories, the extent of local adaptation to estuary conditions remains poorly understood. Among Chinook (*O. tshawytscha*; Healey 1980; Bottom et al. 2005) and coho salmon (*O. kisutch*; Miller and Sadro 2003; Koski 2009; Jones et al. 2014) in particular, there is empirical evidence that juveniles migrate to estuaries throughout the year and at a range of ages and sizes—from recently-emerged fry to yearlings and older—and that estuary-rearing individuals survive, grow, and can constitute a substantial portion of adult returns (Volk et al. 2010, Jones et al. 2021). Migration between habitats can be viewed as a trade-off between maximizing growth opportunities and minimizing mortality risks in each habitat (Werner and Gilliam 1984, Quinn et al.

2009, Satterthwaite et al. 2012). Because growth-mortality trade-offs differ between freshwater and estuarine habitats, and between estuarine and marine habitats, it follows that estuary characteristics may influence migratory traits. For example, when high-productivity estuary habitat is present it may be advantageous to migrate downstream earlier or at a smaller size in order to accelerate growth prior to ocean entry, thereby avoiding pre-smolt competition for space and resources in freshwater habitats. For systems without substantial estuary habitat, juveniles may have evolved to exit freshwater later and at a larger, more uniform size, which would minimize marine predation risk. If estuaries enable expression and success of a greater diversity of migratory life-histories, the evolution of migration traits exhibited by juvenile salmon may therefore be influenced by the extent and quality of downstream estuary habitats.

Here, we examine population diversity in juvenile salmon migratory traits and potential linkages with rearing habitat characteristics, with a focus on coho salmon. Our study considers the full range of juvenile rearing habitats—from freshwater to estuarine—as potential drivers of juvenile trait diversity. Coho salmon are present in systems featuring a diversity of estuary habitat extents, configurations, and conditions. Specifically, we explored the extent to which juvenile coho salmon migration traits are correlated with metrics of estuary habitat quantity and quality, in addition to natal watershed characteristics such as latitude, elevation, lake influence, and catchment area. With respect to migration timing, we expected that migration would generally follow a latitudinal trend, with populations at higher latitudes exhibiting increasingly later and shorter migrations. However, we hypothesized that populations with access to extensive and high-quality estuary rearing habitat would migrate from freshwater on average earlier, and over a broader migration window, than those with access to smaller or poorer-quality estuary habitats (Table A.1). With respect to size, we expected that juveniles would migrate at a smaller mean size, and exhibit a broader range of sizes at migration, in systems featuring extensive and high-quality estuaries relative to those with smaller or more impacted estuaries. Understanding the diversity and distribution of migration traits exhibited by juvenile coho salmon could offer insights into the extent of local adaptation throughout the species' native range, and shed light on population sensitivities to anthropogenic change.

2.3. Methods

2.3.1. Juvenile coho salmon migration data

We assembled juvenile coho salmon migration data from 64 unique juvenile trap sites ranging from central California to southeast Alaska, spanning more than 20 degrees of latitude and representing 947 site-years of sampling (Figure 2.1; Table 2.1). Data were collected by federal, state, and local governments, First Nations and Tribes, not-for-profit organizations, universities, and industry groups. Minimum criteria for site inclusion were 1) availability of at least three years of juvenile migrant trap data, 2) daily or near-daily (e.g., excluding weekends) juvenile counts paired with individual size data collected across the migration window, and 3) little to no hatchery influence. Most data sets comprised only wild fish; however, some systems featured either historic or ongoing hatchery operations. In these cases, systems were included only if hatchery-origin juveniles were clearly marked and distinguishable from natural-origin juveniles, and only natural-origin juveniles were considered in analyses. Therefore, all juveniles in our study reared in the natural environment, but some may be progeny of hatchery strays. Most systems were sampled throughout the typical spring migration window, spanning approximately March through June; to maintain consistency, migration data collected after mid-August (Julian day 200) were excluded from analyses. Trap types varied between systems and included rotary screw traps, smolt fences, and full-river weirs, and as such censused either part or all of the downstream migration. Each unique trap site is hereafter referred to as a “population.” That said, we acknowledge that traps sited near the outlet of major rivers may sample metapopulations, while those sited near headwaters may sample partial populations.



Figure 2.1. Geographic location of juvenile coho salmon trap sites (n = 64).

2.3.2. Estimation of migration trait parameters

For each coho population in the study, migration timing was characterized by four parameters: peak migration date, the lower and upper quartiles of the migration window (hereafter “early migration date” and “late migration date,” respectively), and the interquartile range of the migration window (hereafter “migration duration”). Annual migration timing parameters were calculated for years in which at least 15 sampling dates occurred and 100 total fish were counted.

Peak migration date, early and late migration dates, and migration duration were determined using the methods of Wilson (2021), featuring comparison of four frequentist hierarchical state-space models using Template Model Builder (R package “salmix”). In brief, for each population log daily migration counts for each year were fit to four possible process models: 1) a symmetric normal distribution; 2) a symmetric Student-t distribution, which can accommodate more extreme tails than the normal distribution; 3) a double normal distribution that combines two truncated normal distributions, which share a common mean but can differ in variance; and 4) a double Student-t distribution that combines two truncated Student-t distributions, which share a common mean but can differ in variance and degrees of freedom (Wilson 2021). The latter two process models relax the assumption of normality and result in asymmetric distributions. For each population, log daily migration counts were fit to each of the four distributions and competed with AIC to determine the best-fit model for a given population. The global mean and variance were estimated as random effects. Models estimated annual peak migration date, as well as the early migration date (25th percentile), late migration date (75th percentile), and migration duration (difference between 25th and 75th percentiles). Best-fit model outputs were examined to determine goodness of fit. Where fit was poor, migration timing parameters were compared to parameters describing the cumulative migration of 25% (early), 50% (peak), and 75% (late) of juveniles past the trap. Where state-space model and cumulative model fits were similar, state-space model migration timing parameters were retained; where cumulative fits outperformed state-space model fits, cumulative migration timing parameters were retained. For a given population, annual timing parameters were averaged across sampling years to produce mean parameters used in statistical analyses.

For each coho population in the study, size at migration was characterized by the annual mean and standard deviation of body sizes (fork length) observed. Calculations focused on age-1+ juveniles; age-0 (fry) migrants were identified by age data or by visual inspection of size-at-time data and removed from the data set. Annual migration body size parameters were calculated for years in which timing parameters could be calculated, and at least 50 age-1+ individuals were measured (minimum 25 individuals measured before and after the peak migration date). To produce population-specific size parameters used in statistical analyses, mean body size was averaged across sampling years and standard deviation was weighted by annual sample size and averaged across sample years.

2.3.3. Estuary habitat spatial data

Each coho salmon population was associated with its recipient estuary; in several cases, more than one population in the study was associated with a given estuary. Estuary habitat quantity characteristics included estuary area, estuary shoreline length, and estuary area relative to the total area of the watershed. For estuaries in the United States, current estuary area and shoreline perimeter were calculated using data from the National Wetlands Inventory (NWI; U.S. Fish and Wildlife Service 2021) per methodology outlined in Brophy et al. (2019). In brief, estuary habitat polygons were created by subsetting NWI data for marine, estuarine, and riverine system types classified as subtidal or intertidal, in addition to palustrine system types classified as freshwater tidal. All habitats with diked modifiers were removed, and remaining habitats were dissolved into a single polygon representing each estuary. For estuaries in Canada, current estuary area and shoreline perimeter were derived from spatial data produced by the Pacific Estuary Conservation Program's Estuary Ranking Project (Pacific Estuary Conservation Program 2019). Where applicable, the seaward extent of Canadian estuaries was extended to 4 meters below mean lower low water for consistency with United States estuary data. For both data sets, estuary area was calculated as the area of the polygon (km²), and shoreline length was calculated as the perimeter of the polygon (km) that intersected land.

Estuary shape was characterized by three indices outlined in the estuary environment classification (EEC) framework developed by Hume et al. (2007). Shape indices included the estuary closure index, the estuary elongation index, and the

shoreline complexity index. The estuary closure index is a measure of the openness of the estuary mouth, calculated as the width of the estuary mouth divided by the length of the estuary shoreline. We subtracted this ratio from 1 to accommodate sites without estuaries; therefore, higher closure index values indicate estuaries with narrower mouths. The estuary elongation index is a measure of estuary elongation, calculated as the length of the estuary thalweg (from the upstream extent to the mouth) divided by the length of the estuary shoreline. Higher elongation index values indicate estuaries that are more elongate. With respect to the shoreline complexity index, we note that our metric differs slightly from that proposed in the EEC framework. Hume et al. (2007) calculated the shoreline complexity index as the waterbody's shoreline length divided by the circumference of a circle with the same area as that waterbody (equivalent to the shoreline development index commonly used in limnological applications). Here, we have multiplied this metric by an adjustment factor representing relative shoreline length, defined as the length of the estuary shoreline divided by the total perimeter of the estuary polygon (including the mouth). We made this adjustment because, unlike lake shorelines, estuary shorelines are non-contiguous—each estuary has a mouth that interrupts some proportion of its shoreline. By adjusting for relative shoreline length, our adjustment factor allows for comparisons of shoreline complexity across estuaries with varying mouth widths.

Estuary habitat quality was characterized by extent of 1) protected areas and 2) “natural” areas, defined as areas for which land use was not classified as urban or agricultural. Both habitat quality metrics were assessed within a 1- and 5-km buffer of the estuary polygon. Habitat quality data were obtained from the North American Environmental Atlas (Commission for Environmental Cooperation 2021). Protected areas were subset to include those falling under one of six protected categories defined by the International Union for the Conservation of Nature (IUCN), ranging from strictly protected areas with limited human access to protected areas managed for sustainable natural resource use. For each habitat quality metric of interest, we calculated the total area (km²) within each buffer classified as protected or natural, as well as the proportion of the buffer composed of protected or natural areas.

2.3.4. Watershed covariate spatial data

Watershed covariates of interest included trap latitude, migration distance, Strahler stream order, watershed area and elevation, and lake influence. For systems in the United States, watershed characteristics were calculated using data from the National Hydrography Dataset Plus High Resolution (NHDPlus; U.S. Geological Survey 2021). For systems in Canada, watershed characteristics were calculated using data from the British Columbia Freshwater Atlas (Province of British Columbia 2021). Juvenile trap coordinates were provided by each data holder. Migration distance to the estuary was calculated as the distance along the flowline between the juvenile migrant trap and its intersection with the estuary polygon. All watershed data were extracted using ESRI ArcMap and the Spatial Analyst toolset. For each trap site, we used 10 m raster data to delineate the upstream watershed, calculate its total area, and extract elevation parameters. Lake influence was determined by clipping NHDPlus waterbody data to each watershed and summing the total area of waterbodies that were 1) classified as “Lake,” “Reservoir,” or “Swamp,” and 2) intersected a flowline. Accessible lake habitat was determined by subsetting this layer for lakes that were not located upstream of a fish passage barrier (e.g., impassable dam or known natural barrier).

Table 2.1. Geographic details, trap coordinates, number of years sampled, and data holders associated with each juvenile coho salmon study population (n = 64).

Population	Estuary	State or Province	Trap Latitude	Trap Longitude	Data Range	Years Timing (n)	Years Size (n)	Data Holder
Berners	Berners Bay	AK	58.87	-134.99	2008-2020	11	5	ADFG
Hugh Smith	Boca de Quadra	AK	55.10	-130.71	2000-2020	19	15	ADFG
Kitwanga	Skeena River Complex	BC	55.32	-128.10	2016-2020	5	4	Gitanyow Fisheries Authority
Ksi Ts'oohl Tsap	Nass River Complex	BC	55.17	-129.27	2010-2019	10	10	Nisga'a JFMC
Deena	Deena River	BC	53.14	-132.14	1994-2018	21	16	Council of the Haida Nation
West Arm	West Arm	BC	53.14	-128.98	2001-2008	8	7	DFO
Koeye	Koeye River	BC	51.77	-127.81	2014-2019	6	5	Wild Salmon Center
Keogh	Keogh River	BC	50.67	-127.35	1981-2015	35	10	DFO
Black	Black Creek	BC	49.85	-125.10	1996-2020	25	17	DFO
Myrtle	N/A*	BC	49.79	-124.48	2000-2013	13	8	DFO
Whittall	Whittall Creek	BC	49.78	-124.35	2000-2003	4	4	DFO
Morrison	Courtenay River	BC	49.69	-125.01	2002-2009	8	6	DFO
Waterloo	Mud Bay/Waterloo Creek Complex	BC	49.47	-124.79	2002-2010	9	5	DFO
Mud Bay	Mud Bay/Waterloo Creek Complex	BC	49.47	-124.79	2011-2020	10	5	DFO
Carnation	Carnation Creek	BC	48.91	-125.00	1982-2015	34	12	DFO
Skagit	Skagit Bay	WA	48.44	-122.34	1990-2019	30	15	WDFW
Stillaguamish	Stillaguamish River	WA	48.21	-122.27	2001-2017	13	13	Stillaguamish Tribe
Deep	N/A*	WA	48.17	-124.03	2012-2019	8	3	Lower Elwha Klallam Tribe, NOAA
West Twin	N/A*	WA	48.16	-123.95	2012-2019	8	2	Lower Elwha Klallam Tribe, NOAA

Population	Estuary	State or Province	Trap Latitude	Trap Longitude	Data Range	Years Timing (n)	Years Size (n)	Data Holder
East Twin	East Twin River	WA	48.16	-123.94	2012-2019	8	1	Lower Elwha Klallam Tribe, NOAA
Dungeness	Dungeness Bay	WA	48.15	-123.13	2006-2019	14	13	WDFW
Elwha	Elwha River	WA	48.11	-123.55	2005-2019	7	2	Lower Elwha Klallam Tribe, NOAA
Indian	Elwha River	WA	48.07	-123.58	2013-2019	7	4	Lower Elwha Klallam Tribe, NOAA
Bear	Salmon Bay	WA	47.67	-122.11	1999-2019	20	18	WDFW
Little Anderson	Anderson Creek	WA	47.66	-122.76	1992-2019	24	15	WDFW
Duckabush	Duckabush River	WA	47.66	-122.94	2013-2019	6	6	WDFW
Big Beef	Big Beef Creek	WA	47.65	-122.78	1978-2019	42	16	WDFW
Seabeck	Seabeck Bay	WA	47.64	-122.83	1993-2019	27	16	WDFW
Stavis	Stavis Bay	WA	47.62	-122.87	1993-2019	27	16	WDFW
Cedar	Salmon Bay	WA	47.48	-122.20	2000-2019	20	16	WDFW
Green	Duwamish River	WA	47.29	-122.17	2006-2020	12	11	WDFW
White	Puyallup River	WA	47.24	-122.24	2016-2019	4	4	Puyallup Tribe
Bingham	Grays Harbor	WA	47.15	-123.40	1982-2016	35	15	WDFW
Nisqually	Nisqually River	WA	46.97	-122.63	2009-2019	11	11	WDFW
Germany	Columbia River (A-D)	WA	46.20	-123.12	2001-2020	20	20	WDFW
Abernathy	Columbia River (A-D)	WA	46.20	-123.17	2001-2020	20	19	WDFW
Mill	Columbia River (A-D)	WA	46.19	-123.18	2001-2020	20	20	WDFW
Scappoose NF	Columbia River (A-F)	OR	45.80	-122.93	1999-2019	18	18	ODFW
Nehalem NF	Nehalem River	OR	45.81	-123.74	1998-2017	20	20	ODFW
Wilson Lower NF	Tillamook Bay	OR	45.48	-123.74	1998-2013	14	13	ODFW
Trask EF	Tillamook Bay	OR	45.42	-123.60	2005-2016	12	12	ODFW
Salmon	Salmon River	OR	45.02	-123.94	2008-2016	8	8	ODFW
Mill	Siletz Bay	OR	44.74	-123.79	1997-2019	23	23	ODFW

Population	Estuary	State or Province	Trap Latitude	Trap Longitude	Data Range	Years Timing (n)	Years Size (n)	Data Holder
Mill	Yaquina Bay	OR	44.57	-123.91	1997-2019	22	22	ODFW
Cascade	Alsea Bay	OR	44.32	-123.85	1998-2019	21	21	ODFW
Lobster EF	Alsea Bay	OR	44.25	-123.64	1988-2019	32	32	ODFW
Lobster Upper MS	Alsea Bay	OR	44.25	-123.64	1988-2019	30	30	ODFW
Smith WF	Umpqua River	OR	43.81	-123.77	1998-2019	22	22	ODFW
Winchester	Coos Bay	OR	43.28	-124.32	1999-2019	19	19	ODFW
Mill	Smith River	CA	41.78	-124.10	2014-2018	5	5	CDFW
Prairie	Redwood Creek	CA	41.30	-124.05	2011-2020	9	9	CA Coop. Fish and Wildlife Research Unit
Little Lower SF	Little River	CA	41.03	-124.02	1999-2020	21	20	Green Diamond
Little Upper SF	Little River	CA	41.03	-124.00	2000-2020	13	13	Green Diamond
Carson	Little River	CA	41.01	-124.06	2000-2020	17	17	Green Diamond
Little MS	Little River	CA	41.01	-124.08	2015-2020	6	6	Green Diamond
Freshwater	Humboldt Bay	CA	40.78	-124.08	2010-2020	11	11	CA Coop. Fish and Wildlife Research Unit
Ryan	Humboldt Bay	CA	40.76	-124.13	2004-2014	11	11	Green Diamond
Noyo SF	Noyo River	CA	39.42	-123.73	2007-2019	12	12	CDFW
Caspar	Caspar Creek	CA	39.36	-123.82	2008-2020	12	12	CDFW
Little	Little River	CA	39.27	-123.79	2006-2017	9	8	CDFW
Mill	Russian River	CA	38.58	-122.88	2012-2017	4	4	Sonoma Water
Dutch Bill	Russian River	CA	38.47	-123.01	2013-2020	4	4	Sonoma Water
Willow	Russian River	CA	38.43	-123.07	2014-2018	3	3	Sonoma Water
Lagunitas	Tomales Bay	CA	38.08	-122.78	2010-2019	10	10	Marin Municipal Water District

* N/A indicates where there is no estuary habitat available to a given population.

2.3.5. Statistical analyses

We used partial least-squares regression to examine correlations between juvenile coho salmon migration traits, estuary habitat characteristics, and watershed covariates. Partial least-squares regression is a supervised dimension-reduction technique, whereby multivariate predictor data are decomposed into latent variables (“components”) that best explain variation in a response variable. The first component is constructed to describe maximum covariance between the predictor data and the response variable, and each subsequent component is fit to the residuals of the prior component. As a result, components are fit to orthogonalized data and are uncorrelated with one another (Hastie et al. 2021). Partial least-squares regression is particularly well suited to analysis of data sets with multicollinearity amongst predictor variables and a high number of predictor variables relative to the number of response observations (Carrascal et al. 2009; Scott and Crone 2021; Figure 2.2).

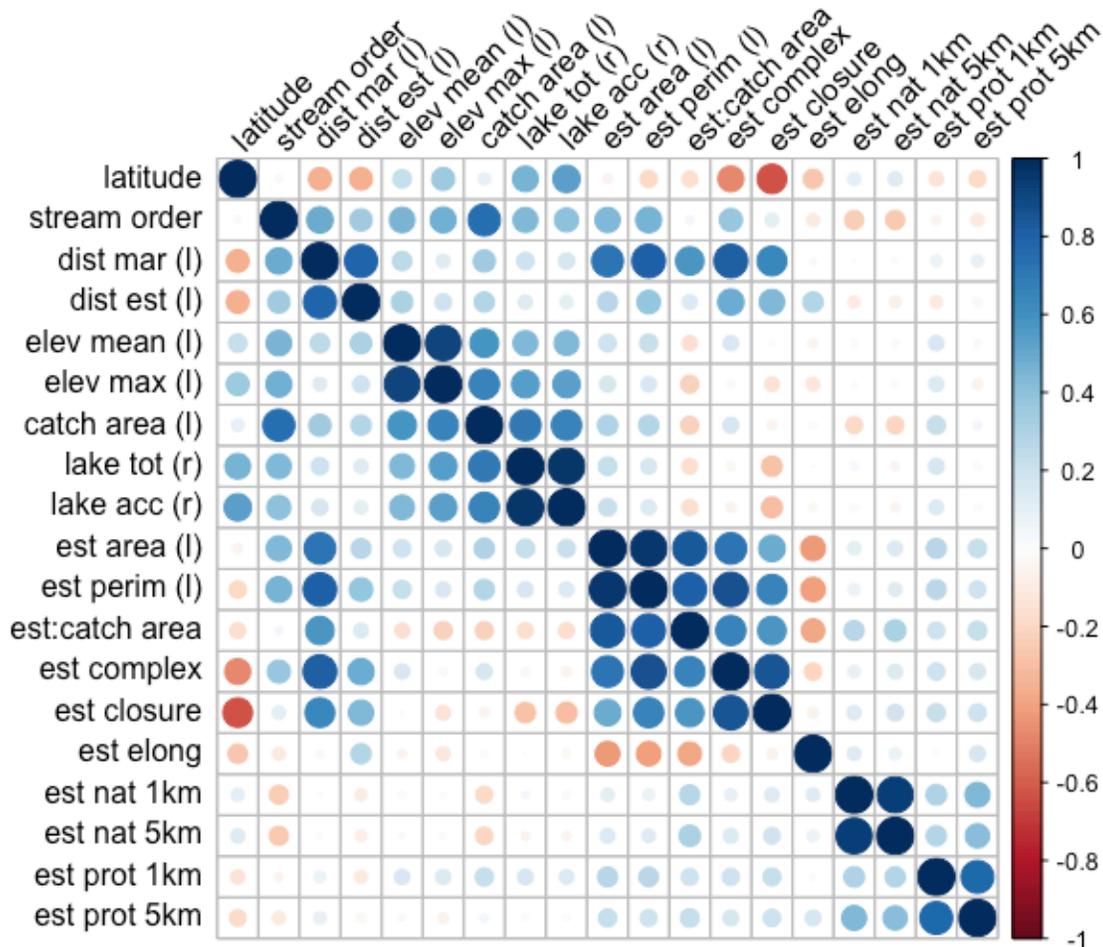


Figure 2.2. Correlation plot for all candidate predictor variables considered in partial least-squares regression models.

Note: Blue circles indicate a positive correlation and red circles indicate a negative correlation; the strength of the correlation is indicated by the size of the circle. Predictor variables with absolute correlation coefficients > 0.7 are generally sufficiently correlated to impact model performance within a traditional regression framework (Dormann et al. 2013). Abbreviations for watershed and estuary predictor variables are as follows. Latitude: trap latitude in decimal degrees; stream order: Strahler stream order; dist mar (l): migration distance from the trap site to the ocean (km; log-transformed); dist est (l): migration distance from the trap site to the upstream extent of the estuary (km; log-transformed); elev mean (l): mean catchment elevation (m; log-transformed); elev max (l): maximum catchment elevation (m; log-transformed); catch area (l): total catchment area (km²; log-transformed); lake tot (r): aggregate surface area of lakes in catchment (km²; fourth-root transformed); lake acc (r): aggregate surface area of accessible lakes in catchment (km², fourth-root transformed); est area (l): total surface area of estuary (km²; log-transformed); est perim (l): total perimeter of estuary shoreline excluding mouth (km, log-transformed); est:catch area: ratio of estuary area to catchment area; est complex: estuary complexity index; est closure: estuary closure index; est elong: estuary elongation index; est nat 1km: proportion of land within 1-kilometre buffer of the estuary not designated as urban or agricultural; est nat 5km: proportion of land within 5-kilometre buffer of the estuary not designated as urban or agricultural; est prot 1km: proportion of protected land within 1-kilometre buffer of the estuary; est prot 5km: proportion of protected land within 5-kilometre buffer of the estuary.

Several of the coho salmon populations in our study encounter the same recipient estuary *en route* to the ocean. To avoid pseudoreplication of estuary habitat data, we determined the number of unique estuaries in our data set ($n = 49$) and used random sampling to create a set of non-pseudoreplicated data subsets that featured only one population per estuary. We created 108 data subsets in total, in order to achieve > 100 replicates and to ensure that each population that shared a given estuary was replicated with equal frequency across data subsets. Non-normally distributed predictor variables were either log-transformed (migration distance, elevation, catchment area, estuary area, and estuary perimeter variables) or fourth-root transformed (lake influence variables). All predictor data were iteratively scaled and centred in the course of model cross-validation.

Partial least-squares regression analyses were performed using *p/s* function in the package “mdatools” in R (Kucheryavskiy 2020). For each migration timing and size response variable, a preliminary round of partial least-squares regression was performed on each of the 108 non-pseudoreplicated data subsets. Preliminary models were “pruned” to remove any candidate predictors which had variable influence on projection (VIP) scores < 0.8 , indicating low influence on the response variable. Pruned models were subsequently rerun to determine the optimal number of components. Selection of the proper number of predictive components is a crucial step in partial least-squares regression, and lessens the likelihood of model overfitting or underfitting (Wold et al. 2001). The optimal number of components for each response variable was selected via the randomization test method described by Wiklund et al. (2007), using 1000 permutations. Preliminary model outputs from all data subsets were examined to determine the number of optimal components occurring most frequently, and to identify any populations that were consistently detected as outliers. A second round of partial least-squares regression was then performed for each data subset to establish final models, forcing adoption of the optimal number of components. Final models were fit using the SIMPLS algorithm and leave-one-out cross validation, and regression coefficient confidence intervals were calculated using the jackknife method—default settings in the “mdatools” package.

Key partial least-squares regression model outputs include component loadings, regression coefficients, and selectivity ratios. For each significant component, loadings describe the covariance between constituent predictor variables and the response

variable (Wold et al. 2001). Loadings are commonly depicted in a biplot format featuring the first two components as x- and y-axes, the position of each predicted response relative to the scaled and centred mean (represented by the biplot origin), and the magnitude and directionality of correlations between the response and each predictor (represented by vectors). Here, reported loadings were derived by averaging the model outputs of 108 non-pseudoreplicated data subsets. Where the best-fit model included only a single predictive component, we have reported results associated with the single-component model but depicted loadings using the two-component biplot format for consistency across response variables. For a given predictor, regression coefficients represent the combined weight of that predictor along each significant component, weighted by the contribution of the component to the best-fit model. Regression coefficients in a partial least-squares regression model are analogous to regression coefficients in a multiple linear regression model; however, we note that partial least-squares regression coefficients are not independent from one another unless the number of significant components is equal to the number of predictor variables (Wold et al. 2001). Here, reported regression coefficients and 95% confidence intervals were derived by averaging model outputs of the 108 data subsets. Finally, selectivity ratios are used to identify the most influential predictor variables in a partial least-squares regression model. For a given predictor, the selectivity ratio is defined as the variance explained by that predictor divided by its residual (unexplained) variance. This approach diminishes the influence of predictor variables with high variance but low covariance with the response variable, and elevates the influence of those with low variance but high covariance with the response variable (Kvalheim 2010).

2.4. Results

2.4.1. Trends in migration traits

The 64 coho salmon populations in our study spanned more than 20 degrees of latitude and represented 947 site-years of sampling. There was considerable variation in migration timing across populations. The earliest population migrated 10 weeks earlier than the latest population, with mean peak migration dates that ranged from 3 April to 11 June (Julian day 93-162). There was also substantial variation in the duration of the migration window, with some populations exhibiting constricted migrations lasting just

one week while others migrated over a period spanning more than 9 weeks. Specifically, migration duration ranged from 7 to 65 days (Figure 2.3a). Mean peak migration date was negatively correlated with mean migration duration ($R^2 = 0.35$). Across populations, standard deviation about the mean migration date ranged from 0.3-15.7 days, and standard deviation about migration duration ranged from 5.2-18.6 days (Figure A.1). For a majority of populations, the best-fit migration timing model was asymmetric with either Student t-tails ($n = 44$) or normal tails ($n = 2$). The lower quartile of the migration window (early to peak migration date) was of longer duration than the upper quartile for approximately half of the populations (peak to late migration date; $n = 33$ of 64); however, approximately one quarter of populations exhibited the opposite trend ($n = 13$ of 64). For most remaining populations, migration timing was best characterized by a symmetric model with t-tails ($n = 16$ of 64), indicating that the migration window was equally distributed about the peak migration date. Migration timing parameters for two populations—Washington’s Duckabush River and the Mill Creek tributary to California’s Russian River—were fit with a cumulative distribution due to poor state-space model fit.

Study populations also exhibited considerable variation in body size at migration. The largest-bodied coho salmon populations were more than 50% larger than the smallest-bodied populations at the time of downstream migration. Population-specific mean body size at migration ranged from 86 to 134 mm, with mean standard deviation (weighted by annual number of measurement observations) ranging from 7 to 25 mm (Figure 2.3b). We note that reported size means and standard deviations represent age-1 (and where present, age-2) juveniles, but exclude age-0 juveniles (fry) as they were not consistently measured across all populations.

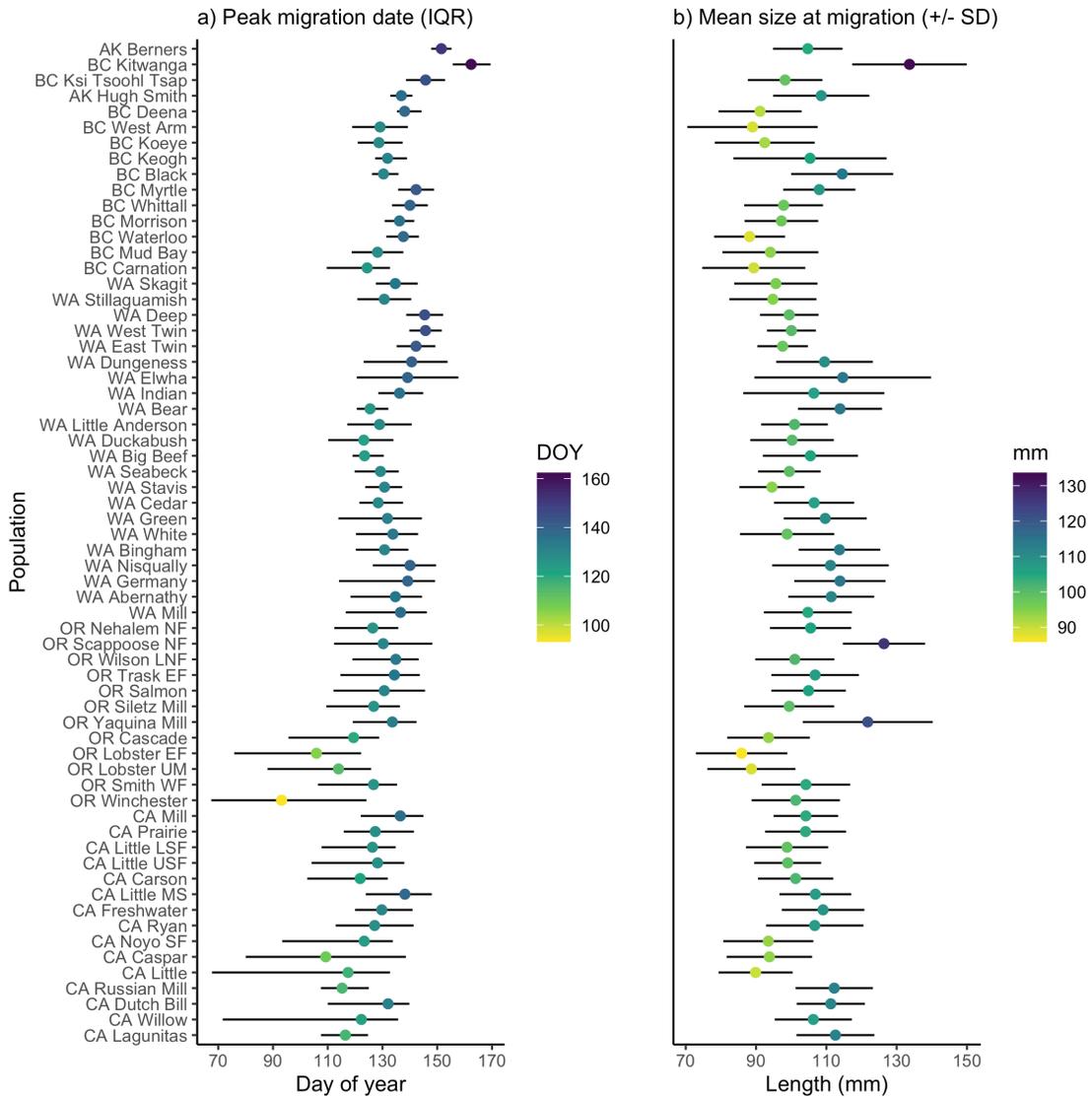


Figure 2.3. Migration timing (peak and interquartile range; panel a) and body size at migration (mean and standard deviation; panel b) for each population included in the study.

Note: Data points represent means across sampling years. Earlier migration timing and smaller size at migration are represented by lighter points; later migration timing and larger size at migration are represented by darker points. Populations arranged by trap latitude (north to south).

2.4.2. Migration timing

The early migration date (date that an estimated 25% of juvenile coho salmon had migrated) was best described by a two-component partial least-squares regression model, which described nearly 60% of observed variation. The first component described 48% of variation ($R^2_Y = 0.48$, $pR^2_Y < 0.001$), while the second component

described an additional 10% ($R^2_Y = 0.10$, $pR^2_Y = 0.02$; Figure 2.4a). Best-fit models for all 108 non-pseudoreplicated data subsets included eight predictors on both component axes: latitude, catchment area, mean and maximum elevation, total and accessible lake habitat, estuary closure, and estuary shoreline complexity. Of these, latitude had the largest effect, with populations situated at higher latitudes initiating migration significantly later in the year ($\beta = 0.41$, 95% CI = 0.25-0.57). Juvenile salmon migrated significantly earlier where estuaries were more enclosed ($\beta = -0.24$, -0.34--0.15) and featured more complex shorelines ($\beta = -0.20$, -0.37--0.04). Total and accessible lake habitat had a positive effect on the early migration date ($\beta = 0.07$, 0.00-0.14; $\beta = 0.10$, 0.02-0.18), as did maximum catchment elevation ($\beta = 0.09$, 0.00-0.18). Selectivity ratios revealed that latitude had the strongest influence on the early migration date (median selectivity ratio = 2.61), followed by estuary closure (median SR = 0.63), estuary complexity (median SR = 0.56), and accessible lake habitat (median SR = 0.50; Figure A.2a).

For peak migration date, the best-fit partial least-squares regression model featured two predictive components, which together described nearly 50% of observed variation in peak migration date. The first component described nearly 40% of observed variation ($R^2_Y = 0.39$, $pR^2_Y < 0.001$), while the second component described an additional 10% of variation ($R^2_Y = 0.10$, $pR^2_Y = 0.04$; Figure 2.4b). All 108 best-fit models included the same eight predictors on both component axes: latitude, mean and maximum elevation, catchment area, total and accessible lake habitat, estuary openness, and shoreline complexity. Latitude was again the strongest predictor, with populations situated at higher latitudes exhibiting significantly later peak migration dates ($\beta = 0.37$, 0.14-0.60). Estuary closure was the second strongest predictor of peak migration date and also had a significant negative effect, with populations encountering more enclosed estuaries exhibiting earlier peak migration dates ($\beta = -0.20$, -0.33--0.07). Peak migration date was also negatively correlated with estuary shoreline complexity, though this correlation was marginally non-significant ($\beta = -0.18$, -0.41-0.05). Mean and maximum elevation had smaller positive effects on peak migration dates ($\beta = 0.15$, 0.01-0.29; $\beta = 0.15$, 0.06-0.25), though the effect of mean elevation was marginally non-significant. The effects of catchment area and lake influence variables were non-significant. Selectivity ratios revealed that latitude had the strongest influence on peak migration date (median SR = 2.38), followed by estuary closure (median SR = 0.48), and estuary complexity (median SR = 0.44; Figure A.2b). The predicted peak migration date

for juveniles with access to the most complex and enclosed estuaries was 13.5 days earlier than that predicted for juveniles with access to the least complex and enclosed estuaries (represented by the 95th and 5th percentile of estuary complexity and closure metrics, respectively, with all other predictor variables held at their mean; Figure 2.5a).

The late migration date (date that an estimated 75% of juvenile coho salmon had migrated) was best described by a single-component partial least-squares regression model, which described 34% of observed variation ($R^2_Y = 0.34$, $pR^2_Y < 0.001$; Figure 2.4c). Nine predictors were included in all 108 best-fit models: latitude, mean and maximum elevation, catchment area, total and accessible lake habitat, estuary closure, estuary elongation, and the proportion of “natural” habitat within a 5 km estuary buffer. Of these, latitude again had the largest effect, with populations situated at higher latitudes exhibiting migrations that extended significantly later into the year ($\beta = 0.16$, 0.08-0.23). Mean and maximum catchment elevation also had a positive effect on the late migration date ($\beta = 0.14$, 0.08-0.21; $\beta = 0.13$, 0.08-0.19), as did total and accessible lake influence and catchment area ($\beta = 0.07$, 0.00-0.13; $\beta = 0.09$, 0.03-0.15, $\beta = 0.07$, 0.02-0.11). Populations exhibited earlier late migration dates where estuaries were more enclosed and elongate ($\beta = -0.09$, -0.18-0.01; $\beta = 0.08$, -0.17-0.02) and featured a greater proportion of “natural” habitat ($\beta = -0.08$, -0.20-0.03); however, all estuary parameters were marginally non-significant. Selectivity ratios revealed that maximum watershed elevation had the strongest influence on the late migration date (median SR = 2.34), followed by mean watershed elevation, accessible lake habitat, total lake habitat, and catchment area (median SR = 1.77, 1.67, 1.39, and 1.15, respectively). Latitude had moderate influence on the late migration date (median SR = 0.61), while influence of estuary characteristics was comparatively low (median SR < 0.20; Figure A.2c).

2.4.3. Migration duration

With respect to migration duration (number of days between early and late migration dates), low-latitude populations with low lake influence, and those with access to more enclosed and complex estuaries, tended to migrate over a broader range of dates. Partial least-squares regression resulted in a model with a single significant predictive component, which described 47% of observed variation in the interquartile range of migration timing ($R^2_Y = 0.47$, $pR^2_Y < 0.001$; Figure 2.4d). Five predictors were included in all best-fit models: latitude, total and accessible lake area, estuary shoreline

complexity, and estuary closure. Latitude had a strong negative effect on migration duration, with populations at high latitudes exhibiting significantly shorter migration windows ($\beta = -0.31, -0.41--0.21$). Migration duration was positively correlated with estuary shoreline complexity ($\beta = 0.18, 0.03-0.33$) and estuary closure ($\beta = 0.19, 0.12-0.25$). Populations from watersheds with greater total and accessible lake influence also exhibited significantly narrower migration windows ($\beta = -0.17, -0.22--0.11$; $\beta = -0.17, -0.23--0.11$). Selectivity ratios revealed that latitude had the strongest influence on migration duration (median SR = 1.98), whereas total and accessible lake habitat each had a moderate influence (median SR = 0.74 and 1.02, respectively). Estuary shoreline complexity and degree of closure also had a moderate influence on migration duration (median SR = 0.46 for both variables; Figure A.2d). The predicted duration of migration for juveniles with access to the most complex and enclosed estuaries was nearly 16 days longer than that predicted for juveniles with access to the least complex and enclosed estuaries (95th and 5th percentile of estuary complexity and closure metrics, respectively; Figure 2.5b).

2.4.4. Body size at migration

The first predictive axis was non-significant ($pR^2_{\gamma} > 0.05$) for both mean size at migration and standard deviation of size at migration. Accordingly, partial least-squares regression models did not outperform the null model. Counter to our predictions, and despite widespread apparent variation in juvenile body size at migration across populations, juvenile body size was not significantly correlated with any of the estuary habitat characteristics (area, perimeter, configuration, habitat quality) or watershed covariates (latitude, catchment area, elevation, lake influence) included in our analyses.

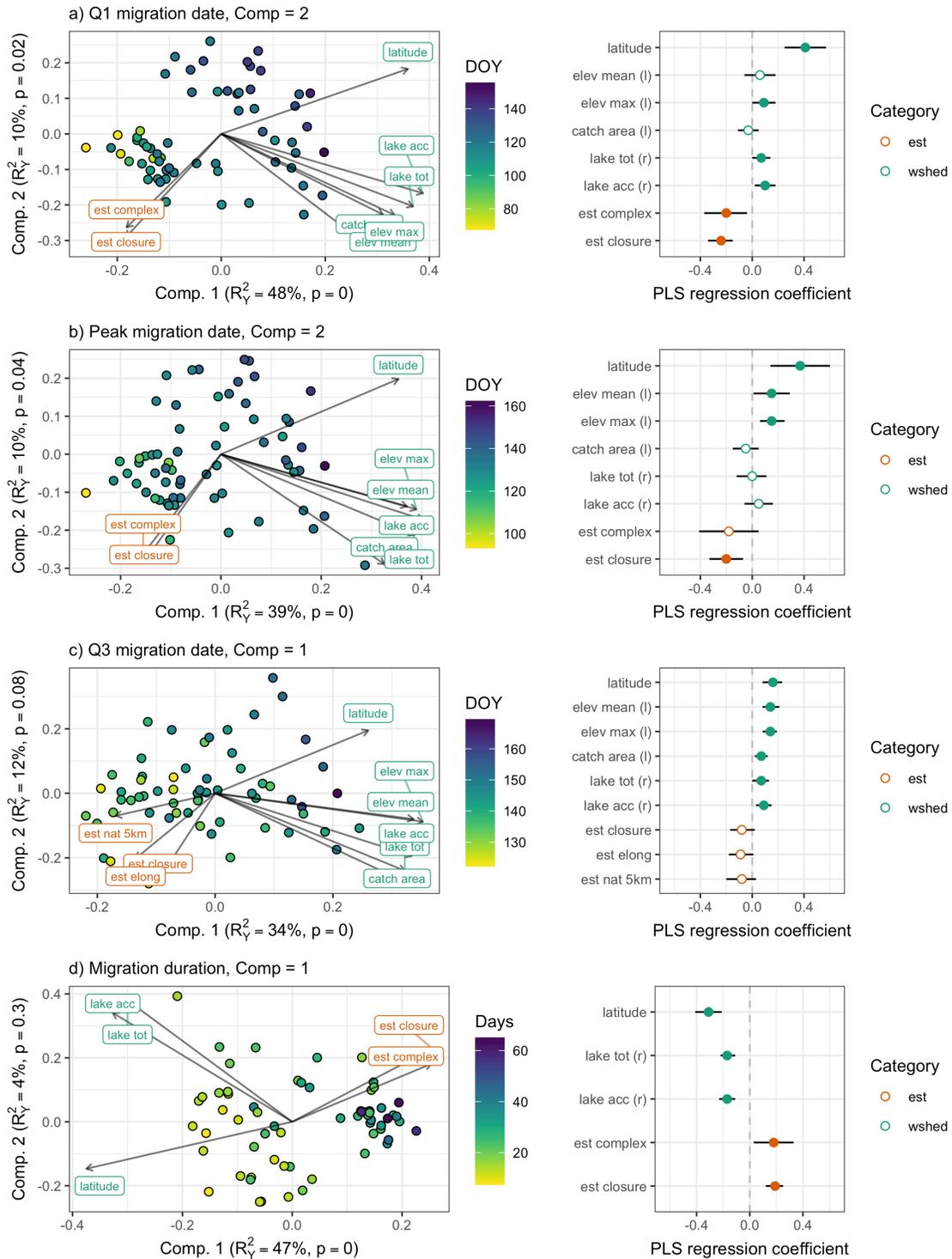


Figure 2.4. Partial least-squares regression biplots and associated regression coefficients for a) early migration date (25th percentile), b) peak migration date, c) late migration date (75th percentile), and d) migration duration (interquartile range).

Note: For late migration date (panel c) and migration duration (panel d), the second PLS component was not statistically significant and has been included for plotting purposes only.

Regression coefficients describe the contribution of each scaled and centred predictor variable to the response variable, weighted by the respective weight of each significant component axis. For regression coefficient plots, points indicate regression coefficients for watershed (teal) and estuary (orange) predictors. Black lines indicate 95% confidence intervals. Solid points indicate predictors that were significant at the 95% confidence level; open points indicate predictors whose 95% confidence intervals span zero. Alongside each biplot title, “Comp” indicates the number of significant components associated with the given response variable.

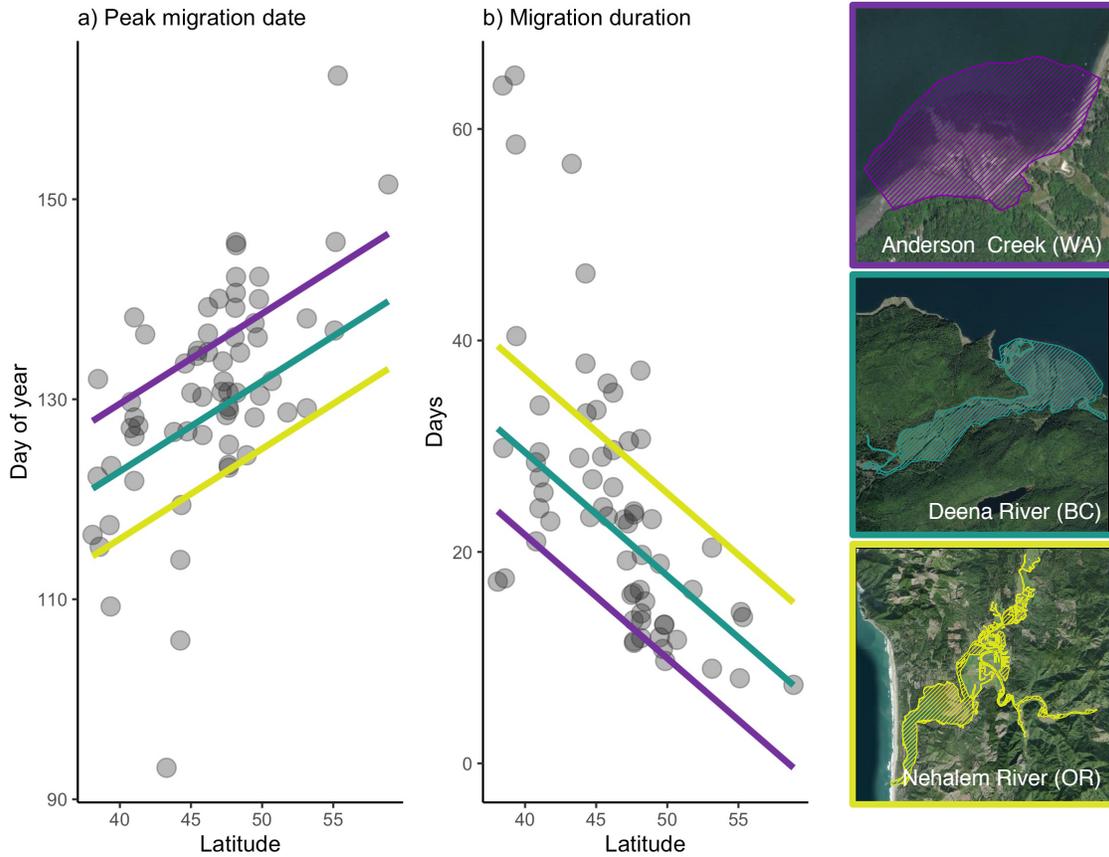


Figure 2.5. Comparison of observed data and partial least-squares model predictions for a) peak migration date and b) migration duration.

Note: Grey points represent observed migration timing and duration data for each site included in the study. Lines represent model predictions as a function of latitude and varying degrees of estuary closure and complexity (purple = 5th percentile, blue = 50th percentile, yellow = 95th percentile), with all other predictor variables held at their mean. Righthand panel images depict study estuaries whose configurations best approximate the 10th (Anderson Creek estuary, WA), 50th (Deena River estuary, BC), and 90th (Nehalem River estuary, OR) percentiles of estuary closure and complexity. True estuary closure and complexity percentiles for these study estuaries are as follows: Anderson Creek: closure = 0.0, complexity = 0.02; Deena River: closure = 0.70, complexity = 0.15; Nehalem River: closure = 1.0, complexity = 0.89.

2.5. Discussion

Our study demonstrates that coho salmon exhibit diverse juvenile migration traits across populations, which vary with estuary habitat configuration and latitudinal clines in marine and freshwater processes. Populations with access to more complex, more enclosed estuaries exhibited earlier juvenile migrations that occurred over a broader timeframe. In addition to estuary characteristics, our findings build on past research (e.g., Sandercock 1991; Pearcy 1992; Spence and Hall 2010) identifying latitude and elevation as key drivers of variation in juvenile coho salmon migration traits. Migration timing was generally positively correlated with latitude and elevation, while migration duration was negatively correlated with both variables. We also found that populations with greater lake access exhibited later and shorter migrations. Broadly, these findings showcase underappreciated dimensions of local adaptation in salmon watersheds—namely, adaptation to estuary habitat characteristics. This lends support to the notion that migratory life-histories reflect adaptation not only to current habitats (for juvenile salmon, freshwater rearing habitats), but also to future habitats (i.e., estuarine and marine habitats), thus adding to our understanding of controls on salmonid migration traits.

Both the timing and duration of juvenile salmon migrations were influenced by estuary habitat configuration—specifically, shoreline complexity and degree of enclosure. Estuary habitat configuration is influenced by the relative balance of river and ocean influence, in combination with basin morphometry (Hume et al. 2007). These factors interact to structure the estuary seascape, including physical characteristics such as temperature, salinity and turbidity and biological characteristics such as zooplankton assemblages. Across response variables, juvenile salmon migration timing was consistently influenced by degree of estuary enclosure. Where estuaries featured a high degree of enclosure (i.e., a narrow mouth relative to shoreline perimeter), juvenile migrations tended to be earlier and more protracted, while those that encountered more open estuaries exhibited later seaward migrations of shorter duration. Estuary complexity was another key driver of variation in migration timing traits. Populations with access to more complex (i.e., less circular) estuary shorelines tended to migrations that occurred earlier in the year, and unfolded over a longer period relative to those that encountered estuaries with simpler shorelines. For juvenile coho salmon with access to

maximally enclosed and complex estuaries, model predictions indicate that the migration window will last more than two weeks longer, and peak nearly two weeks earlier, than for populations with access to comparatively open and simple estuaries (Figure 2.5). Given that migration between freshwater and estuarine habitats likely reflects a trade-off between growth opportunity and mortality risk (Werner and Gilliam 1984, Quinn et al. 2009, Satterthwaite et al. 2012), early migration to complex, relatively enclosed estuaries may reflect their inherent value as nursery habitats. For juvenile salmon, estuary nurseries are defined by their ability to provision prey, offer refuge from predators and other environmental stressors, and serve as a physiological transition zone from freshwater to saltwater (Simenstad et al. 1982, Thorpe 1994). In a study comparing physical and biological characteristics associated with various estuary configurations, Lucena-Moya and Duggan (2017) reported that highly complex, enclosed estuaries featured salinity profiles and zooplankton assemblages similar to those found in the nearshore marine environment. Comparatively, simpler riverine estuaries more closely reflected the salinity and zooplankton characteristics of freshwater habitats. Early migrations to complex, enclosed estuaries may therefore reflect the improved foraging and growth opportunities in nursery habitats replete with marine-derived prey. While few studies specifically compare juvenile salmon predation risk in estuaries relative to freshwaters (but see Seitz et al. 2020), structurally complex shorelines could also offer improved predator refugia (Simenstad and Cordell 2000) and high estuary growth rates may enable juveniles to quickly outgrow certain predators, including piscivorous fishes (Koski 2009).

While juvenile coho salmon migration timing and duration were significantly influenced by estuary shape metrics, latitude was the strongest predictor of migration timing traits. Consistent with previous research (e.g., Pearcy 1992, Spence and Hall 2010), more northerly salmon populations exhibited later juvenile migrations that occurred over a narrower timeframe (Figure 2.5). For coho salmon populations in northern British Columbia and southeast Alaska—the northernmost in our study—mean peak migration occurred between 16 May and 11 June and spanned a relatively narrow window of 7-14 days. Comparatively, central and northern California populations—the southernmost in our study—migrated 4-8 weeks earlier and over a longer timeframe, with peak migrations occurring between 19 April and 12 May and lasting 17-65 days. Our findings of latitudinal clines in migration timing and duration closely mirror those

reported by Spence and Hall (2010), who propose that these trends reflect local adaptations to “windows of opportunity” in the coastal marine zone. Broadly, the timing and magnitude of coastal primary productivity along the North American continental shelf are shaped by interactions between physical ocean processes affecting nutrient availability, coastal physiography, and freshwater inputs into the coastal zone (Gargett 1997). Timing and variability in coastal productivity varies along a latitude gradient. Primary productivity in the Northern California Current, which extends from Baja California to Northern Vancouver Island, is highly variable (February-June) and driven by nutrient-replenishing upwelling events. By comparison, primary productivity in the Alaskan Current, which circulates north of Haida Gwaii and in the Gulf of Alaska, is light-limited and therefore peaks relatively predictably in accordance with lengthening photoperiod (May-June; Gargett 1997). By extension, the earlier, protracted migrations exhibited by southerly coho salmon populations likely reflect adaptation to optimal marine conditions that occur earlier in the spring and are interannually variable, while the later, constricted migrations of northerly populations reflect optimal marine conditions that occur later and are more predictable. Migration timing windows are likely further constrained by latitudinal clines in freshwater habitat processes, such as seasonal drying of ephemeral streams in southerly regions and the timing of ice-off in northern lakes and rivers (Spence and Hall 2010, Carr-Harris et al. 2018).

Relative to latitude, catchment elevation and lake influence generally had smaller, though directionally similar effects on migration timing, such that juvenile salmon from higher-elevation watersheds and with greater lake access exhibited later and shorter migrations. We note that latitude, catchment elevation, and lake influence variables were moderately to highly collinear across populations in our study (Figure 2.2). However, the relative effect of latitude decreased as the migration window progressed, while the influence of catchment elevation and lake influence simultaneously increased such that these factors had a dominant effect on the late migration date. Together, these trends suggest the influence of catchment-related dynamics that cue juvenile salmon migration decisions (e.g., photoperiod, stream flow, and temperature conditions), although the mechanisms underlying these relationships are likely context-specific (Spence and Dick 2014). For example, the timing of seaward migration by higher-latitude, higher-elevation populations with access to ample lake rearing habitat could be delayed by spring ice-off, as inferred for lake-rearing sockeye

salmon (*O. nerka*, Carr-Harris et al. 2018; Quinn 2018). Alternatively, where lake-rearing habitats are highly productive, juvenile coho salmon may delay downstream migration as a means of maximizing the freshwater rearing period, toward increasing body size prior to ocean entry. Such a scenario could indicate growth-mortality trade-offs between lacustrine and estuarine rearing habitats, whereby the value of an extended lake rearing period outweighs the potential growth benefits (and mortality risks) associated with early migration to the estuary.

Interestingly, we did not find substantial linkages between migration traits and either absolute estuary size or estuary habitat quality. This finding runs counter to our hypothesis that systems with more and higher quality estuary habitat may feature earlier and more extended juvenile migrations. Recent research suggests that productivity scales with estuary size, such that smaller estuaries tend to be more productive per unit size than larger estuaries (Nidzieko 2018). If superior foraging opportunities are indeed a driver of earlier migrations, then perhaps bigger is not necessarily better when it comes to the estuarine prey landscape. We also note that metrics of estuary habitat quality generally did not influence migration timing traits. One exception was the late migration date, whereby juvenile salmon tended to migrate earlier when estuaries featured a higher proportion of “natural” (non-urban or agricultural) habitat; that said, this effect was slight. Although tangential to juvenile migration timing, previous research suggests a positive relationship between estuary habitat quality and marine survival rates. For example, Magnusson and Hilborn (2003) reported increased marine survival for Chinook and coho salmon that transited estuaries with a high proportion of “pristine” habitat. Similarly, populations of Puget Sound Chinook salmon rearing in less chemically-contaminated estuaries exhibited higher smolt-to-adult survival rates; however, a similar effect was not observed for coho salmon (Meador 2014). Estuaries are subject to diverse terrestrial and aquatic stressors that may impair nursery function (Hodgson et al. 2020), and the terrestrial-based metrics considered by our study may not fully capture the degree of current impact across diverse estuaries (e.g., to water quality or aquatic vegetation).

Contrary to our hypotheses, our analyses did not reveal correlations between juvenile coho body size at downstream migration and estuary or watershed characteristics. We hypothesize that this lack of result is driven by a variety of interacting population-specific factors—such as latitude, density- and temperature-dependent

growth, and juvenile freshwater age composition—which may have masked size-habitat relationships. Coho salmon populations at higher latitudes and colder growing conditions tend to feature a higher proportion of fish that remain in freshwater for two years before migrating to sea (Quinn 2018). These age-2 migrants are consistently larger than age-1 migrants from the same population, given their additional year of growth. However, because higher-latitude populations tend to experience cooler water temperatures, age-2 juveniles from a northerly population may not differ substantially in size from age-1 juveniles from a more southerly population (Bradford et al. 1997). It is also possible that the principal biological mechanisms driving population-specific variation in juvenile body size (e.g., juvenile density in freshwaters, freshwater habitat extent and productivity) were not adequately captured by the catchment-scale habitat characteristics we considered. For example, in populations where juvenile densities approach or exceed habitat carrying capacity or prey availability, ensuing resource competition can constrain individual body size. Density-dependence can operate at fine spatial scales (Walters et al. 2013, Thorson et al. 2014) and therefore may be independent of the catchment-scale characteristics considered in our analyses. Additionally, although we aimed to account for broad-scale thermal variation across populations (i.e., with latitude and elevation parameters), evidence suggests that juvenile salmon exploit thermal microhabitats to maximize growth potential. For example, juvenile coho salmon in Alaska have been observed making diel and seasonal migrations that track shifting thermal mosaics, suggesting fine-scale behavioural thermoregulation to maximize prey intake, digestion efficiency, and freshwater growth (Armstrong and Schindler 2013, Baldock et al. 2016). Thermal determinants such as habitat configuration, groundwater inputs, and flow conditions at the reach or tributary scale may therefore exert greater influence over juvenile salmon body size than thermal proxies such as latitude and elevation. Finally, we note that our analyses focused on age-1 and age-2 migrants (where present) migrants and excluded fry migrants. For populations where fry migrant dynamics are consistently captured, incorporation of these data into future analyses could reveal linkages between size- or age-at migration and estuary rearing habitats.

Broadly, our results suggest that juvenile coho salmon migrations are locally adapted to estuary habitat characteristics, based on populations ranging from California to Alaska. Although estuaries are increasingly recognized for their role as nursery habitats for juvenile fishes including salmon (Healey 1982, Beck et al. 2001,

Nagelkerken et al. 2015), little is known about geographic variation in estuary reliance, and describing the estuary contributions to life-history diversity and fitness across the salmon life-cycle remains a challenge. To date, much of the literature on estuary-related trait diversity stems from population-specific case studies (e.g., Miller and Sadro 2003, Bennett et al. 2011, Hoem Neher et al. 2013, Craig et al. 2014, Jones et al. 2014, Rebenack et al. 2015, Moore et al. 2016; Chapter 3). Here, we consider wide-ranging coho salmon populations and the spectrum of estuary configurations and conditions they encounter—including systems without estuaries, systems with estuaries of various sizes and shapes, and with various degrees of human impact—and show that juveniles migrate earlier when they have access to enclosed, complex estuary rearing habitats. Where estuaries offer sufficient prey resources and refuge from predators and environmental stressors, early migration may be the precursor to an extended period of estuary stopover that enables additional growth prior to marine entry (Chapter 3). Within the context of prevailing marine survival literature, early migration could reflect an adaptive migratory strategy whereby juvenile coho salmon increase their body size—and likely their probability of survival—prior to entering the size-selective marine environment. Once in the ocean, larger smolts may be better equipped to avoid predation by larger fishes and seabirds (Tucker et al. 2016, Duncan and Beaudreau 2019) and pursue larger, more energy-dense prey (Pope et al. 1994, Daly et al. 2009, Duffy et al. 2010). We expect that phenotypic diversity in migration timing and duration will vary according to the range of freshwater and estuarine rearing environments available to juvenile salmon, and the growth-mortality trade-offs inherent therein.

If early estuary migration is an adaptive migratory trait, widespread loss of estuary rearing habitats could conceivably result in this trait becoming maladaptive—at least in the short term. As hotspots of human activity, estuaries rank among the most degraded habitats on earth and increasingly face dual pressures of coastal development and sea level rise (Lotze et al. 2006, Kirwan and Murray 2008). Estuary degradation (e.g., via dredging, stormwater pollution, nutrient inputs) or structural simplification (e.g., via diking, shoreline armoring) could imperil foraging opportunities (Munsch et al. 2014, David et al. 2016) or increase susceptibility to predators (Munsch et al. 2017) for early-migrating juveniles reliant on estuary rearing habitats for pre-ocean growth. At the population level, such impacts could reduce juvenile survival both in the estuary and in the ocean, and ultimately reduce adult returns (Magnusson and Hilborn 2003, Meador

2014). Simultaneously, rapid evolution could potentially modulate the impact of estuary habitat loss (Bowlin et al. 2010). Evidence suggests that Pacific salmon have the potential to rapidly adapt their migratory strategies in the face of massive habitat change. In the case of Snake River fall Chinook, for example, hydrological changes to upstream spawning and rearing grounds prompted by dam construction were followed by a rapid shift in the relative occurrence of ocean- and stream-type juvenile migration strategies within just a few decades (Williams et al. 2008). Reciprocally, habitat restoration can enable re-emergence of lost migratory life-history diversity. In Oregon's Salmon River estuary, dike removal and salt marsh restoration was followed by re-emergent estuary-rearing juvenile Chinook salmon, which were previously rare in the system (Bottom et al. 2005). The implications are twofold: while major habitat alteration can alter the fitness landscape and prompt rapid evolution toward different (or differently-distributed) traits, it also has the potential to erode population-level life-history diversity (Beechie et al. 2006, McClure et al. 2008, Cordoleani et al. 2021). By extension, while estuary-adapted coho populations could theoretically shift to later, more contracted migrations in the face of estuary habitat loss, such a shift could also lead to homogenization of juvenile traits, with negative implications for population-level resilience to future perturbations. Although our study did not reveal impacts of estuary habitat quality on migration timing (except for a non-significant negative effect on the late migration date), we speculate that this discrepancy reflects a time lag between impact and adaptation.

Our study illustrates the diversity of migratory traits present amongst wide-ranging coho salmon populations, and suggests that migration timing is locally adapted to estuary habitats in addition to latitudinal clines in marine and freshwater habitat processes. Exploring linkages between habitat diversity, life-history diversity, and resilience is a major theme in the study of Pacific salmon (Schindler et al. 2008). Within and across populations, habitat and life-history diversity can confer resilience and act as a buffer against dynamic and changing environmental conditions (Schindler et al. 2010, Moore et al. 2014, Schroeder et al. 2015, Brennan et al. 2019, Jones et al. 2021). In many salmon watersheds, habitat degradation is accelerating across the range of freshwater and estuary rearing habitats that juveniles rely upon for growth and survival (McClure et al. 2008, Hodgson et al. 2020). Future adaptive capacity could depend on ensuring continued access to varied habitat types, as a means of sustaining genotypic and phenotypic diversity including that evident in juvenile migratory traits (Williams et al.

2008, Cordoleani et al. 2021). Conservation and restoration of diverse rearing habitats could permit successful expression of alternative life-history strategies (Bottom et al. 2005, Craig et al. 2014), and help sustain reserves of population-level diversity that are crucial for resilience to future natural and anthropogenic change.

2.6. Acknowledgements

This project would not have been possible without the extensive monitoring efforts and data contributions of numerous federal, state, and local agencies, First Nations and Tribes, academic research groups, not-for-profit organizations, and industry groups. We extend our gratitude to the many scientists, technicians, and data stewards whose countless hours have contributed to building and maintaining these rich data sets. Specifically, we thank the following individuals for their willingness to share data, discuss ideas, and contribute time to this project: Mark Cleveland and Melissa Shirey with the Gitanyow Fisheries Authority; Mark Spoljaric with the Haida Fisheries Department; Charlotte Scofield with the Stillaguamish Tribe; Andrew Berger with the Puyallup Tribe; Mike McHenry with the Lower Elwha Klallam Tribe; members of the Nisga'a Joint Fisheries Management Committee; Cameron Noble and Richard Alexander with LGL Limited; Matt Sloat and Will Atlas with the Wild Salmon Center; George Pess, Todd Bennett, and Martin Liermann with the National Oceanic and Atmospheric Administration; Nicolette Watson, Karalea Cantera, Andrew Pereboom, and Ryan Whitmore with Fisheries and Oceans Canada; Justin Priest with the Alaska Department of Fish and Game; Clayton Kinsel, Marisa Litz, Jamie Lamperth, Peter Topping, Peter Lisi, Matthew Klungle, and Joshua Weinheimer with the Washington Department of Fish and Wildlife; Erik Suring, Kim Jones, and Trevan Cornwell with the Oregon Department of Fish and Wildlife and Oregon State University; Shaun Thompson and Justin Garwood with the California Department of Fish and Wildlife; Mark Henderson, Mike Sparkman, and John Deibner-Hanson with the California Cooperative Fish and Wildlife Research Unit and Humboldt State University; Gregg Horton with Sonoma Water, Eric Ettlinger with Marin Municipal Water District; and Pat Righter and Matt House with Green Diamond. This project also benefitted greatly from recent collaborative efforts to map and characterize estuary habitats along the Pacific Coast of the United States (Pacific Marine and Estuarine Fish Habitat Partnership) and Canada (Pacific Estuary Conservation Program). Specifically, we thank Kate Sherman with the Pacific States

Marine Fisheries Commission, Kathleen Moore with Environment Canada, and Courtney Hamilton with Ducks Unlimited Canada for sharing and contextualizing estuary spatial data. Support for this research came from the Nature Trust of British Columbia, the National Science and Engineering Research Council of Canada, and the Liber Ero Research Chair in Coastal Science and Management.

Chapter 3. State-dependent estuary stopover boosts marine survival for juvenile salmon

3.1. Abstract

Stopover habitats can allow migratory animals to bolster energy stores prior to resumption of migration, which in turn can increase an individual's likelihood of survival. Carryover effects from prior habitats may mediate use of stopover habitats: some evidence suggests that low-condition migrants exhibit longer stopovers and attain more growth in these habitats relative to high-condition individuals. For Pacific salmon (*Oncorhynchus* spp.), estuaries may be important stopover habitats during the juvenile migration from natal freshwaters to the ocean. High-productivity estuaries offer favourable growth conditions, and growth in the estuary could improve marine survival prospects as body size at marine entry can be positively correlated with survival to adulthood. Yet the contribution of the estuarine life stage to individual fitness across the salmon life-cycle remains poorly understood. Here, we show that body size at freshwater exit mediates estuary stopover behaviour by juvenile coho salmon (*O. kisutch*), and that estuary growth can increase the probability of marine survival. We performed a multi-year mark-recapture study of juvenile coho salmon in the Koeye River and its estuary, located on the remote Central Coast of British Columbia. We found that estuary stopover duration decreased with increasing body size: small juveniles spent more than three times longer in the estuary than their larger conspecifics. Estuary growth rates ranged from 0.58-0.95 mm/day, and the smallest juveniles grew by up to 30% during estuary stopover. Consequently, each outmigrating juvenile cohort entered the ocean both larger and less variable in size than it was at freshwater exit. Analysis of returning spawners indicated that larger juveniles had higher ocean survival rates than smaller individuals, and that growth achieved in the estuary improved marine survival by 44-46% across juvenile size classes. Together these results, from a watershed unaltered by intensive logging or development, suggest that growth achieved during estuary stopover can mitigate freshwater carryover effects, substantially boost watershed-level carrying capacity, and buffer size-selective survival in a changing ocean. More broadly, these findings highlight the importance of state-dependent use of stopover habitats in the study of migration ecology and conservation of migratory species.

3.2. Introduction

Through migration, animals connect disparate habitats that vary in their inherent opportunities and constraints. Through predictable, directional movement between habitats, migratory animals can optimize access to spatially and temporally variable resources needed for survival, growth, and reproduction (Alerstam et al. 2003, Dingle and Drake 2007). Traits exhibited by migratory animals within a given habitat, such as body size and timing of seasonal occupancy, reflect both ecological forces and evolutionary strategies toward maximizing fitness (Alerstam et al. 2003). Variation in resource availability and acquisition can produce carryover effects that manifest as individual differences in biological condition (e.g., body size, lipid storage, hormone levels; Harrison et al. 2011), and may influence performance in later habitats and life stages (Norris 2005, O'Connor et al. 2014, Chasco et al. 2021). At the same time, migratory animals must hew to fitness constraints imposed by future habitats (i.e., habitats they are *en route* to), such as the timing of resource availability. Such selective pressures, often operating in geographically-distinct habitats, represent crucial links between successive phases of animal migrations (McNamara et al. 1998, Bowlin et al. 2010). Together, these “upstream” and “downstream” forces interact to shape the evolution and expression of life-history decisions (Werner and Gilliam 1984, Mangel and Clark 1988).

Migration can be an energetically costly process, and stopover habitats offer migratory animals critical opportunities for rest and refuelling (Alerstam et al. 2003, Sawyer et al. 2009). Situated along migratory routes, these habitats allow animals to recoup depleted energy stores while limiting exposure to predators and other environmental stressors (Moore et al. 1995). Use of stopover habitats has been documented extensively for migratory birds (reviewed in Alerstam and Hedenstrom 1998), and to a lesser degree for ungulates (Sawyer et al. 2009), whales (Mate et al. 2011), and salmonid fishes (Moore et al. 2016, Chalde and Fernández 2017). While there is increasing evidence documenting the usage of stopover habitats by various migratory taxa, our understanding of the fitness benefits provided by these habitats—and thus their conservation value—is nascent (Moore et al. 1995, Bowlin et al. 2010, Sheehy et al. 2011, Runge et al. 2014).

Use of stopover habitats may be state-dependent, whereby body condition upon arrival is a key determinant of behaviour at a stopover site. In particular, duration of stay and intensity of feeding activity at stopover habitats can reflect carryover effects from previous life stages (Moore et al. 1995). For example, studies of migratory birds suggest that those with lower fat reserves exhibit longer residence times and higher rates of mass gain during migratory stopover (Biebach et al. 1986; Loria and Moore 1990). Thus, carryover effects from prior habitats may mediate use of stopover habitats, and low-condition individuals may derive outsized benefits from extended stopovers.

For juvenile Pacific salmon (*Oncorhynchus* spp.), estuary stopover between natal freshwaters and the ocean may provide growth opportunities that bolster marine survival prospects. While all Pacific salmon migrate from freshwater to marine environments as juveniles (Thorpe 1994), the size, configuration, and quality of estuary nursery habitats encountered in the course of migration can vary from negligible habitat area to extensive, interconnected habitats spanning a range of biophysical and ecological conditions. Accordingly, behavioural patterns of estuary stopover vary both within and across populations, and with the types of estuary habitats available (reviewed in Levings, 2016). Comparative studies indicate that juvenile salmon prey intake and growth rates can be higher in high-productivity estuaries relative to upstream freshwater habitats (e.g., Bond et al. 2008; Hayes et al. 2008; Hoem Neher et al. 2014; Goertler et al. 2016; Chalde and Fernández 2017), owing in part to an abundance of energy-dense prey such as copepods, mysids, and adult and larval insects (Simenstad et al. 1982, Arbeider et al. 2019, Woo et al. 2019). Further, estuary shorelines commonly feature shallow waters with aquatic and overhanging vegetation, which may offer superior refuge from piscivorous predators when compared with deepwater marine habitats (Paterson and Whitfield 2000, Simenstad and Cordell 2000, Seitz et al. 2020). Understanding the value of estuary habitats to migrating juvenile salmon is of timely importance, especially as estuaries have high exposure to multiple and ongoing human stressors (Hodgson et al. 2020) and their degradation can erode salmon population productivity and resilience (Magnusson and Hilborn 2003, Meador 2014, Jones et al. 2021).

Estuary stopover by juvenile Pacific salmon may be shaped by both freshwater carryover effects and future constraints, namely size-selective pressures encountered in the subsequent marine stage. Juvenile body size at ocean entry is generally positively

correlated with survival to adulthood (Ward et al. 1989, Henderson and Cass 1991, Koenings et al. 1993; but see Ulaski et al. 2020). While survival rates fluctuate across space and time, as few as <1-10% of juvenile salmon that enter the ocean survive to reproductive maturity (Pearcy 1992). Within this high-mortality seascape, a larger body size can improve fitness by increasing the success of prey pursuit and predator avoidance, and decreasing the likelihood of overwinter starvation (Pope et al. 1994, Sogard 1997, Beamish and Mahnken 2001). Several studies cite growth attained prior to marine entry and during the first few months at sea as critical for juvenile salmon to survive the physiological and environmental challenges encountered during this period (Beamish et al. 2004, Duffy and Beauchamp 2011, Tomaro et al. 2012, Woodson et al. 2013). However, we note that within the size-selective marine survival literature, “marine entry” and “freshwater exit” are often conflated; this false equivalence fails to account for the estuary stage of juvenile salmon migration (Jones et al. 2021), and consequently disregards the role of estuaries as stopover habitats for juvenile salmon.

Given size-selective marine survival pressures, estuary stopover may be particularly important for smaller-bodied juvenile salmon *en route* to the ocean. Theory indicates that size-structured trade-offs in growth opportunity and mortality risk control the evolution of life-history decisions, such as the duration of habitat use and timing of migration between habitats (Werner and Gilliam 1984, Satterthwaite et al. 2009). Differences in freshwater habitat characteristics, foraging success, and overwintering conditions often produce considerable within-population variation in juvenile salmon body size (Gosselin and Anderson 2017), which in turn may have carryover effects on the duration of estuary residence by juvenile salmon migrating to sea. Thus, for juvenile salmon that exit freshwaters at a relatively small size, extended estuary stopover could allow them to grow larger and potentially lessen the threat of size-related marine mortality. Indeed, there is some evidence that smaller-bodied juvenile salmonids exhibit long estuary stopovers relative to their larger counterparts, and experience high growth rates in estuary habitats (Bond et al. 2008, Moore et al. 2016). However, this potential size-dependency of estuary stopover behaviour is relatively poorly described, with unknown fitness implications.

With this study, we examined the size-dependency of estuary stopover behaviour by juvenile coho salmon (*O. kisutch*) and its consequences for individual survival. Quantifying the extent to which juvenile salmon reside and feed in estuaries is key to

understanding their function as stopover habitats (Thorpe 1994), yet there remains a relative dearth of information regarding this critical portion of the salmon life-cycle (Weitkamp et al. 2014). Our study was conducted in the Koeye River estuary, which is located in the Central Coast region of British Columbia, Canada, and has not undergone intensive land-use activities such as logging or development. Given that estuaries are among the most heavily-altered habitats on earth (Lotze et al. 2006), this location provides a rare exemplar of a fully-intact estuary ecosystem and its role in the salmon life-cycle. Using a mark-recapture study, we quantified estuary residence and growth and examined linkages between estuary stopover characteristics and marine survival. Specifically, we 1) determined the relationship between size at freshwater exit and duration of estuary stopover; 2) quantified growth achieved during estuary stopover, and 3) quantified the predicted contribution of estuary growth to observed patterns of size-selective marine survival. We hypothesized that small-bodied individuals would exhibit longer estuary stopovers and consequently grow more in the estuary relative to their larger conspecifics. If marine survival was size-selective, we expected that additional growth attained during estuary stopover would translate to a higher probability of survival to adulthood, and that smaller juveniles would derive greater relative survival benefits from estuary growth.

3.3. Methods

3.3.1. Overview of methods

In each of three years, from 2017 to 2019, we conducted a life-cycle study of coho salmon in the Koeye River watershed (51.7791°N, 127.8718°W) on the Central Coast of British Columbia, Canada (Figure 3.1). This study was conducted in partnership with the Heiltsuk Nation and supported by the Heiltsuk Integrated Resource Management Department (HIRMD), in alignment with HIRMD goals and objectives for the management of salmon habitat. Each spring, we captured, measured, and tagged juvenile coho salmon at freshwater exit using a rotary screw trap (RST; $n_{2017} = 1,258$, $n_{2018} = 1,533$, $n_{2019} = 2,003$). Juvenile salmon smolt year (SY) cohorts are hereafter identified by the year they were tagged at the RST (e.g., SY2017). We note that this study focused on coho salmon yearlings migrating downstream; though present in the system, subyearling (fry) migrants were not tagged or tracked due to their small body

size. We seined the downstream estuary to recapture and remeasure tagged individuals prior to marine entry ($n_{2017} = 16$, $n_{2018} = 19$, $n_{2019} = 29$). Each fall, we re-detected adult coho salmon that survived the marine environment using a full-river weir and RFID arrays deployed throughout the system ($n_{SY2017} = 23$, $n_{SY2018} = 60$). Together, we used these data to quantify (1) duration of estuary residence by juvenile salmon, (2) growth attained in the estuary, and (3) smolt-to-adult marine survival. Although the terms “freshwater exit” and “marine entry” are often used interchangeably in the size-selective marine survival literature, here our mark-recapture study allowed us to quantify growth achieved in the estuary—between freshwater exit and marine entry—and subsequently predict the extent to which that growth contributed to observed marine survival rates.

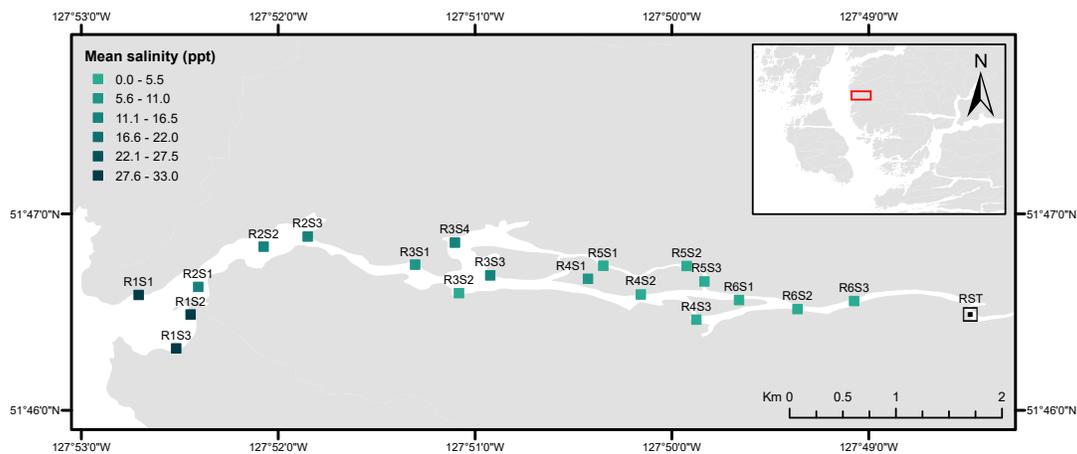


Figure 3.1. Map of the Koeye River estuary, indicating location of rotary screw trap (RST) and estuary sampling sites.

Note: Estuary sampling sites are labelled by reach and site numbers and color-coded by mean salinity from April-June in 2017, 2018, and 2019; darker colour represents higher salinity. Reach 1 sites (R1S1, R1S2, R1S3) were considered a proxy for estuary exit and marine entry. RFID arrays were located upstream of the RST.

3.3.2. Data collection

The 35-km Koeye River drains approximately 180 km² of temperate old-growth rainforest and is connected to marine waters via a 5-km tidal estuary (Figure 3.1). We deployed a floating RST (2-m diameter) 0.5 km upstream of the upper extent of tidal influence to capture juvenile coho salmon exiting freshwater. The RST was monitored daily from late April through early June, except on dates when high flows prevented trap access. Juvenile salmon were collected from the trap box and lightly anaesthetized in

holding tanks using Tricaine methanesulfonate. Anaesthetized individuals were measured (fork length, mm) and weighed (g). All individuals weighing at least 4.0 g were inserted with a 12-mm Passive Integrated Transponder (PIT) tag (Oregon RFID) using an injector syringe and a 2.15 mm-gauge needle. Handled individuals were allowed to recover in freshwater holding tanks and subsequently released back into the river immediately downstream of the RST.

We conducted periodic beach seining at 19 sites throughout the Koeye River estuary to recapture juvenile coho salmon tagged at the RST. Per methodology outlined in Seitz et al. (2020), estuary habitats were classified into six reaches based on their habitat characteristics (Figure 3.1). Reach 1, located at the mouth of the Koeye River, functionally represents the outer transitional edge of the Koeye River estuary; we considered date of recapture in this reach a suitable proxy for date of estuary exit and marine entry. Reach 1 sampling sites are exposed to wave and tidal action from adjacent Fitz Hugh Sound and feature sandy substrates with minimal structural complexity. Seasonal mean salinities at these sites approached typical marine levels ($\mu_{2017} = 27.3$ ppt; $\mu_{2018} = 29.3$ ppt; $\mu_{2019} = 34.9$ ppt) and were nearly double the salinity levels observed at reaches immediately upstream. Reaches 2-6, located upstream of Reach 1, become progressively less saline and are characterized by a range of habitats including dense eelgrass beds, rockweed mudflats, salt marsh, and riverine pool-riffle morphology. Beach seining was conducted in each reach every 10 to 14 days from May through September, though intensity of seining effort varied by year ($n_{2017} = 244$ seine sets, $n_{2018} = 170$, $n_{2019} = 141$). Due to site-specific variation in estuary habitat characteristics, three types of seine nets were deployed. In Reaches 1 and 2, fish were captured using a 22 x 3.1 m net (3 mm bunt mesh) deployed from a skiff; due to tidal strength, net sets were deployed with the direction of tidal flow. For most sites in Reaches 3-6, fish were captured using a 30 x 1.8 m net (1.5 mm bunt mesh) deployed in an identical manner. For particularly shallow or constrained sites in Reaches 3-6, we hand-deployed a 13.7 x 1.2 m pole seine (6 mm bunt mesh; see Seitz et al. 2020 for a full description of estuary sampling methods). Together, use of these three net types effectively sampled the target size range of juvenile salmon migrating through the Koeye River estuary. All captured fish were measured (fork length, mm) and scanned for PIT tags using a handheld reader (Oregon RFID, Portland, OR). Captured individuals were

allowed to recover from handling in holding tanks filled with water collected *in situ* and subsequently returned to the site of capture.

To quantify marine survival, we installed four Radio Frequency Identification (RFID) arrays upstream of the estuary to detect adult salmon that were PIT tagged as juveniles returning to their upstream spawning grounds. Adult salmon were also scanned for PIT tags when captured at a weir located approximately 0.5 km downstream of the RST. Survival analyses were conducted on SY2017 and SY2018 cohorts, for which complete adult return data were available. While a majority of coho salmon spend one full year in the ocean before returning to their natal rivers and streams to spawn in fall, a small proportion of males consistently return upstream to spawn after their first summer at sea (“jack” males; Quinn 2018). Jacks were included in our survival analyses; therefore, SY2017 juveniles were redetected as adults in either fall 2017 or 2018, and SY2018 juveniles were redetected in either fall 2018 or 2019.

Fish sampling was authorized by permits from Fisheries and Oceans Canada and Simon Fraser University (Animal Care Protocol #1158B-11-23 and #1270B-14).

3.3.3. Estuary residence analysis

Data from juvenile coho salmon recaptured in the estuary were used to quantify the relationship between size at freshwater exit and duration of estuary residence. Residence analyses pooled data across the three sampling years (SY2017-2019) but considered only those individuals recaptured in the estuary prior to 30 June. This date was used to delineate juvenile coho salmon exhibiting the species’ predominant life-history strategy (freshwater exit in the spring followed by ocean entry in the late spring or early summer) from those exhibiting alternative strategies. Such strategies may include extended residence in the stream-estuary ecotone before returning upstream to overwinter in freshwater (e.g., Miller and Sadro 2003; Koski 2009) or overwintering in the estuary followed by ocean entry the subsequent spring (e.g., Quinn et al. 2013; Jones et al. 2014). Our choice to use 30 June as a cut-off was corroborated by the fact that juvenile coho salmon tagged at the RST were never observed in Reach 1 (estuary exit/marine entry) after this date. Individuals recaptured in the upper estuary after 30 June were presumed to be exhibiting one of the aforementioned alternative life-history strategies and excluded from subsequent analyses.

We compared generalized linear models (GLMs) with various underlying error distributions (Gaussian, Poisson, and negative binomial) to identify drivers of variation in estuary residence S_i , calculated as the number of days between tagging at the RST and recapture in the estuary. Estuary residence GLMs considered a subset of individuals recaptured at sites approximating estuary exit and marine entry (Reach 1; $n_{2017} = 4$, $n_{2018} = 8$, $n_{2019} = 6$). to avoid bias from individuals recaptured further upstream that likely continued to rear in the estuary prior to entering marine waters. Model comparison using Akaike Information Criteria corrected for small sample sizes (AICc; Akaike 1973; Burnham and Anderson 2002) revealed that a GLM with a negative binomial error distribution outperformed other candidate distributions. The most parsimonious model included a fixed term for individual size $FL_{RST(i)}$, but not terms for sampling year, date of freshwater exit, or individual daily growth rate:

$$S_i = DOY_{est(i)} - DOY_{RST(i)} \quad (1.1)$$

$$\log(\hat{S}_i) \sim \beta_0 + \beta_{FL} FL_{RST(i)} \quad (1.2)$$

where $DOY_{RST(i)}$ was the day of year when an individual fish was initially captured at the RST, and $DOY_{est(i)}$ was the day of year when the same fish was recaptured in Reach 1 of the estuary (marine entry). β_{FL} was the coefficient describing the effect of fork length at freshwater exit $FL_{RST(i)}$ on predicted duration of estuary residence.

We tested two alternative approaches for predicting the relationship between body size at freshwater exit and apparent duration of estuary residence, including a log-linear quantile regression model and a Cormack Jolly Seber mark-recapture model. Alternative approaches considered all individuals recaptured in the estuary, and estuary residence predictions derived from these approaches supported predictions derived from the aforementioned GLM approach (Appendix B: Figure B.1, Table B.1). We selected the best-fit model from the GLM approach for use in subsequent analyses because it produced the most precise estimates.

3.3.4. Estuary growth analysis

We predicted annual estuary growth rates using observed residence and growth data from juvenile coho salmon recaptured in the estuary prior to 30 June of each sampling year. One individual tagged and recaptured in 2017 was excluded from growth analyses due to clear measurement error. Observed absolute growth rates GR_i were calculated for each individual tagged at the RST and recaptured in the estuary. A linear relationship between growth and days since freshwater exit was deemed appropriate due to the relatively short estuary residence periods observed (< 40 days); therefore, growth rates represent growth (mm) per day. Predicted growth rates \widehat{GR}_i were calculated for all individuals tagged at the RST, based on individual growth rates observed for individuals recaptured in the estuary. Model comparison using AICc supported inclusion of a fixed term for smolt year:

$$GR_i = \frac{FL_{est(i)} - FL_{RST(i)}}{DOY_{est(i)} - DOY_{RST(i)}} \quad (2.1)$$

$$\widehat{GR}_i \sim \beta_{SY} SY_j + \varepsilon_i \quad (2.2)$$

where $DOY_{RST(i)}$ and $FL_{RST(i)}$ were the day of year and fork length at which an individual fish was initially captured at the RST, and $DOY_{est(i)}$ and $FL_{est(i)}$ were the day of year and fork length at which the same individual was recaptured in any reach of the estuary. β_{SY} was the coefficient describing the effect of a categorical variable denoting smolt year SY_j on predicted growth rate.

To predict size at marine entry, we first estimated estuary residence duration for each individual tagged at freshwater exit. We then applied the daily growth rate model to individual residence estimates to predict growth achieved during estuary residence. Finally, we added predicted estuary growth to observed size at freshwater exit to predict individual size at marine entry $\widehat{FL}_{mar(i)}$:

$$\widehat{FL}_{mar(i)} = FL_{RST(i)} + (\widehat{S}_i \cdot \widehat{GR}_i) \quad (2.3)$$

where $FL_{RST(i)}$ was observed fork length at the RST, \hat{S}_i was predicted duration of estuary residence, and \widehat{GR}_i was predicted estuary growth rate for each individual juvenile coho salmon i tagged in SY2017, SY2018, and SY2019.

3.3.5. Marine survival analysis

For each cohort of juvenile coho salmon with complete adult return data (SY2017 and SY2018), we used quasibinomial logistic regression to determine a) the observed relationship between marine survival and size at freshwater exit in the presence of estuary rearing habitat, and b) the predicted relationship between marine survival and size at freshwater exit in the absence of estuary rearing habitat. Each individual i in our study had 1) an observed size at freshwater exit ($FL_{RST(i)}$), 2) a predicted size at marine entry as derived from residence and growth models ($\widehat{FL}_{mar(i)}$), and 3) an observed binary marine survival value (0 = died, 1 = survived). To determine the size-survival relationship in the presence of estuary rearing habitat, we related observed size at freshwater exit to observed marine survival; the most parsimonious model included a fixed term for smolt year. Any estuary growth is implicit in this relationship, as all juvenile coho salmon that exit the Koeye River transit its estuary before reaching the ocean. However, the specific contribution of estuary growth to marine survival remains obscured (Figure 3.2a). Next, we determined the size-survival relationship in the absence of estuary rearing habitat by relating predicted size at marine entry to observed marine survival. In this hypothetical scenario, no growth occurs between freshwater exit and marine entry because these points are coincident in time and space; in other words, size at freshwater exit is equivalent to size at marine entry (Figure 3.2b). For the estuary-absent scenario, we weighted predicted size at marine entry by the inverse joint variance associated with estuary residence and growth model predictions as a means of propagating error between models.

$$\text{logit}(\phi_{ij}) \sim \beta_0 + \beta_{FL}FL_i + \beta_{SY}SY_j + \beta_{est}estuary + \varepsilon_i \quad (3)$$

Here, survival probability was ϕ_{ij} , which was coded as either zero or one to denote the death or survival of each tagged juvenile coho salmon in the marine environment (taken to include estuarine and marine habitats, in addition to freshwater habitats transited by returning adults that were located downstream of RFID arrays). β_{FL}

was the coefficient describing the effect of individual fork length FL_i on marine survival; FL_i was the observed fork length at freshwater exit for the estuary-present marine survival model, and the predicted length at marine entry for the estuary-absent model. β_{SY} was the coefficient describing the effect of smolt year SY_j on marine survival. β_{est} was the coefficient describing the effect of a categorical variable *estuary* denoting the theoretical presence or absence of estuary habitat, which adjusted the survival intercept. For individuals of a given size, we quantified the estuary contribution to marine survival by comparing observed survival rates in the presence of estuary habitat to predicted survival rates in the absence of estuary habitat.

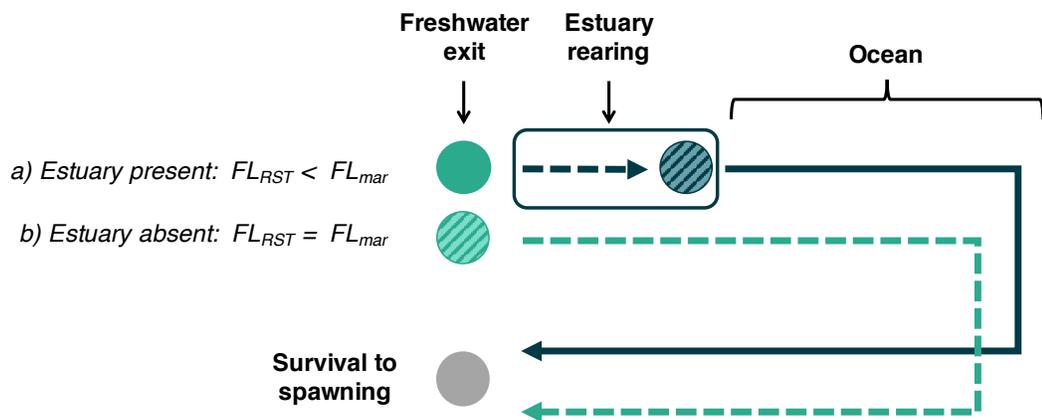


Figure 3.2. Conceptual figure showing data used to determine size-selective marine survival relationships a) observed in the presence of estuary habitat and b) predicted in the absence of estuary habitat.

Note: Solid circles and lines indicate observations; dashed circles and lines indicate predictions. In the “estuary present” scenario, observed length at freshwater exit (solid green circle) is related to observed marine survival (solid grey circle). Estuary rearing and growth is implicit in this relationship, with predicted length at marine entry following estuary rearing indicated by the dashed blue circle. In the estuary-absent scenario, length at freshwater exit is equivalent to length at marine entry; therefore, predicted length at marine entry (dashed green circle) is related to observed marine survival data. No additional estuary growth occurs in the estuary-absent scenario.

Our marine survival models are predicated on the following set of assumptions, which we believe to be biologically defensible but warrant description. First, we assumed that there is not substantial size-selective mortality in the estuary. We used Kolmogorov-Smirnov tests to check for annual differences in the freshwater exit size distribution for 1) all individuals tagged at the RST and 2) the subset of individuals recaptured in the estuary. We found no significant differences, suggesting a lack of size-selective mortality between the RST and marine entry ($p_{2017} = 0.4883$, $p_{2018} = 0.4131$, $p_{2019} = 0.8555$).

Second, we assumed that absence of estuary habitat would not result in a longer period of freshwater rearing prior to ocean entry. The timing of juvenile coho salmon migration and smoltification is primarily influenced by a combination of environmental factors including photoperiod, lunar phase, temperature, and flow (e.g., DeVries et al. 2005; Björnsson et al. 2011; Spence and Dick 2013); we found no literature suggesting that presence or absence of estuary habitat influences freshwater emigration timing on ecological timescales. Finally, we assumed that estuary stopover does not increase mortality risk to juvenile salmon in comparison with direct migration to the ocean. Indeed, available data indicate that juvenile salmonids experience high survival rates in estuaries relative to the coastal ocean (Moore et al. 2010, Rechisky et al. 2012, 2014, Clark et al. 2016). Following this assumption, the only impact of estuary residence is additional growth prior to ocean entry. Accordingly, the estuary-absent model addresses the extent to which a lack of estuary growth reduces the probability of marine survival for individual juvenile salmon of a given size.

All analyses were conducted in the R statistical environment, version 4.0.5 (R Core Team 2021; see Data S1 for data files and model code). Generalized linear modelling and model comparison were conducted using the packages 'MASS' (Venables and Ripley 2002) and 'bbmle' (Bolker 2020). Plots were made using the packages 'ggplot2' (Wickham 2016) and 'patchwork' (Pedersen 2020).

3.4. Results

3.4.1. Estuary residence

Residence analyses revealed that small juveniles exhibited longer estuary stopovers than their larger counterparts. Each of the three residence approaches tested indicated a negative relationship between size at freshwater exit and duration of estuary stopover, and estuary stopover duration estimates were similar across approaches (negative binomial GLM: $\beta_{FL} = -0.034$, quantile regression: $\beta_{FL} = -0.020$, CJS mark-recapture: $\beta_{FL} = -0.011$; Appendix S1: Table S1). The negative binomial GLM predicted an estuary stopover duration of 14.5 days (95% CI 11.1-19.1 days) for median-sized individuals ($Q_{0.5} = 93$ mm, Figure 3.3). For individuals exiting freshwater in the lower 10% of the size distribution ($Q_{0.1} = 78$ mm), predicted estuary stopover duration was 24.4 days (95% CI 14.8-40.0). For individuals exiting freshwater in the upper 10% of the size

distribution ($Q_{0.9} = 112$ mm), predicted estuary stopover duration was 7.6 days (95% CI 4.8-12.0). Broadly, all three analytical approaches revealed that juvenile salmon that were small at freshwater exit reared in the estuary for longer than those that were comparatively large.

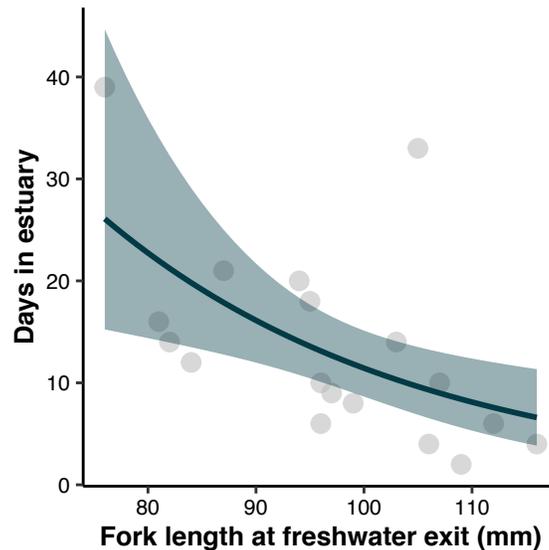


Figure 3.3. Relationship between fork length at freshwater exit and estuary residence (with 95% CI), derived from GLM with a negative binomial error distribution.

Note: Points represent juvenile coho salmon tagged at freshwater exit and recaptured at sites approximating estuary exit and marine entry (Reach 1) in SY2017, 2018, and 2019.

3.4.2. Estuary growth

Daily growth rates in the estuary were high and interannually variable, with the highest annual growth rates exceeding the lowest by nearly twofold (Figure 3.4). In 2017, juvenile salmon growth in the estuary averaged 0.61 mm/day (95% CI about the mean 0.43-0.80 mm/day). Growth rates in 2018 were substantially higher, at 0.95 mm/day (95% CI 0.70-1.11 mm/day). Growth rates in 2019 more closely resembled those observed in 2017, at 0.58 mm/day (95% CI 0.45-0.72 mm/day). Post-hoc Tukey pairwise comparisons indicated that 2017 and 2019 growth rates were significantly different from 2018 growth rates ($p < 0.001$), but not from each other ($p = 0.42$).

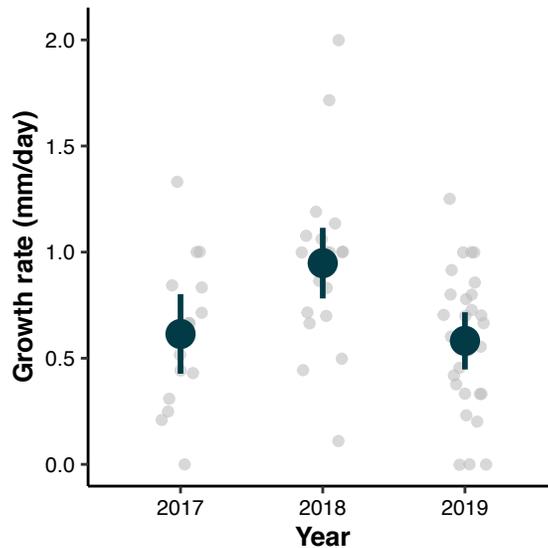


Figure 3.4. Mean daily estuary growth rates (with 95% CI about the mean) of juvenile coho salmon for each sampling year.

Note: Grey points depict individual daily growth rates observed during estuary rearing.

Because estuary stopover duration decreased with size, small juveniles spent more time in the estuary and thus achieved more growth than their larger conspecifics (Figure 3.5). Thus, our models predict that the net effect of estuary rearing was that each cohort entered the ocean larger and less variable in size than it was at freshwater exit. Due to interannually variable growth rates, the magnitude of this impact differed between years. Residence and growth models predicted that SY2017 individuals exiting freshwater in the lower 10% of the size distribution ($Q_{0.1}$) grew an additional 19% in the estuary before entering the ocean. Comparatively, median-sized SY2017 individuals ($Q_{0.5}$) grew an additional 10% in the estuary, while those exiting freshwater in the upper 10% of the size distribution ($Q_{0.9}$) only grew 4% before marine entry. SY2018 individuals had higher estuary growth rates relative to SY2017, resulting in greater contraction of the size distribution between freshwater exit and marine entry. Here, $Q_{0.1}$ individuals grew an additional 30% in the estuary before entering the ocean, while $Q_{0.5}$ individuals grew an additional 15% and those in $Q_{0.9}$ grew only 6%. SY2019 was similar to SY2017, whereby residence and growth models predicted that $Q_{0.1}$ individuals grew 18%, $Q_{0.5}$ individuals grew 9%, and $Q_{0.9}$ individuals grew 4% in the estuary.

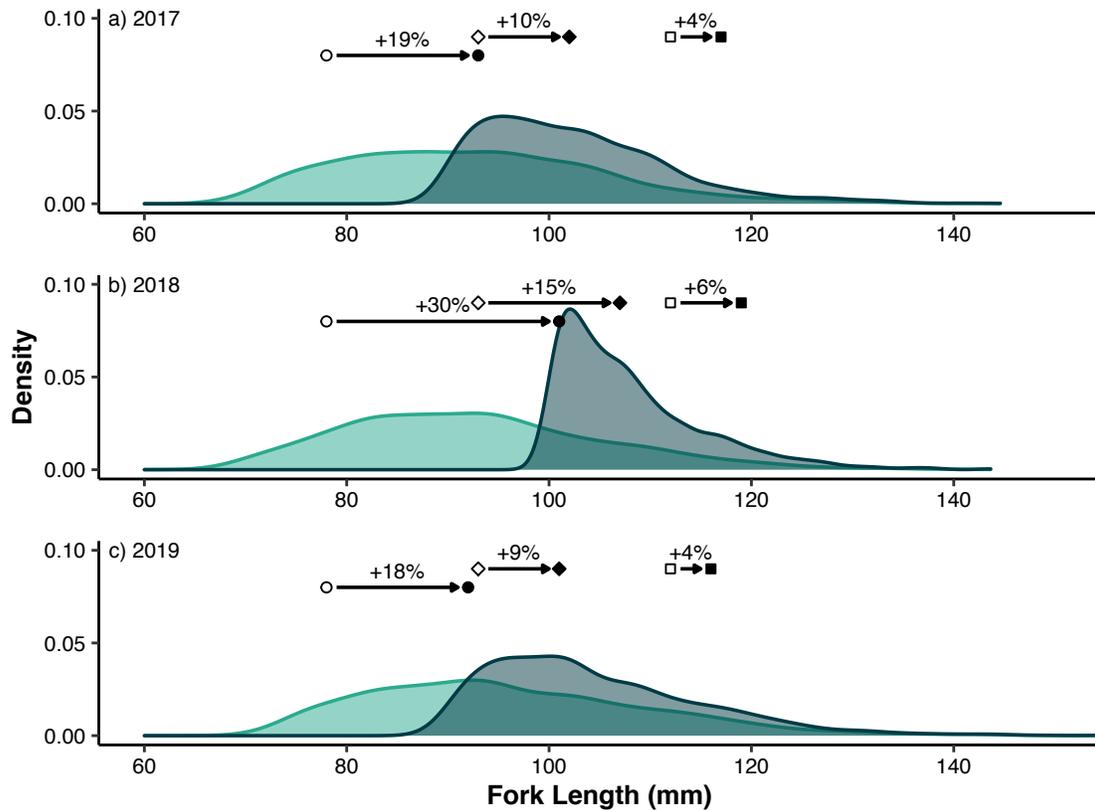


Figure 3.5. Density plots depicting observed size at freshwater exit (green) and predicted size at marine entry after estuary rearing (blue) for all juvenile coho salmon sampled at the RST in a) 2017, b) 2018, and c) 2019.

Note: Points represent juvenile coho salmon in the lower 10% ($Q_{0.1}$), in the middle ($Q_{0.5}$), and in the top 10% ($Q_{0.9}$) of the size distribution at freshwater exit (circles, diamonds, and squares, respectively). Open points depict observed size at freshwater exit; closed points depict predicted size at marine entry. Arrows and labels indicate growth in body size achieved during estuary stopover for individuals in each size quantile.

3.4.3. Marine survival

Between 2017 and 2019, we detected 83 tagged adult coho salmon from SY2017 and SY2018 returning to the Koeye River to spawn. SY2017 saw 23 tagged adults return to spawn; of these, 87% exhibited the predominant coho salmon life-history strategy of one year at sea ($n = 20$) while 13% returned as jacks ($n = 3$). SY2018 saw 60 tagged adults return to spawn, of which 75% had spent a full year at sea ($n = 45$) and 25% returned as jacks ($n = 15$).

For both SY2017 and SY2018, marine survival was positively correlated with juvenile body size at freshwater exit and estuary habitat presence increased the

probability of marine survival (Table 3.1). Post-hoc Tukey pairwise comparisons indicated that marine survival was significantly higher for SY2018 than SY2017 ($p = 0.001$).

Table 3.1. Estimated effect sizes, 95% confidence intervals, and p-values for parameters included in the best-fit marine survival model.

Parameter	β	2.5%	97.5%	p-value
FL _{RST}	0.030	0.017	0.043	<0.001
SY2017	-7.222	-8.669	-5.767	<0.001
SY2018	-6.477	-7.900	-5.038	<0.001
estuary	0.385	0.046	0.724	0.026

Note: Parameter abbreviations are as follows: FL_{RST}: fork length at which individual juvenile salmon were captured at the rotary screw trap (freshwater exit); SY2017: categorical variable denoting juvenile salmon that exited freshwater in 2017; SY2018: categorical variable denoting juvenile salmon that exited freshwater in 2018; estuary: categorical variable denoting theoretical presence or absence of estuary rearing habitat.

Marine survival rates observed for SY2017 were higher for larger individuals, and estuary growth increased the probability of survival. The SY2017 marine survival rate for coho salmon with access to estuary rearing habitat ranged from 0.011 (95% CI 0.007-0.016) for $Q_{0.1}$ individuals to 0.031 (95% CI 0.019-0.042) for $Q_{0.9}$ individuals. For median-sized individuals, the observed marine survival rate was 0.018 (95% CI 0.012-0.023; Figure 3.6). When the estuary contribution to size at marine entry was hypothetically eliminated—such that juvenile salmon entered the ocean at the size they exited freshwater—predicted marine survival rates were lower, ranging from 0.008 (95% CI 0.004-0.012) for $Q_{0.1}$ individuals to 0.021 (95% CI 0.013-0.030) for $Q_{0.9}$ individuals. In the absence of estuary rearing, the predicted marine survival rate for median-sized individuals was 0.012 (95% CI 0.007-0.017). Across size classes, estuary rearing boosted marine survival prospects by approximately 46% relative to the estuary-absent scenario.

Marine survival rates observed for the SY2018 cohort were comparatively higher than those of the SY2017 cohort, ranging from 0.023 (95% CI 0.016-0.031) for $Q_{0.1}$ individuals to 0.063 (95% CI 0.046-0.080) for $Q_{0.9}$ individuals. For median-sized individuals, observed marine survival was 0.036 (95% CI 0.028-0.045; Figure 3.6). Elimination of the estuary contribution to size at marine entry again resulted in lower predicted marine survival rates, ranging from 0.016 (95% CI 0.009-0.023) for $Q_{0.1}$ individuals to 0.044 (95% CI 0.034-0.054) for $Q_{0.9}$ individuals. In the absence of estuary

rearing, the predicted marine survival rate for median-sized individuals was 0.025 (95% CI 0.018-0.033). Similar to SY2017, estuary rearing boosted marine survival prospects relative to the estuary-absent scenario and was relatively consistent across size classes, ranging from 44% for $Q_{0.9}$ individuals to 46% for $Q_{0.1}$ individuals.

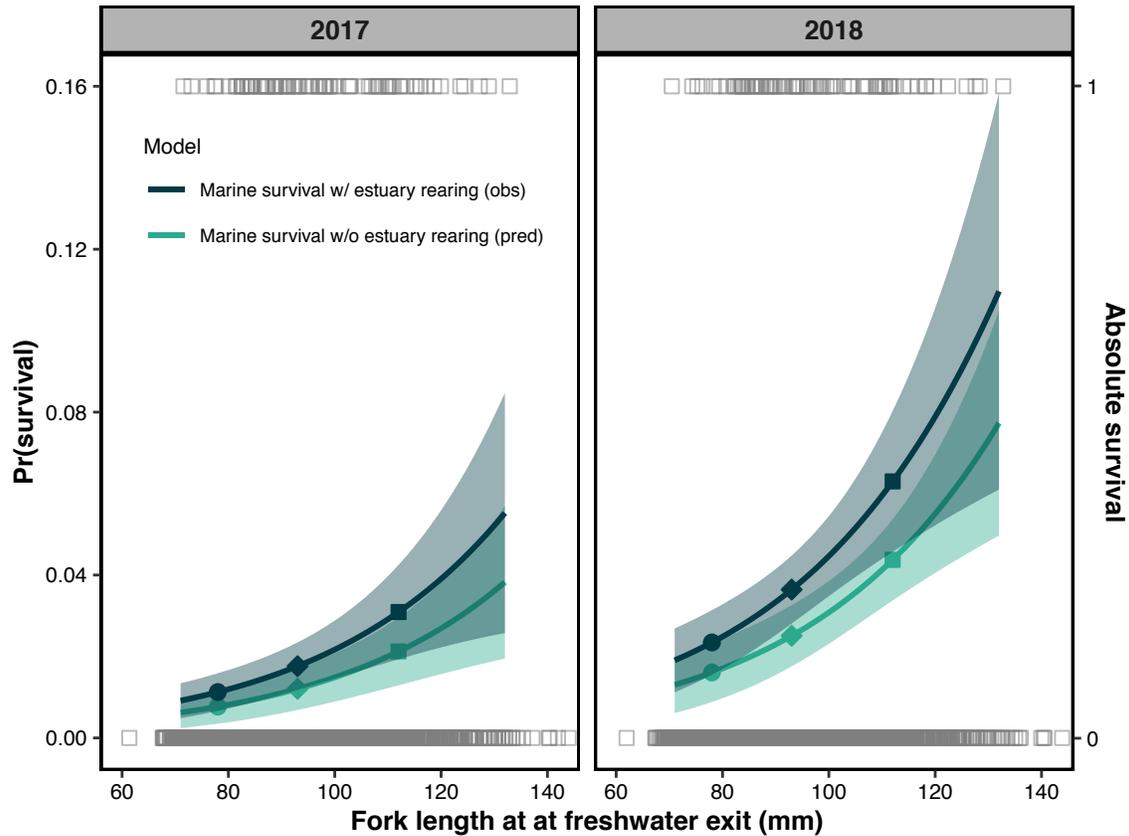


Figure 3.6. Relationship between fork length at freshwater exit and marine survival of juvenile coho salmon.

Note: The primary y-axis indicates the probability of marine survival observed for juvenile coho salmon with access to estuary rearing habitats (blue) and predicted in the absence of estuary rearing (green). Closed points indicate juvenile coho salmon representative of the 10% ($Q_{0.1}$), 50% ($Q_{0.5}$) and 90% ($Q_{0.9}$) quantiles in the size distribution at freshwater exit (circles, diamonds, and squares, respectively). The secondary y-axis depicts absolute survival of juvenile coho salmon tagged at the Koeve River upon freshwater exit. Grey points with an absolute survival value of 1 indicate tagged individuals that survived the ocean and were redetected in the Koeve River as adults; grey squares with an absolute survival value of 0 indicate tagged individuals were not detected returning as adults.

3.5. Discussion

Our results suggest that estuary stopover behaviours exhibited by migrating juvenile coho salmon reflect carryover effects from freshwater life-stages and modulate

future constraints imposed by the marine environment. Individuals that left freshwater at a small size had longer estuary stopovers than their larger counterparts, and consequently grew relatively more prior to marine entry. Notably, we estimate that growth attained during estuary stopover increased the likelihood of marine survival by 44-46% for individuals spanning the juvenile size distribution. Prolonged estuary residence by juvenile coho salmon *en route* to the ocean appears to reflect an adaptive migratory strategy by which small individuals increase their body size prior to entering the higher-risk marine environment. By using estuaries as stopover habitats, juvenile coho salmon can improve their prospects for survival in a size-selective ocean.

Our analyses provide empirical evidence of the state-dependent nature of estuary stopover behaviour by juvenile salmon. While sample sizes were small due to a low recapture rate, three independent approaches for estimating estuary stopover duration indicated a negative relationship between size at freshwater exit and estuary stopover, whereby individuals in the lower 10% of the freshwater size distribution spent 2-3 times longer rearing in the estuary than individuals in the upper 10% of the size distribution. Similar patterns of size-dependent estuary stopover by juvenile salmonids have been indirectly inferred for coho salmon in the Skeena River estuary (Moore et al. 2016), and observed for sockeye salmon (*O. nerka*) in Rivers Inlet (Egorova 2016) and steelhead trout (*O. mykiss*) in California's Scott Creek estuary (Bond et al. 2008). Similarly, there is some evidence that the size-dependency of migratory behaviours extends to juvenile salmon moving through nearshore habitats. For example, large sockeye smolts migrating seaward from the Fraser River and Vancouver Island demonstrated rapid, direct movement through the Strait of Georgia, while smaller individuals tended to linger near marine entry points for up to several weeks (Freshwater et al. 2016). As such, size-dependent estuary stopover by juvenile salmonids may be a common but underappreciated phenomenon.

We found that high growth rates in the estuary partially attenuated freshwater carryover effects, resulting in each juvenile outmigrant cohort entering the ocean both larger and less variable in size than it was at freshwater exit. Across our three sampling years, coho salmon yearlings exited freshwater at sizes ranging from 61-155 mm. This broad size range remained remarkably consistent across years, and likely reflects a suite of freshwater processes acting at various spatial scales to produce a diversity of juvenile salmon body sizes (e.g., water temperature, density dependence, competition

for food resources, nutrient subsidies, adult spawn timing; Quinn 2018). Following freshwater exit, growth rates observed in the estuary ranged from 0.58-0.95 mm/day. An informal review of the literature suggests that these greatly exceed growth rates observed in freshwaters, which range from 0.01-0.18 mm/day for comparably-sized juvenile coho salmon (Dolloff 1987, Kahler et al. 2001, Roni et al. 2012, Hauer 2013). Similar findings of high growth rates in estuaries relative to freshwaters have been reported for restored tidal wetlands (Craig et al. 2014), brackish river deltas (Davis et al. 2019), and glacially-fed estuary channels (Hoem Neher et al. 2014). Interannual variation in observed estuary growth rates may be related to variability in environmental characteristics such as water temperature, precipitation, saltwater intrusion, and the productivity of the adjacent marine environment. For example, the 2018 sampling season—which featured the highest growth rates observed in our study—was characterized by high temperatures and little rainfall, resulting in a high degree of saltwater intrusion upstream. This combination of environmental factors may have resulted in thermally favourable growth conditions (e.g., Mortensen et al. 2000) or enhanced the prey landscape for juvenile coho salmon rearing in the estuary. Regardless, our study supports the idea that intact estuaries can provide opportunities for exceptionally high, albeit interannually variable, growth rates relative to freshwater habitats.

While estuary habitat mosaics are widely recognized as important nursery grounds for juvenile fishes including salmon (Healey 1982, Beck et al. 2001, Nagelkerken et al. 2015), to date it has proven challenging to quantify the relationship between estuary rearing and lifetime fitness. Here we offer novel empirical estimates of the survival benefits afforded by facultative rearing in an intact, productive estuary with high growth potential relative to freshwater habitats. We predicted that, following estuary stopover, marine survival for Koeye River coho salmon is 44-46% higher across juvenile size classes than it would be if access to estuary rearing habitat were lost, assuming that growth is the primary impact of estuary stopover. This estimate from our mark-recapture study corroborates cross-system correlative studies that observed decreased salmon population productivity associated with estuary degradation (Magnusson and Hilborn 2003, Meador 2014). We note that our findings reflect the site-specific contribution of the Koeye River estuary, which is largely ecologically intact and minimally altered by modern human impact. Across salmon watersheds, there is likely variation in estuary residence

and growth potential depending on the characteristics of available rearing habitats. Regardless, our findings contribute to a growing body of literature indicating that the state of estuary habitats can be an important control on individual survival and population productivity.

The marine survival benefits associated with estuary stopover were similar across juvenile coho salmon size classes, counter to our prediction that individuals that were small at freshwater exit would derive the greatest benefits from extended estuary rearing. While survival benefits were slightly higher for smaller individuals, the difference relative to larger individuals was negligible. The consistency of the estuary contribution to individual fitness appears to be the product of opposing nonlinear relationships between 1) estuary residence and 2) marine survival, whereby estuary residency (and thereby relative growth) decreased with juvenile salmon size while marine survival increased with size. We note that marine survival estimates derived from our analysis do not account for imperfect detection of returning adult coho salmon at freshwater RFID arrays; therefore, marine survival values should be considered minimum estimates. However, since the probability of detecting a returning adult is unrelated to its body size at outmigration, our analysis provides an unbiased estimate of the influence of juvenile size on marine survival.

Juvenile body size is likely a key determinant of the ability to overcome new challenges encountered in the ocean (Sogard 1997, Saloniemi et al. 2004), with larger individuals better able to evade predation by larger fishes (Duncan and Beaudreau 2019) and seabirds (Tucker et al. 2016) and pursue larger, energy-dense prey types (Pope et al. 1994, Daly et al. 2009, Duffy et al. 2010). Although our study revealed a positive relationship between juvenile size, estuary growth, and marine survival across years, body size is one of several potential factors that may contribute to observed patterns of marine survival. Perhaps most notably, shifting ocean conditions are known to exert substantial influence on marine survival and may either amplify or modulate size-selective pressures (Walsworth et al. 2020). Given that the direction and magnitude of marine size-selective survival can vary interannually (Ulaski et al. 2020), and that estuary growth rates varied substantially across years in this study, we speculate that survival benefits derived from estuary stopover will be dynamic through time, depending on environmental conditions.

The estuary-absence scenario underlying our marine survival analysis is analogous to rapid degradation and loss of an intact and productive estuary (e.g., via extensive diking and draining, industrial or urban development, or other forms of drastic habitat alteration; Hodgson et al. 2020). For juvenile salmon populations whose natal watersheds historically featured intact and productive estuaries, the size and timing at which downstream migration occurs have presumably evolved to maximize fitness in the presence of estuary habitat (Chapter 2). If that habitat is rapidly lost, migration traits that evolved over millennia may no longer be optimal for survival. Juvenile salmon reliant on estuary habitats for pre-ocean growth may instead encounter constricted areas of lower-quality estuary habitat with increased density-dependence, decreased food availability, and higher predation risk—thus negatively impacting survival in a critical life-history phase (Magnusson and Hilborn 2003, Meador 2014, David et al. 2016). Over time, salmon populations could potentially adapt to estuary habitat loss through evolutionary changes in their migration traits. However, these traits simultaneously depend upon trade-offs associated with the freshwater rearing stage, and freshwater habitats are also being degraded by human activities (McClure et al. 2008). Broadly, we speculate that evolution could ameliorate some negative impacts of estuary habitat loss (Bowlin et al. 2010), but the pace and possible extent of this potential adaptive response remain unknown.

Together, our findings indicate that juvenile coho salmon use intact estuaries as flexible “solution spaces” for maximizing fitness before entering a size-selective ocean. Until recently, juvenile coho salmon life-histories were considered relatively fixed (Jones et al. 2014) with fry rearing for one year in natal freshwaters before migrating directly to sea (Thorpe 1994). It is now known that coho salmon exhibit a variety of estuary rearing strategies, ranging from opportunistic seasonal use of the stream-estuary ecotone to yearlong estuary residence by subyearling (fry) migrants (Miller and Sadro 2003, Koski 2009, Jones et al. 2014). We note that our study only considered yearling migrants; though abundant, subyearling migrants were too small to PIT tag and were not consistently enumerated at freshwater exit. Thus, our estimates of the benefits of estuary rearing were focused specifically on individuals that were undergoing smoltification and would migrate to sea within a few months of tagging, and should be considered conservative. Numerous studies demonstrate that juvenile coho salmon that rear in estuaries during their early life-histories constitute a meaningful proportion of

adult returns (Jones et al. 2014, 2021, Bennett et al. 2015). Had it been feasible, we anticipate that inclusion of subyearlings would substantially increase the magnitude of the estuary contribution to marine survival and overall production in the Koeye River watershed.

Estuaries are among the most degraded habitats on earth, and are increasingly squeezed by coastal development and sea level rise (Lotze et al. 2006, Kirwan and Murray 2008). For example, under high sea level rise projections, up to 83% of estuarine marsh habitats along the United States Pacific Coast may be lost by 2110 (Thorne et al. 2018). Our study adds to mounting evidence that conservation or restoration of estuaries could provide disproportionately positive benefits in salmon ecosystems (e.g., Moore et al. 2015; Ellings et al. 2016; Toft et al. 2018; Hodgson et al. 2020). Complex estuary nursery habitats—as exemplified by the Koeye River estuary—offer myriad potential benefits to juvenile salmon, including diverse and abundant prey resources (Arbeider et al. 2019, Woo et al. 2019), lower rates of density-induced competition (David et al. 2016), and structurally complex microhabitats (Chalifour et al. 2019, Sharpe et al. 2019) that offer refugia from predators (Simenstad and Cordell 2000, Seitz et al. 2020). Our findings contribute to the estuary nursery concept by demonstrating that estuary stopover can directly boost an individual’s chance of marine survival. The correlation between juvenile salmon body size at freshwater exit and duration of estuary stopover suggests that this migratory stage represents a critical—yet flexible—period for maximizing individual fitness in later life stages. Conservation of estuary stopover habitats—and restoration where they have been degraded—could bolster marine survival and recruitment in the face of increasingly unpredictable environmental conditions.

Our study is broadly relevant to understanding the fitness benefits of stopover habitats for migratory species. For juvenile salmonids, the joint influence of upstream carryover effects and downstream constraints appears to shape size-dependent estuary stopover decisions, toward maximizing survival prospects across the life-cycle. These findings align with predictions from state-dependent life-history theory, whereby the state (e.g., body size) of an individual during key decision windows determines the optimal timing of life-history transitions (e.g., smolt migration to the ocean; Werner and Gilliam 1984, Satterthwaite et al. 2009). For migratory species, access to productive stopover habitats can have population-level consequences for migration success, survival, and

reproduction (Sheehy et al. 2011, Runge et al. 2014, Studds et al. 2017). Therefore, understanding the fitness implications of stopover habitat use is fundamental to migration ecology and the successful conservation of migratory species.

3.6. Acknowledgements

This research was a product of collaboration between Simon Fraser University, the Heiltsuk Nation, and the Hakai Institute. We are grateful to the Heiltsuk Integrated Resource Management Department and the Qqs Projects Society for their continued partnership on research conducted in the Koeye River watershed. We thank Jeremy Jorgenson, Jared Reid, Jessel Housty, Melvin Innes, Jefferson Brown, Howard Duncan, Robert Duncan, Liam Nazarek, Ray Wilson, Jess Housty, and William Housty for their essential contributions to data collection and to the broader collaborative research program. We also thank William Housty for his helpful feedback on the manuscript. Funding for this research was provided by the Hakai Institute and Tula Foundation, Pacific Salmon Foundation, TIDES Canada (MakeWay), the Vancouver Foundation, the McLean Foundation, the Nature Trust of British Columbia, and the Liber Ero Foundation.

Chapter 4. General Discussion

In this thesis, I combined a multi-population analysis with a population-specific study to elucidate linkages between estuary rearing habitats and juvenile salmon migration traits, stopover behaviour, and marine survival. Specifically, my research offers insight into two subsequent stages of juvenile salmon migration: exit from natal freshwaters (Chapter 2) and estuary stopover prior to marine entry (Chapter 3). In Chapter 2, I compiled freshwater emigration data from 64 coho salmon populations, ranging from Southeast Alaska to Central California, to investigate the extent to which migratory traits were correlated with estuary rearing habitats and watershed covariates. In Chapter 3, I used a mark-recapture study to examine individual migratory behaviour from juvenile coho salmon from British Columbia's Koeeye River, with a focus on quantifying estuary residence and growth, and linkages between estuary stopover and marine survival. In this concluding chapter, I review key findings and discuss their implications, as well as explore possible directions for future research. Collectively, my findings indicate that certain juvenile salmon migration traits are locally adapted to estuary habitats, and that state-dependent estuary stopover can mitigate freshwater carryover effects and boost marine survival.

Pacific salmon exhibit considerable trait diversity, which can reflect local adaptations to habitat conditions experienced throughout their migratory life-histories (Hodgson and Quinn 2002, Beechie et al. 2006). My second chapter shed light on the breadth of migratory trait diversity exhibited by juvenile coho salmon, and revealed that timing-related traits were correlated with characteristics of both estuary and freshwater rearing habitats. There was considerable diversity in migration timing traits across populations: peak migration date ranged from early-April to mid-June, and the duration of the migration window ranged from 7 to 65 days. Analyses revealed that juvenile salmon migration timing and duration were correlated with latitudinal clines and various metrics of estuary configuration: migrations were earlier and more protracted for populations at southerly latitudes, and for those with access to estuaries that were more enclosed and featured more complex shorelines. At northerly latitudes, and where estuaries were more open and had simpler shorelines, migration occurred later and over a more constricted timeframe. Although there was also substantial variation in

population-specific body size at migration, analyses surprisingly did not reveal correlations between size-related traits and estuary or watershed characteristics.

Migration from one habitat to another can be viewed as a trade-off between maximizing growth opportunities and minimizing mortality risks (Werner and Gilliam 1984, Quinn et al. 2009, Satterthwaite et al. 2012). For juvenile coho salmon with access to complex, enclosed estuaries, early downstream migration indicates local adaptation to estuarine habitats that can feature superior growth opportunities relative to freshwater, combined with predation risk that is presumably lower than that encountered in the ocean. Where downstream estuaries are relatively enclosed, juvenile salmon that leave freshwaters early can access a zooplankton prey assemblage which reflects that found in the nearshore coastal zone (Lucena-Moya and Duggan 2017). Access to such energy-dense prey can lead estuary growth rates to be much higher than freshwater growth rates (Hayes et al. 2008, Hoem Neher et al. 2013, Chalde and Fernández 2017). Simultaneously, shallow, complex estuary shorelines can serve as predator refugia, leading to mortality risk that is presumably lower in estuaries relative to offshore marine waters (Paterson and Whitfield 2000, Willette 2001, Seitz et al. 2020). Therefore, early migration to estuaries could help juvenile salmon maximize growth while minimizing mortality risk.

For long-distance migrants, stopover habitats can be critical sites for rest and refuelling, toward maximizing the likelihood of surviving migration (Moore et al. 1995, Alerstam et al. 2003, Sawyer et al. 2009). My third chapter revealed distinct patterns of state-dependent estuary stopover by juvenile coho salmon from the Koeys River. Juvenile salmon that were small at freshwater exit exhibited relatively long estuary stopovers lasting up to 40 days, while those that were large migrated through the estuary and to the ocean rapidly, in as few as two days. Regardless of the duration of estuary residence, nearly all recaptured individuals grew at high rates in the estuary, with growth ranging from 0.58-0.95 mm/day. Due to their long stopovers, small juvenile salmon achieved more growth as compared to their larger counterparts. As a result, each juvenile cohort entered the ocean larger and less variable in size than it was at freshwater exit. Analysis of returning adults revealed that marine survival was positively correlated with juvenile body size, and that estuary-associated growth after freshwater exit improved the marine survival prospects by 44-46% across size classes. Together, these findings offer evidence for state-dependent estuary stopover by juvenile coho

salmon *en route* to the ocean, and demonstrate that growth achieved during this period can boost marine survival rates.

Estuary habitats are widely considered important nursery grounds for juvenile fishes including Pacific salmon (Healey 1982, Beck et al. 2001, Sheaves et al. 2015), but it has proven difficult to quantify the relationship between estuary use and lifetime fitness. Understanding drivers of fitness is challenged by the need to track individuals throughout their life-cycles (Harrison et al. 2011, O'Connor et al. 2014). In the case of Pacific salmon, this challenge is magnified by migratory life-histories that commonly span thousands of kilometres, in addition to the fundamental complications associated with tracking small fishes through large and dynamic bodies of water. In recent decades, advances in tracking technologies—and their increasing availability—have transformed our ability to follow individual migratory animals throughout their life-cycles as a means of better understanding the habitats and behaviours that shape individual fitness. My Chapter 3 analyses relied on Passive Integrated Transponder (PIT) technology to characterize linkages across habitats: between freshwater experience and estuary stopover behaviour, and between estuary stopover behaviour and marine survival. By implanting each juvenile with a unique PIT tag at freshwater exit, we were able to quantify how freshwater carryover effects influenced individual residence and growth in the estuary, and subsequently identify those juveniles that returned as adults to spawn—thus providing empirical data to link estuary stopover with marine survival. Individual tracking technologies such as PIT tags can be especially useful for characterizing use of habitats that are only occupied for a relatively brief period, such as stopover sites. Broadly, such technological advances increasingly enable scientists to track the fates of migratory animals across the continuum of habitats they occupy, and therefore more fully describe both life-history diversity and drivers of individual fitness.

Collectively, my two thesis chapters offer insights into the interplay between local adaptation and behavioural plasticity by migrating juvenile coho salmon. While my Chapter 2 findings suggest that freshwater emigration timing is locally adapted to both latitude and estuary habitat characteristics, my Chapter 3 findings indicate that migratory behaviour in the estuary is plastic, influenced by individual body condition (i.e., freshwater carryover effects) at the time of downstream migration. Freshwater carryover effects often reflect processes such as density dependence, competition, and thermal experience that can unfold at fine spatial scales (Walters et al. 2013, Thorson et al.

2014) and produce considerable within-population variation in body size. Such variation is common across populations, as evidenced in both of my data chapters. For example, body size at freshwater exit ranged from 61-155 mm for age-1+ individuals from three consecutive Koeve River cohorts. This variation remained remarkably consistent across years, suggesting freshwater rearing conditions that vary spatially throughout the watershed (as opposed to interannually-variable conditions affecting the entire watershed). Where suitable estuary habitat is available, it may therefore be adaptive for migration to commence earlier, allowing the contingent of juveniles whose freshwater experience invariably results in a small body size time to “catch up” via estuary stopover and improve their survival prospects in the size-selective marine environment. While neither of my chapters examined how body size at migration changes with the progression of the migration window, I speculate that protracted migrations by populations with access to complex, enclosed estuaries (as observed in Chapter 2) likely feature a greater proportion of smaller migrants at the outset and progressively larger migrants as the migration window progresses. That said, while the availability of estuary stopover habitat likely makes early migration particularly advantageous for small-bodied juvenile salmon, research indicates that early migration can also benefit large juveniles. Although large juveniles will likely exhibit estuary shorter stopovers than their smaller counterparts (as observed in Chapter 3), evidence suggests that marine survival can be highest for large-bodied juveniles that migrate early relative to the rest of their cohort (Scheuerell et al. 2009, Wilson et al. 2021). As such, where favourable estuary conditions exist, early migration appears to benefit small- and large-bodied juveniles alike. By extension, the improved rates of marine survival (and presumed successful reproduction) of these individuals would favour persistence of the early migration trait within the population. Broadly, this reinforces the concept of the estuary as a flexible “solution space” where juvenile coho salmon traits and behaviours reflect the combined forces of local adaptation and plasticity.

Broadly, my findings contribute to a growing body of literature demonstrating that estuary habitats play an important yet underappreciated role in the life-histories of coho salmon. Until recently, estuaries were considered minimally important habitats for coho salmon (Jones et al. 2014). Juveniles were thought to transit estuaries rapidly after freshwater exit, using these habitats as migratory corridors rather than as rearing or stopover areas. Thorpe (1994) states that juvenile coho salmon “move quickly to the sea

without delay in the estuary,” attributing this behaviour to rapid smoltification after a year of freshwater rearing. Historically, this view was sufficiently pervasive to lead some scientists to reject findings of apparent estuary reliance by juvenile coho salmon. For example, in a study relating smolt-to-adult survival to characteristics of estuary rearing habitats, Magnusson and Hilborn (2003) dismiss a significant relationship between coho salmon survival and estuary area for lack of a known causal linkage. However, there is growing support for such a linkage: it is increasingly recognized that coho salmon can and do rely extensively on estuary habitats as juveniles, and exhibit a spectrum of estuary rearing strategies ranging from facultative seasonal use of the stream-estuary ecotone to long-term estuary residence by fry and parr migrants (Miller and Sadro 2003, Koski 2009, Jones et al. 2014, Moore et al. 2016). My research further contextualizes the role of estuaries in the coho salmon life-cycle by describing their role as stopover habitats. I demonstrate that estuaries are more than just salinity acclimatization zones for juvenile coho salmon—rather, they are valuable foraging grounds that enable rapid growth prior to marine entry, which confers survival benefits across the life-cycle.

Future analyses would do well to explore linkages between estuary rearing habitats and the full range of migratory strategies exhibited by juvenile coho salmon, toward understanding their role in sustaining population-level productivity and buffering the effects of environmental change. Notably, both my Chapter 2 and Chapter 3 analyses focused on the “typical” yearling life-history strategy, wherein juveniles rear for one to two years in freshwater before initiating seaward migration. My research could be extended to incorporate subyearling migrants, such as fry that migrate downstream in spring and parr that migrate downstream in fall. For example, replication of my Chapter 2 analyses with inclusion of subyearling migrant data could reveal links between estuary rearing habitats and body size at migration, which were possibly obfuscated by my focus on yearling migrants. Subyearling migratory strategies may also be more common in systems with favourable estuary rearing conditions, reflecting the improved viability of early migration. For example, in the Koye River we observed a consistent annual cohort of spring subyearling migrants, which were too small to PIT tag at freshwater exit but were routinely encountered rearing in the estuary through the summer months. Similar subyearling migrant behaviour has been documented elsewhere (e.g., Miller and Sadro 2003, Bennett et al. 2011, Jones et al. 2014, Rebenack et al. 2015), and its prevalence could feasibly covary with the extent, configuration, or quality of accessible

estuary rearing habitats. For managers, a failure to incorporate diverse juvenile life-histories in salmon population assessments can lead to flawed estimates of smolt abundance and smolt-to-adult survival (Bennett et al. 2015, Rebenack et al. 2015), in addition to a fundamental misunderstanding of the relative contributions of freshwater and estuarine rearing habitats to population productivity (Jones et al. 2021). In general, expanding my research to incorporate a fuller range of juvenile salmon migratory strategies would help situate the estuary rearing phase, and its relative opportunities and constraints, within the continuum of habitats occupied by salmon throughout their complex life-cycles.

Human encroachment on coastal habitats has altered the extent, structure, and function of estuaries throughout the native range of Pacific salmon. Estuaries have long been focal points of human activity, and estuary habitat degradation and loss has rapidly accelerated in the course of the past 150 years (Lotze et al. 2006). This has driven population declines in aquatic and terrestrial species that rely on estuaries for part or all of their life-cycles, accompanied by decreases in aquatic vegetation and water quality and a rise in species invasions (Lotze et al. 2006). Along the Pacific Coast of the United States, an estimated 85% of vegetated tidal wetlands have been lost (Brophy et al. 2019), and losses of similar magnitude are projected in the course of the next century (Thorne et al. 2018). In coastal British Columbia, an assessment of 376 estuaries revealed that more than half were considered either “highly threatened” or “moderately threatened” by human activities such as urbanization, agriculture, and vessel traffic (Robb 2014). Of the 49 estuaries included in my Chapter 2 analyses, urban and agricultural land use dominated shorelines (> 50% land use) in fourteen estuaries. Land conversion is commonly accompanied by efforts to fortify and simplify estuary shorelines (e.g., armouring, diking). These modifications can alter physical structure by disrupting sediment transport, truncating the intertidal zone, and introducing steep gradients and pier shade into nearshore habitats (Dugan et al. 2008, Bulleri and Chapman 2010, Munsch et al. 2014). Such structural changes disrupt the terrestrial-aquatic linkages characteristic of complex estuary shorelines, and can subsequently reduce terrestrial prey inputs and submerged aquatic vegetation coverage—key components of estuary nursery function for juvenile salmon (Munsch et al. 2015).

Beyond persistent human encroachment, climate change threatens to further alter estuary structure and function to the detriment of juvenile Pacific salmon (Munsch

et al. 2019, Davis et al. 2021). For example, rising sea levels in coastal areas already impacted by human development could cause “coastal squeeze,” whereby vegetated estuary habitats are prevented from moving landward in line with salinity gradients (Kirwan and Murray 2008, Elliott et al. 2019). Where this constraint occurs, the projected consequence is a loss of preferred rearing habitats (e.g., emergent salt marsh, eelgrass meadows) and associated prey provisioning for estuary-reliant juvenile salmon (Davis et al. 2021). Simultaneously, warming temperatures could decrease the habitability of shallow nearshore areas preferred by juvenile salmon, or exacerbate estuary habitat fragmentation via decreased freshwater flows (Munsch et al. 2019, Davis et al. 2021). Together, these impacts threaten to erode the nursery function of estuary habitats, and compromise their value as stopover sites for juvenile salmon.

In the face of widespread and ongoing estuary loss, my findings highlight the importance of increased estuary conservation and restoration efforts. Evidence suggests that Pacific salmon have the potential to rapidly adapt their migratory strategies in the face of habitat change, but these shifts presumably come with trade-offs. While habitat loss can lead to shifts in predominant juvenile life-history strategies and possible trait homogenization (Williams et al. 2008), habitat restoration can create conditions that are conducive to re-emergence of lost diversity. Indeed, studies have shown that juvenile salmon can rapidly recolonize restored estuary habitats (Ellings et al. 2016) and that restoration can promote expression of renascent life-history strategies (Bottom et al. 2005). For Pacific salmon, migratory life-histories exhibited by a minority of juveniles—such as extended estuary rearing—can contribute disproportionately to adult returns, especially in the face of changing environmental conditions (Bennett et al. 2015, Cordoleani et al. 2021, Jones et al. 2021). Given my Chapter 2 finding that coho salmon migrations are locally adapted to estuary shoreline complexity, restoring the structure and function of nearshore habitats (e.g., through “living shoreline” projects; Gittman et al. 2016) may be particularly important. Where estuary habitats are degraded or threatened, conservation and restoration is crucial for ensuring continued estuary nursery and stopover functions for juvenile salmon, and to sustaining life-history diversity into the future.

Preserving connectivity and integrity of habitats used across the life-cycle is essential for the conservation of migratory species (Bowlin et al. 2010, Runge et al. 2014), including Pacific salmon. Even habitats occupied for relatively short periods, such

as migratory corridors and stopover sites, can be vital for population viability and persistence (Moore et al. 1995, Weber et al. 1999, Sheehy et al. 2011, Runge et al. 2014). Broadly, my thesis research helps contextualize the role of estuary habitats within the migratory life-histories of coho salmon, and describes estuary contributions to migratory adaptations, behaviour, and survival across the salmon life-cycle. Specifically, I have shown that the migration timing of juvenile coho salmon is linked to estuary habitat characteristics, and that state-dependent estuary stopover can mitigate freshwater carryover effects and improve marine survival prospects. As evidence mounts for the crucial role of estuaries in the early life-histories of Pacific salmon, we would do well to protect and restore these critical yet flexible rearing habitats—toward ensuring that salmon persist in a rapidly changing world.

References

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Page *in* B. . Petrov and F. Csaki, editors. 2nd International Symposium on Information Theory. Budapest, Hungary.
- Alerstam, T., and A. Hedenstrom. 1998. The development of bird migration theory. *Journal of Avian Biology* 29:343–369.
- Alerstam, T., A. Hedenström, and S. Åkesson. 2003. Long-distance migration: evolution and determinants. *Oikos* 103:247–260.
- Arbeider, M., C. Sharpe, C. Carr-Harris, and J. W. Moore. 2019. Integrating prey dynamics, diet, and biophysical factors across an estuary seascape for four fish species. *Marine Ecology Progress Series* 613:151–169.
- Armstrong, J. B., and D. E. Schindler. 2013. Going with the flow: spatial distributions of juvenile coho salmon track an annually shifting mosaic of water temperature. *Ecosystems* 16:1429–1441.
- Baldock, J. R., J. B. Armstrong, D. E. Schindler, and J. L. Carter. 2016. Juvenile coho salmon track a seasonally shifting thermal mosaic across a river floodplain. *Freshwater Biology* 61:1454–1465.
- Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography* 49:423–437.
- Beamish, R. J., C. Mahnken, and C. M. Neville. 2004. Evidence that reduced early marine growth is associated with lower marine survival of coho salmon. *Transactions of the American Fisheries Society* 133:26–33.
- Beck, M. W., K. L. Heck, K. W. Able, D. L. Childers, D. B. Eggleston, B. M. Gillanders, B. Halpern, C. G. Hays, K. Hoshino, T. J. Minello, R. J. Orth, P. F. Sheridan, and M. P. Weinstein. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* 51:633–641.
- Beechie, T., E. Buhle, M. Ruckelshaus, A. Fullerton, and L. Holsinger. 2006. Hydrologic regime and the conservation of salmon life history diversity. *Biological Conservation* 130:560–572.
- Bennett, T. R., P. Roni, K. Denton, M. Mchenry, and R. Moses. 2015. Nomads no more: early juvenile coho salmon migrants contribute to the adult return. *Ecology of Freshwater Fish* 24:264–275.

- Bennett, T. R., R. C. Wissmar, and P. Roni. 2011. Fall and spring emigration timing of juvenile coho salmon from East Twin River, Washington. *Northwest Science* 85:562–570.
- Biebach, H., W. Friedrich, and G. Heine. 1986. Interaction of bodymass, fat, foraging and stopover period in trans-Sahara migrating passerine birds. *Oecologia* 69:370–379.
- Björnsson, B. T., S. O. Stefansson, and S. D. McCormick. 2011. Environmental endocrinology of salmon smoltification. *General and Comparative Endocrinology* 170:290–298.
- Bolker, B. 2020. *bbmle: Tools for general maximum likelihood estimation*. R package version 1.0.23.1. <https://cran.r-project.org/package=bbmle>.
- Bond, M. H., S. A. Hayes, C. V. Hanson, and R. B. MacFarlane. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. *Canadian Journal of Fisheries and Aquatic Sciences* 65:2242–2252.
- Bottom, D. L., K. K. Jones, T. J. Cornwell, A. Gray, and C. A. Simenstad. 2005. Patterns of Chinook salmon migration and residency in the Salmon River estuary (Oregon). *Estuarine, Coastal and Shelf Science* 64:79–93.
- Bowlin, M. S., I. A. Bisson, J. Shamoun-Baranes, J. D. Reichard, N. Sapir, P. P. Marra, T. H. Kunz, D. S. Wilcove, A. Hedenström, C. G. Guglielmo, S. Åkesson, M. Ramenofsky, and M. Wikelski. 2010. Grand challenges in migration biology. *Integrative and Comparative Biology* 50:261–279.
- Bradford, M. J., G. C. Taylor, and J. A. Allan. 1997. Empirical review of coho salmon smolt abundance and the prediction of smolt production at the regional level. *Transactions of the American Fisheries Society* 126:49–64.
- Brennan, S. R., D. E. Schindler, T. J. Cline, T. E. Walsworth, G. Buck, and D. P. Fernandez. 2019. Shifting habitat mosaics and fish production across river basins. *Science* 364:783–786.
- Brophy, L. S., C. M. Greene, V. C. Hare, B. Holycross, A. Lanier, W. N. Heady, K. O'Connor, H. Imaki, T. Haddad, and R. Dana. 2019. Insights into estuary habitat loss in the western United States using a new method for mapping maximum extent of tidal wetlands. *Page Plos One*.
- Bulleri, F., and M. G. Chapman. 2010. The introduction of coastal infrastructure as a driver of change in marine environments. *Journal of Applied Ecology* 47:26–35.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Second Edi. Springer, New York, NY.

- Carr-Harris, C. N., J. W. Moore, A. S. Gottesfeld, J. A. Gordon, W. M. Shepert, J. D. J. Henry, H. J. Russell, W. N. B. Helin, D. J. Doolan, and T. D. Beacham. 2018. Phenological diversity of salmon smolt migration timing within a large watershed. *Transactions of the American Fisheries Society* 147:775–790.
- Carrascal, L. M., I. Galván, and O. Gordo. 2009. Partial least squares regression as an alternative to current regression methods used in ecology. *Oikos* 118:681–690.
- Chalde, T., and D. A. Fernández. 2017. Early migration and estuary stopover of introduced Chinook salmon population in the Lapataia River Basin, southern Tierra del Fuego Island. *Estuarine, Coastal and Shelf Science* 199:49–58.
- Chalifour, L., D. Scott, M. MacDuffee, J. Iacarella, T. Martin, and J. Baum. 2019. Habitat use by juvenile salmon, other migratory fish, and resident fish species underscores the importance of estuarine habitat mosaics. *Marine Ecology Progress Series* 625:145–162.
- Chasco, B., B. Burke, L. Crozier, and R. Zabel. 2021. Differential impacts of freshwater and marine covariates on wild and hatchery Chinook salmon marine survival. *PLoS ONE* 16:1–23.
- Chittenden, C. M., J. L. A. Jensen, D. Ewart, S. Anderson, S. Balfry, E. Downey, A. Eaves, S. Saksida, B. Smith, S. Vincent, D. Welch, and R. S. McKinley. 2010. Recent salmon declines: a result of lost feeding opportunities due to bad timing? *PLoS ONE* 5.
- Clark, T. D., N. B. Furey, E. L. Rechisky, M. K. Gale, K. M. Jeffries, A. D. Porter, M. T. Casselman, A. G. Lotto, D. A. Patterson, S. J. Cooke, A. P. Farrell, D. W. Welch, and S. G. Hinch. 2016. Tracking wild sockeye salmon smolts to the ocean reveals distinct regions of nocturnal movement and high mortality. *Ecological Applications* 26:959–978.
- Commission for Environmental Collaboration. 2021. North American Environmental Atlas. Commission for Environmental Collaboration, Montreal, Quebec. <http://www.cec.org/naatlas/>.
- Cordoleani, F., C. C. Phillis, A. M. Sturrock, A. M. FitzGerald, A. Malkassian, G. E. Whitman, P. K. Weber, and R. C. Johnson. 2021. Threatened salmon rely on a rare life history strategy in a warming landscape. *Nature Climate Change* 11:982–988.
- Craig, B. E., C. A. Simenstad, and D. L. Bottom. 2014. Rearing in natural and recovering tidal wetlands enhances growth and life-history diversity of Columbia Estuary tributary coho salmon *Oncorhynchus kisutch* population. *Journal of Fish Biology* 85:31–51.

- Daly, E. A., R. D. Brodeur, and L. A. Weitkamp. 2009. Ontogenetic shifts in diets of juvenile and subadult coho and Chinook salmon in coastal marine waters: Important for marine survival? *Transactions of the American Fisheries Society* 138:1420–1438.
- David, A. T., C. A. Simenstad, J. R. Cordell, J. D. Toft, C. S. Ellings, A. Gray, and H. B. Berge. 2016. Wetland loss, juvenile salmon foraging performance, and density dependence in Pacific Northwest estuaries. *Estuaries and Coasts* 39:767–780.
- Davis, M. J., I. Woo, C. S. Ellings, S. Hodgson, D. A. Beauchamp, G. Nakai, and S. E. W. De La Cruz. 2019. Freshwater tidal forests and estuarine wetlands may confer early life growth advantages for delta-reared Chinook salmon. *Transactions of the American Fisheries Society* 148:289–307.
- Davis, M. J., I. Woo, C. S. Ellings, S. Hodgson, D. A. Beauchamp, G. Nakai, and S. E. W. De La Cruz. 2021. A climate-mediated shift in the estuarine habitat mosaic limits prey availability and reduces nursery quality for juvenile salmon. *Estuaries and Coasts*.
- DeVries, P., F. Goetz, K. Fresh, and D. Seiler. 2005. Evidence of a lunar gravitation cue on timing of estuarine entry by Pacific salmon smolts. *Transactions of the American Fisheries Society* 133:1379–1395.
- Dingle, H., and V. A. Drake. 2007. What is migration? *BioScience* 57:113–121.
- Dolloff, C. A. 1987. Seasonal population characteristics and habitat use by juvenile coho salmon in a small Southeast Alaska stream. *Transactions of the American Fisheries Society* 116:829–838.
- Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B. Reineking, B. Schröder, A. K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:27–46.
- Duffy, E. J., and D. A. Beauchamp. 2011. Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 68:232–240.
- Duffy, E. J., D. A. Beauchamp, R. M. Sweeting, R. J. Beamish, and J. S. Brennan. 2010. Ontogenetic diet shifts of juvenile Chinook salmon in nearshore and offshore habitats of Puget Sound. *Transactions of the American Fisheries Society* 139:803–823.
- Dugan, J. E., D. M. Hubbard, S. Schroeter, D. L. Revell, and I. F. Rodil. 2008. Ecological effects of coastal armoring on sandy beaches. *Marine Ecology* 29:160–170.

- Duncan, D. H., and A. H. Beaudreau. 2019. Spatiotemporal variation and size-selective predation on hatchery- and wild-born juvenile chum salmon at marine entry by nearshore fishes in Southeast Alaska. *Marine and Coastal Fisheries* 11:372–390.
- Efford, M. G. 2005. Migrating birds stop over longer than usually thought: comment. *Ecology* 86:3415–3418.
- Egorova, Y. 2016. Temporal and spatial patterns of outmigration of juvenile sockeye salmon in Rivers Inlet. University of British Columbia.
- Ellings, C. S., M. J. Davis, E. E. Grossman, I. Woo, S. Hodgson, K. L. Turner, G. Nakai, J. E. Takekawa, and J. Y. Takekawa. 2016. Changes in habitat availability for outmigrating juvenile salmon (*Oncorhynchus* spp.) following estuary restoration. *Restoration Ecology* 24:415–427.
- Elliott, M., J. W. Day, R. Ramachandran, E. Wolanski, Q. Fang, M. R. Sheehan, A. J. Seen, and J. C. Ellison. 2019. A synthesis: what is the future for coasts, estuaries, deltas and other transitional habitats in 2050 and beyond? Page Coasts and Estuaries: The Future. Elsevier Inc.
- Freshwater, C., B. J. Burke, M. D. Scheuerell, S. C. H. Grant, M. Trudel, and F. Juanes. 2018. Coherent population dynamics associated with sockeye salmon juvenile life history strategies. *Canadian Journal of Fisheries and Aquatic Sciences* 75:1346–1356.
- Freshwater, C., M. Trudel, T. D. Beacham, L. Godbout, C. E. M. Neville, S. Tucker, and F. Juanes. 2016. Divergent migratory behaviours associated with body size and ocean entry phenology in juvenile sockeye salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 73:1723–1732.
- Gargett, A. E. 1997. The optimal stability “window”: a mechanism underlying decadal fluctuations in North Pacific salmon stocks? *Fisheries Oceanography* 6:109–117.
- Geraci, M. 2016. Qtools: A collection of models and tools for quantile inference. *R Journal* 8:117–138.
- Gittman, R. K., C. H. Peterson, C. A. Currin, F. Joel Fodrie, M. F. Piehler, and J. F. Bruno. 2016. Living shorelines can enhance the nursery role of threatened estuarine habitats. *Ecological Applications* 26:249–263.
- Goertler, P. A. L., C. A. Simenstad, D. L. Bottom, S. Hinton, and L. Stamatiou. 2016. Estuarine habitat and demographic factors affect juvenile Chinook (*Oncorhynchus tshawytscha*) growth variability in a large freshwater tidal estuary. *Estuaries and Coasts* 39:542–559.
- Gosselin, J. L., and J. J. Anderson. 2017. Combining migration history, river conditions, and fish condition to examine cross-life-stage effects on marine survival in Chinook Salmon. *Transactions of the American Fisheries Society* 146:408–421.

- Greene, C. M., J. E. Hall, K. R. Guilbault, and T. P. Quinn. 2010. Improved viability of populations with diverse life-history portfolios. *Biology Letters* 6:382–386.
- Gross, M. R., R. M. Coleman, and R. M. McDowall. 1988. Aquatic productivity and the evolution of diadromous fish migration. *Science* 239:1291–1293.
- Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* 80:4–18.
- Hastie, T., R. Tibshirani, G. James, and D. Witten. 2021. An introduction to statistical learning (2nd edition). Page Springer Texts.
- Hauer, J. J. 2013. Overwinter survival and growth of juvenile coho salmon, *Oncorhynchus kisutch*, in Freshwater Creek, California.
- Hayes, S. A., M. H. Bond, C. V. Hanson, E. V. Freund, J. J. Smith, E. C. Anderson, A. J. Ammann, and R. B. MacFarlane. 2008. Steelhead growth in a small Central California watershed: upstream and estuarine rearing patterns. *Transactions of the American Fisheries Society* 137:114–128.
- Healey, M. C. 1980. Utilization of the Nanaimo River estuary by juvenile Chinook salmon *Oncorhynchus Tshawytscha*. *Fishery Bulletin* 77:653–668.
- Healey, M.C. 1982. Juvenile Pacific salmon in estuaries: The life support system. Pages 315–341 in V. S. Kennedy, editor. *Estuarine Comparisons*. Academic Press, New York.
- Heerhartz, S. M., and J. D. Toft. 2015. Movement patterns and feeding behavior of juvenile salmon (*Oncorhynchus* spp.) along armored and unarmored estuarine shorelines. *Environmental Biology of Fishes* 98:1501–1511.
- Henderson, M. A., and A. J. Cass. 1991. Effect of smolt size on smolt-to-adult survival for Chilko Lake sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* 48:988–994.
- Hilborn, R., T. P. Quinn, D. E. Schindler, and D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences of the United States of America* 100:6564–6568.
- Hoar, S. 1974. Smolt transformation: evolution, behavior, and physiology. *Journal of the Fisheries Research Board of Canada* 33:1234–1252.
- Hodgson, E. E., S. M. Wilson, and J. W. Moore. 2020. Changing estuaries and impacts on juvenile salmon: a systematic review. *Global Change Biology* 26:1986–2001.

- Hodgson, S., and T. P. Quinn. 2002. The timing of adult sockeye salmon migration into fresh water: Adaptations by populations to prevailing thermal regimes. *Canadian Journal of Zoology* 80:542–555.
- Hoem Neher, T. D., A. E. Rosenberger, C. E. Zimmerman, C. M. Walker, and S. J. Baird. 2013. Estuarine environments as rearing habitats for juvenile coho salmon in contrasting south-central Alaska watersheds. *Transactions of the American Fisheries Society* 142:1481–1494.
- Hoem Neher, T. D., A. E. Rosenberger, C. E. Zimmerman, C. M. Walker, and S. J. Baird. 2014. Use of glacier river-fed estuary channels by juvenile coho salmon: transitional or rearing habitats? *Environmental Biology of Fishes* 97:839–850.
- Holtby, L. B., B. C. Andersen, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 47:2181–2194.
- Hume, T. M., T. Snelder, M. Weatherhead, and R. Liefing. 2007. A controlling factor approach to estuary classification. *Ocean and Coastal Management* 50:905–929.
- Hutchings, J. A. 2004. Norms of reaction and phenotypic plasticity in Salmonid life histories. *Evolution Illuminated: Salmon and Their Relatives*:154–174.
- Jones, K. K., T. J. Cornwell, D. L. Bottom, L. A. Campbell, and S. Stein. 2014. The contribution of estuary-resident life histories to the return of adult *Oncorhynchus kisutch*. *Journal of Fish Biology* 85:52–80.
- Jones, K. K., T. J. Cornwell, D. M. Bottom, S. Stein, and S. Starceвич. 2021. Interannual variability in life-stage specific survival and life history diversity of coho salmon in a coastal Oregon basin. *Canadian Journal of Fisheries and Aquatic Sciences*.
- Kahler, T. H., P. Roni, and T. P. Quinn. 2001. Summer movement and growth of juvenile anadromous salmonids in small western Washington streams. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1947–1956.
- Kirwan, M. L., and A. B. Murray. 2008. Ecological and morphological response of brackish tidal marshland to the next century of sea level rise: Westham Island, British Columbia. *Global and Planetary Change* 60:471–486.
- Koenings, J. P., H. J. Geiger, and J. J. Hasbrouck. 1993. Smolt-to-adult survival patterns of sockeye salmon (*Oncorhynchus kisutch*): effects of smolt length and geographic latitude when entering the sea. *Canadian Journal of Fisheries and Aquatic Sciences* 50:600–611.
- Koenker, R. 2020. quantreg: Quantile regression. R package version 5.75. <https://cran.r-project.org/package=quantreg>.

- Koski, K. V. 2009. The fate of coho salmon nomads: the story of an estuarine-rearing strategy promoting resilience. *Ecology and Society* 14:1–15.
- Kucheryavskiy, S. 2020. mdatools – R package for chemometrics. *Chemometrics and Intelligent Laboratory Systems* 198:103937.
- Kvalheim, O. M. 2010. Interpretation of partial least squares regression models by means of target projection and selectivity ratio plots. *Journal of Chemometrics* 24:496–504.
- Laake, J. L., D. S. Johnson, and P. B. Conn. 2013. marked: an R package for maximum likelihood and Markov Chain Monte Carlo analysis of capture-recapture data. *Methods in Ecology and Evolution* 4:885–890.
- Levings, C.D. *Ecology of salmonids in estuaries around the world*. UBC Press, 2016.
- Loria, D. E., and F. R. Moore. 1990. Energy demands of migration on red-eyed vireos, *Vireo olivaceus*. *Behavioral Ecology* 1:24–35.
- Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson, J. B. C. Jackson, and M. Bay. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806–1809.
- Lucena-Moya, P., and I. C. Duggan. 2017. Correspondence between zooplankton assemblages and the Estuary Environment Classification system. *Estuarine, Coastal and Shelf Science* 184:1–9.
- Magnusson, A., and R. Hilborn. 2003. Estuarine influence on survival rates of coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the U.S. Pacific Coast. *Estuaries* 26:1094–1103.
- Mangel, M., and C. W. Clark. 1988. *Dynamic modeling in behavioral ecology*. Page Princeton University Press.
- Mate, B. R., P. B. Best, B. A. Lagerquist, and M. H. Winsor. 2011. Coastal, offshore, and migratory movements of South African right whales revealed by satellite telemetry. *Marine Mammal Science* 27:455–476.
- McClure, M. M., S. M. Carlson, T. J. Beechie, G. R. Pess, J. C. Jorgensen, S. M. Sogard, S. E. Sultan, D. M. Holzer, J. Travis, B. L. Sanderson, M. E. Power, and R. W. Carmichael. 2008. Evolutionary consequences of habitat loss for Pacific anadromous salmonids. *Evolutionary Applications* 1:300–318.
- McCormick, S. D., L. P. Hansen, T. P. Quinn, and R. L. Saunders. 1998. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 55:77–92.

- McNamara, J. M., R. K. Welham, and A. I. Houston. 1998. The timing of migration within the context of an annual routine. *Journal of Avian Biology* 29:416–423.
- Meador, J. P. 2014. Do chemically contaminated river estuaries in Puget Sound (Washington, USA) affect the survival rate of hatchery-reared Chinook salmon? *Canadian Journal of Fisheries and Aquatic Sciences* 71:162–180.
- Miller, B., and S. Sadro. 2003. Residence time and seasonal movements of juvenile coho salmon in the ecotone and lower estuary of Winchester Creek, South Slough, Oregon. *Transactions of the American Fisheries Society* 132:546–559.
- Moore, F. R., S. A. Gauthreaux, P. Kerlinger, and T. R. Simons. 1995. Habitat requirements during migration: important link in conservation. Pages 121–144 *Ecology and Management of Neotropical Migratory Birds: A Synthesis and Review of Critical Issues*.
- Moore, J. W., C. Carr-Harris, A. S. Gottesfeld, D. Radies, C. Barnes, G. Williams, B. Shepert, T. McIntyre, J. Gordon, and W. Joseph. 2015. Selling First Nations down the river. *Science* 349:596.
- Moore, J. W., J. Gordon, C. Carr-Harris, A. S. Gottesfeld, S. M. Wilson, and J. H. Russell. 2016. Assessing estuaries as stopover habitats for juvenile Pacific salmon. *Marine Ecology Progress Series* 559:201–215.
- Moore, J. W., J. D. Yeakel, D. Peard, J. Lough, and M. Beere. 2014. Life-history diversity and its importance to population stability and persistence of a migratory fish: Steelhead in two large North American watersheds. *Journal of Animal Ecology* 83:1035–1046.
- Moore, M. E., B. A. Berejikian, and E. P. Tezak. 2010. Early marine survival and behavior of steelhead smolts through Hood Canal and the Strait of Juan de Fuca. *Transactions of the American Fisheries Society* 139:49–61.
- Mortensen, D., A. Wertheimer, S. Taylor, and J. Landingham. 2000. The relation between early marine growth of pink salmon, *Oncorhynchus gorbuscha*, and marine water temperature, secondary production, and survival to adulthood. *Fishery Bulletin* 98:319–335.
- Munsch, S. H., J. R. Cordell, and J. D. Toft. 2015. Effects of seawall armoring on juvenile Pacific salmon diets in an urban estuarine embayment. *Marine Ecology Progress Series* 535:213–229.
- Munsch, S. H., J. R. Cordell, and J. D. Toft. 2017. Effects of shoreline armoring and overwater structures on coastal and estuarine fish: opportunities for habitat improvement.
- Munsch, S. H., J. R. Cordell, J. D. Toft, and E. E. Morgan. 2014. Effects of seawalls and piers on fish assemblages and juvenile salmon feeding behavior. *North American Journal of Fisheries Management* 34:814–827.

- Munsch, S. H., C. M. Greene, R. C. Johnson, W. H. Satterthwaite, H. Imaki, and P. L. Brandes. 2019. Warm, dry winters truncate timing and size distribution of seaward-migrating salmon across a large, regulated watershed. *Ecological Applications* 29:1–14.
- Nagelkerken, I., M. Sheaves, R. Baker, and R. M. Connolly. 2015. The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish and Fisheries* 16:362–371.
- Nidzicko, N. J. 2018. Allometric scaling of estuarine ecosystem metabolism. *Proceedings of the National Academy of Sciences of the United States of America* 115:6733–6738.
- Norris, D. R. 2005. Carry-over effects and habitat quality in migratory populations. *Oikos* 109:178–186.
- O'Connor, C. M., D. R. Norris, G. T. Crossin, and S. J. Cooke. 2014. Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. *Ecosphere* 5:1–11.
- Pacific Estuary Conservation Program. 2019. Identified estuaries of British Columbia mapping and ranking project: 2019 update.
- Paterson, A. W., and A. K. Whitfield. 2000. Do shallow-water habitats function as refugia for juvenile fishes? *Estuarine, Coastal and Shelf Science* 51:359–364.
- Pearcy, W.G. Ocean ecology of North Pacific salmonids. Washington Sea Grant Program, 1992.
- Pedersen, T.L. 2020. patchwork: The composer of plots. R package version 1.1.1. <https://cran.r-project.org/package=patchwork>.
- Pope, J. G., J. G. Shepherd, and J. Webb. 1994. Successful surf-riding on size spectra: the secret of survival in the sea. *Philosophical Transactions - Royal Society of London, B* 343:41–49.
- Province of British Columbia. 2021. British Columbia Freshwater Atlas. Province of British Columbia, Ministry of Forests, Lands, Natural Resource Operations and Rural Development, Vancouver, B.C. <https://www2.gov.bc.ca/gov/content/data/geographic-data-services/topographic-data/freshwater>
- Quinn, T.P. The behavior and ecology of Pacific salmon and trout. University of Washington Press, 2018.
- Quinn, T. P., K. Doctor, N. W. Kendall, and H. B. Rich. 2009. Diadromy and the life history of sockeye salmon: Nature, nurture, and the hand of man. *American Fisheries Society Symposium* 69:23–42.

- Quinn, T. P., N. Harris, J. A. Shaffer, C. Byrnes, and P. Crain. 2013. Juvenile coho salmon in the Elwha river estuary prior to dam removal: seasonal occupancy, size distribution, and comparison to nearby Salt Creek. *Transactions of the American Fisheries Society* 142:1058–1066.
- R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rebenack, J. J., S. Ricker, C. Anderson, M. Wallace, and D. M. Ward. 2015. Early emigration of juvenile coho salmon: implications for population monitoring. *Transactions of the American Fisheries Society* 144:163–172.
- Rechisky, E. L., D. W. Welch, A. D. Porter, J. E. Hess, and S. R. Narum. 2014. Testing for delayed mortality effects in the early marine life history of Columbia River Basin yearling Chinook salmon. *Marine Ecology Progress Series* 496:159–180.
- Rechisky, E. L., D. W. Welch, A. D. Porter, M. C. Jacobs-Scott, P. M. Winchell, and J. L. McKern. 2012. Estuarine and early-marine survival of transported and in-river migrant Snake River spring Chinook salmon smolts. *Scientific Reports* 2:1–9.
- Reed, T. E., D. E. Schindler, and R. S. Waples. 2011. Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. *Conservation Biology* 25:56–63.
- Robb, C. K. 2014. Assessing the impact of human activities on British Columbia's estuaries. *PLoS ONE* 9.
- Roni, P., T. Bennett, R. Holland, G. Pess, K. M. Hanson, R. Moses, M. McHenry, W. Ehinger, and J. Walter. 2012. Factors affecting migration timing, growth, and survival of juvenile coho salmon in two coastal Washington watersheds. *Transactions of the American Fisheries Society* 141:890–906.
- Runge, C. A., T. G. Martin, H. P. Possingham, S. G. Willis, and R. A. Fuller. 2014. Conserving mobile species. *Frontiers in Ecology and the Environment* 12:395–402.
- Ryding, K. E., and J. R. Skalski. 1999. Multivariate regression relationships between ocean conditions and early marine survival of coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 56:2374–2384.
- Saloniemi, I., E. Jokikokko, I. Kallio-Nyberg, E. Jutila, and P. Pasanen. 2004. Survival of reared and wild Atlantic salmon smolts: size matters more in bad years. *ICES Journal of Marine Science* 61:782–787.
- Sandercock, F. K. 1991. Life history of coho salmon (*Oncorhynchus kisutch*). Pages 395–446 *Pacific Salmon Life Histories*.

- Satterthwaite, W. H., M. P. Beakes, E. M. Collins, D. R. Swank, J. E. Merz, R. G. Titus, S. M. Sogard, and M. Mangel. 2009. Steelhead life history on California's Central Coast: insights from a state-dependent model. *Transactions of the American Fisheries Society* 138:532–548.
- Satterthwaite, W. H., S. M. Carlson, S. D. Allen-Moran, S. Vincenzi, S. J. Bograd, and B. K. Wells. 2014. Match-mismatch dynamics and the relationship between ocean-entry timing and relative ocean recoveries of Central Valley fall run Chinook salmon. *Marine Ecology Progress Series* 511:237–248.
- Satterthwaite, W. H., S. A. Hayes, J. E. Merz, S. M. Sogard, D. M. Frechette, and M. Mangel. 2012. State-dependent migration timing and use of multiple habitat types in anadromous salmonids. *Transactions of the American Fisheries Society* 141:781–794.
- Sawyer, H., M. J. Kauffman, R. M. Nielson, and J. S. Horne. 2009. Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecological Applications* 19:2016–2025.
- Schaub, M., R. Pradel, L. Jenni, and J.-D. Lebreton. 2001. Migrating birds stop over longer than usually thought: an improved capture-recapture analysis. *Ecology* 82:852–859.
- Scheuerell, M. D., R. W. Zabel, and B. P. Sandford. 2009. Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (*Oncorhynchus* spp.). *Journal of Applied Ecology* 46:983–990.
- Schindler, D. E., X. Augerot, E. Fleishman, N. J. Mantua, B. Riddell, M. Ruckelshaus, J. Seeb, and M. Webster. 2008. Climate change, ecosystem impacts, and management for Pacific salmon. *Fisheries* 33:502–506.
- Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. *Nature* 465:609–612.
- Schroeder, R. K., L. D. Whitman, B. Cannon, and P. Olmsted. 2015. Juvenile life-history diversity and population stability of spring Chinook salmon in the Willamette River basin, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 73:921–934.
- Scott, E. R., and E. E. Crone. 2021. Using the right tool for the job: the difference between unsupervised and supervised analyses of multivariate ecological data. *Oecologia* 196:13–25.
- Seitz, K. M., W. I. Atlas, B. Millard-Martin, J. R. Reid, J. H. Heavyside, B. P. V. Hunt, and J. W. Moore. 2020. Size-spectra analysis in the estuary: assessing fish nursery function across a habitat mosaic. *Ecosphere* 11:e03291.

- Sharpe, C., C. Carr-Harris, M. Arbeider, S. M. Wilson, and J. W. Moore. 2019. Estuary habitat associations for juvenile Pacific salmon and pelagic fish: implications for coastal planning processes. *Aquatic Conservation: Marine and Freshwater Ecosystems* 29:1636–1656.
- Sheaves, M., R. Baker, I. Nagelkerken, and R. M. Connolly. 2015. True value of estuarine and coastal nurseries for fish: incorporating complexity and dynamics. *Estuaries and Coasts* 38:401–414.
- Sheehy, J., C. M. Taylor, and D. R. Norris. 2011. The importance of stopover habitat for developing effective conservation strategies for migratory animals. *Journal of Ornithology* 152:161–168.
- Simenstad, C. A., and J. R. Cordell. 2000. Ecological assessment criteria for restoring anadromous salmonid habitat in Pacific Northwest estuaries. *Ecological Engineering* 15:283–302.
- Simenstad, C. A., K. L. Fresh, and E. O. Salo. 1982. The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: an unappreciated function. Pages 343–364 *Estuarine Comparisons: Proceedings of the Sixth Biennial International Estuarine Research Conference*. Glenden Beach, OR.
- Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* 60:1129–1157.
- Spence, B. C., and E. J. Dick. 2014. Geographic variation in environmental factors regulating outmigration timing of coho salmon (*Oncorhynchus kisutch*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences* 71:56–69.
- Spence, B. C., and J. D. Hall. 2010. Spatiotemporal patterns in migration timing of coho salmon (*Oncorhynchus kisutch*) smolts in North America. *Canadian Journal of Fisheries and Aquatic Sciences* 67:1316–1334.
- Stearns, S. C. 2000. Life history evolution: Successes, limitations, and prospects. *Naturwissenschaften* 87:476–486.
- Studds, C. E., B. E. Kendall, N. J. Murray, H. B. Wilson, D. I. Rogers, R. S. Clemens, K. Gosbell, C. J. Hassell, R. Jessop, D. S. Melville, D. A. Milton, C. D. T. Minton, H. P. Possingham, A. C. Riegen, P. Straw, E. J. Woehler, and R. A. Fuller. 2017. Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. *Nature Communications* 8:1–7.
- Sturrock, A. M., S. M. Carlson, J. D. Wikert, T. Heyne, S. Nusslé, J. E. Merz, H. J. W. Sturrock, and R. C. Johnson. 2020. Unnatural selection of salmon life histories in a modified riverscape. *Global Change Biology* 26:1235–1247.

- Sykes, G. E., C. J. Johnson, and J. M. Shrimpton. 2009. Temperature and flow effects on migration timing of Chinook salmon smolts. *Transactions of the American Fisheries Society* 138:1252–1265.
- Thorne, K., G. MacDonald, G. Guntenspergen, R. Ambrose, K. Buffington, B. Dugger, C. Freeman, C. Janousek, L. Brown, J. Rosencranz, J. Holmquist, J. Smol, K. Hargan, and J. Takekawa. 2018. U.S. Pacific coastal wetland resilience and vulnerability to sea-level rise. *Science Advances* 4:1–11.
- Thorpe, J. E. 1994. Salmonid fishes and the estuarine environment. *Estuaries* 17:76–93.
- Thorson, J. T., M. D. Scheuerell, E. R. Buhle, and T. Copeland. 2014. Spatial variation buffers temporal fluctuations in early juvenile survival for an endangered Pacific salmon. *Journal of Animal Ecology* 83:157–167.
- Toft, J. D., S. H. Munsch, J. R. Cordell, K. Siitari, V. C. Hare, B. M. Holycross, L. A. DeBruyckere, C. M. Greene, and B. B. Hughes. 2018. Impact of multiple stressors on juvenile fish in estuaries of the northeast Pacific. *Global Change Biology* 24:2008–2020.
- Tomaro, L. M., D. J. Teel, W. T. Peterson, and J. A. Miller. 2012. When is bigger better? Early marine residence of middle and upper Columbia River spring Chinook salmon. *Marine Ecology Progress Series* 452:237–252.
- Tucker, S., J. M. Hipfner, and M. Trudel. 2016. Size- and condition-dependent predation: a seabird disproportionately targets substandard individual juvenile salmon. *Ecology* 97:461–471.
- Ulaski, M. E., H. Finkle, and P. A. H. Westley. 2020. Direction and magnitude of natural selection on body size differ among age-classes of seaward-migrating Pacific salmon. *Evolutionary Applications* 13:2000–2013.
- U. S. Fish and Wildlife Service. 2021. National Wetlands Inventory. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C.
<http://www.fws.gov/wetlands/>
- U.S. Geological Survey. 2021. National Hydrography Dataset Plus High Resolution. U.S. Department of the Interior, Geological Survey, Washington, D.C.
<https://www.usgs.gov/core-science-systems/ngp/national-hydrography/access-national-hydrography-products>.
- Venables, W.N. and Ripley, B.D. 2002. *Modern applied statistics with S*. Fourth Edition. Springer, New York. <https://www.stats.ox.ac.uk/pub/MASS4/>.
- Volk, E. C., D. L. Bottom, K. K. Jones, and C. A. Simenstad. 2010. Reconstructing juvenile Chinook salmon life history in the Salmon River estuary, Oregon, using otolith microchemistry and microstructure. *Transactions of the American Fisheries Society* 139:535–549.

- Walsworth, T. E., J. R. Baldock, C. E. Zimmerman, and D. E. Schindler. 2020. Interaction between watershed features and climate forcing affects habitat profitability for juvenile salmon. *Ecosphere* 1:e03266.
- Walters, A. W., T. Copeland, and D. A. Venditti. 2013. The density dilemma: limitations on juvenile production in threatened salmon populations. *Ecology of Freshwater Fish* 22:508–519.
- Waples, R. S., R. G. Gustafson, L. A. Weitkamp, J. M. Myers, O. W. Johnson, P. J. Busby, J. J. Hard, G. J. Bryant, F. W. Waknitz, K. Neely, D. Teel, W. S. Grant, G. A. Winans, S. Phelps, A. Marshall, and B. M. Baker. 2001. Characterizing diversity in salmon from the Pacific Northwest. *Journal of Fish Biology* 59:1–41.
- Ward, B. W., P. A. Slaney, A. R. Faccin, and R. W. Land. 1989. Size-biased survival in steelhead trout (*Oncorhynchus mykiss*): back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1853–1858.
- Weber, T. P., A. I. Houston, and B. J. Ens. 1999. Consequences of habitat loss at migratory stopover sites: a theoretical investigation. *Journal of Avian Biology* 30:416.
- Weitkamp, L. A., G. Goulette, J. Hawkes, M. O'Malley, and C. Lipsky. 2014. Juvenile salmon in estuaries: comparisons between North American Atlantic and Pacific salmon populations. *Reviews in Fish Biology and Fisheries* 24:713–736.
- Weitkamp, L. A., D. J. Teel, M. Liermann, S. A. Hinton, D. M. Van Doornik, and P. J. Bentley. 2015. Stock-specific size and timing at ocean entry of columbia river juvenile Chinook salmon and steelhead: implications for early ocean growth. *Marine and Coastal Fisheries* 7:370–392.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*.
- Wickham, H. 2016. *ggplot2: Elegant graphics for data analysis*. Springer-Verlag, New York. <https://ggplot2.tidyverse.org>.
- Wiklund, S., D. Nilsson, L. Eriksson, M. Sjöström, S. Wold, and K. Faber. 2007. A randomization test for PLS component selection. *Journal of Chemometrics* 21:427–439.
- Willette, T. M. 2001. Foraging behaviour of juvenile pink salmon (*Oncorhynchus gorbusha*) and size-dependent predation risk. *Fisheries Oceanography* 10:110–131.
- Williams, J. G., R. W. Zabel, R. S. Waples, J. A. Hutchings, and W. P. Connor. 2008. Potential for anthropogenic disturbances to influence evolutionary change in the life history of a threatened salmonid. *Evolutionary Applications* 1:271–285.

- Wilson, S. M. 2021. Assessing species- and population-level vulnerability to climate-driven phenological mismatch in Pacific salmon. Simon Fraser University.
- Wilson, S. M., T. W. Buehrens, J. L. Fisher, K. L. Wilson, and J. W. Moore. 2021. Phenological mismatch, carryover effects, and marine survival in a wild steelhead trout *Oncorhynchus mykiss* population. *Progress in Oceanography* 193:102533.
- Wold, S., M. Sjöström, and L. Eriksson. 2001. PLS-regression: a basic tool of chemometrics. *Chemometrics and Intelligent Laboratory Systems* 58:109–130.
- Woo, I., M. J. Davis, C. S. Ellings, S. Hodgson, J. Y. Takekawa, G. Nakai, and S. E. W. De La Cruz. 2019. A mosaic of estuarine habitat types with prey resources from multiple environmental strata supports a diversified foraging portfolio for juvenile Chinook salmon. *Estuaries and Coasts* 42:1938–1954.
- Woodson, L. E., B. K. Wells, P. K. Weber, R. B. MacFarlane, G. E. Whitman, and R. C. Johnson. 2013. Size, growth, and origin-dependent mortality of juvenile Chinook salmon *Oncorhynchus tshawytscha* during early ocean residence. *Marine Ecology Progress Series* 487:163–175.

Appendix A. Supplemental Material for Chapter 2

Table A.1. Hypothesized relationships between juvenile salmon migration traits, watershed covariates, and estuary habitat characteristics.

Predictor variable	Hypothesized effects on migration timing	Hypothesized effects on migration size
Trap latitude (decimal degrees)	Latitudinal clines in marine and freshwater processes (e.g., coastal productivity, timing of ice-off, timing and magnitude of spring freshet) could affect the optimal timing and duration of juvenile migration. Populations from higher-latitude systems may exhibit later migrations of shorter duration.	Water temperatures generally decline with latitude, leading to slower growth and smaller average body size at high latitudes. However, high-latitude populations may have a higher proportion of age-2 migrants, which may moderate this effect and lead to a broader range of sizes at migration.
Migration distance from trap to estuary (km)	Migration distance may influence when juveniles leave rearing grounds to reach the estuary/ocean at an optimal time.	Migration distance may exert selective pressure on juvenile body size (e.g., swim performance, predation risk), such that populations further from the ocean produce larger juveniles.
Migration distance from trap to ocean (km)	Juveniles that migrate downstream over longer distances may initiate migration earlier.	
Catchment area above trap (km ²)	These variables indicate catchment size, and (by proxy) potential population-level variability. Traps with a larger upstream catchment area, or sited on higher-order streams, may integrate a greater diversity of migration phenologies and be characterized by broader migration windows.	As per migration timing hypotheses, traps with a larger upstream catchment area, or sited on higher-order streams, may integrate a greater diversity of freshwater rearing conditions and be characterized by a broader range of juvenile sizes.
Strahler stream order		
Mean catchment elevation above trap (m)	In combination with latitude, elevation-related variables can indicate snow-dominated vs. rain-dominated hydrology. High elevation, high latitude systems are more likely to be snow-dominated, leading to more predictable hydrologic regimes. Populations from such systems may exhibit later migrations of shorter duration.	Due to cooler instream temperatures, populations that rear at higher elevations may exhibit slower growth and attain a smaller average size prior to migration.
Max catchment elevation above trap (m)		

Predictor variable	Hypothesized effects on migration timing	Hypothesized effects on migration size
Total lake area in catchment (km ²) Accessible lake area in catchment (km ²)	Lake influence can impact both watershed hydrology and type of rearing habitat available to juvenile salmonids. Systems with more lake habitat may have more stable hydrologic regimes, leading to a narrower migration timing window. Those with accessible lake habitat may have a higher proportion of lake-rearing juveniles, which could further influence migration timing.	Fish-accessible lakes may serve as rearing habitats that are more thermally stable than lotic freshwater habitats. This could improve growth conditions for lake-rearing juveniles, leading to a greater mean size and broader range of sizes at migration.
Total estuary area (km) Total estuary shoreline length (km) Estuary area relative to catchment area	Estuary habitats may offer alternative or superior rearing and growth opportunities for juveniles en route to the ocean. Where there is ample estuary habitat available, it may be advantageous for juveniles to migrate downstream earlier to accelerate growth prior to ocean entry and avoid pre-smolt competition for space/resources in freshwater habitats. For systems with little to no estuary habitat, juveniles may have evolved to exit freshwater later and over a shorter duration to facilitate optimal ocean entry timing.	Availability of estuary rearing habitats may enable a greater diversity of successful juvenile life-history strategies. Earlier migration by estuary-rearing juveniles may manifest in a smaller mean size and greater range of sizes at migration. For systems with little to no estuary habitat, juveniles may have evolved to exit freshwater at a larger, more uniform size to minimize marine predation risk.
Shoreline complexity index Closure index Estuary elongation index	Estuary configuration may mediate habitat suitability for juvenile salmon. For example, estuaries that are more enclosed may offer superior refuge to those characterized by a high degree of ocean exposure. Alternatively, estuaries with complex shorelines may offer superior terrestrial prey inputs and vegetative cover relative to those with simplified shorelines. Where estuary habitat suitability is high, juveniles may migrate downstream earlier.	As above, earlier migration by estuary-rearing juveniles may manifest in a smaller mean size and a greater range of sizes at migration. For systems with little to no suitable estuary habitat, juveniles may have evolved to exit freshwater at a larger, more uniform size to minimize marine predation risk.

Predictor variable	Hypothesized effects on migration timing	Hypothesized effects on migration size
Proportion estuary buffer protected (1- or 5-km)	Estuaries surrounded more protected area may comprise higher-quality habitats with less anthropogenic impact. Estuaries with a high degree of protection may more closely reflect historic conditions. Such conditions may enable a greater range of life-history strategies, leading juveniles to migrate on average earlier or over a longer duration.	As above, earlier migration by estuary-rearing juveniles may manifest in a smaller mean size and a greater range of sizes at migration. For systems with little to no suitable estuary habitat, juveniles may have evolved to exit freshwater at a larger, more uniform size to minimize marine predation risk.
Proportion estuary buffer in “natural” land use (1- or 5-km)	Where urban and agricultural impact is low, estuaries may undergo fewer anthropogenic alterations (e.g., armoring and diking, deforestation, stormwater and nutrient inputs) and therefore comprise higher-quality habitats. Such estuaries may more closely reflect historic conditions and permit a greater range of successful life-history strategies— leading juveniles to migrate on average earlier or over a longer duration.	As above, earlier migration by estuary-rearing juveniles may manifest in a smaller mean size and a greater range of sizes at migration. For systems with little to no suitable estuary habitat, juveniles may have evolved to exit freshwater at a larger, more uniform size to minimize marine predation risk.

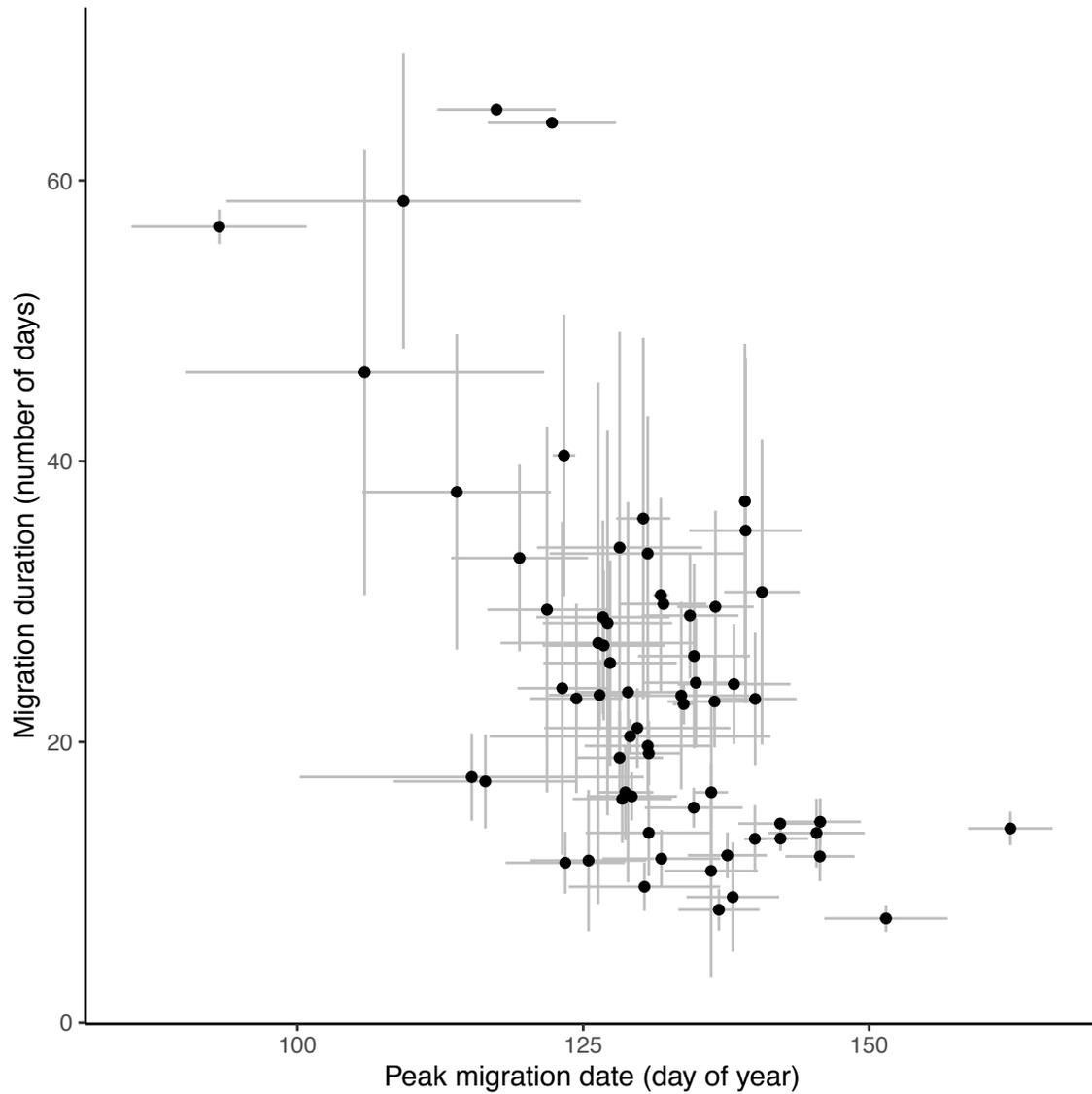


Figure A.1. Relationship between juvenile coho salmon peak migration date and duration of the migration window.

Note: For each population, points represent the mean peak migration date and migration duration calculated across years. Horizontal lines indicate one standard deviation about the mean peak migration date. Vertical lines indicate one standard deviation about the mean migration duration.

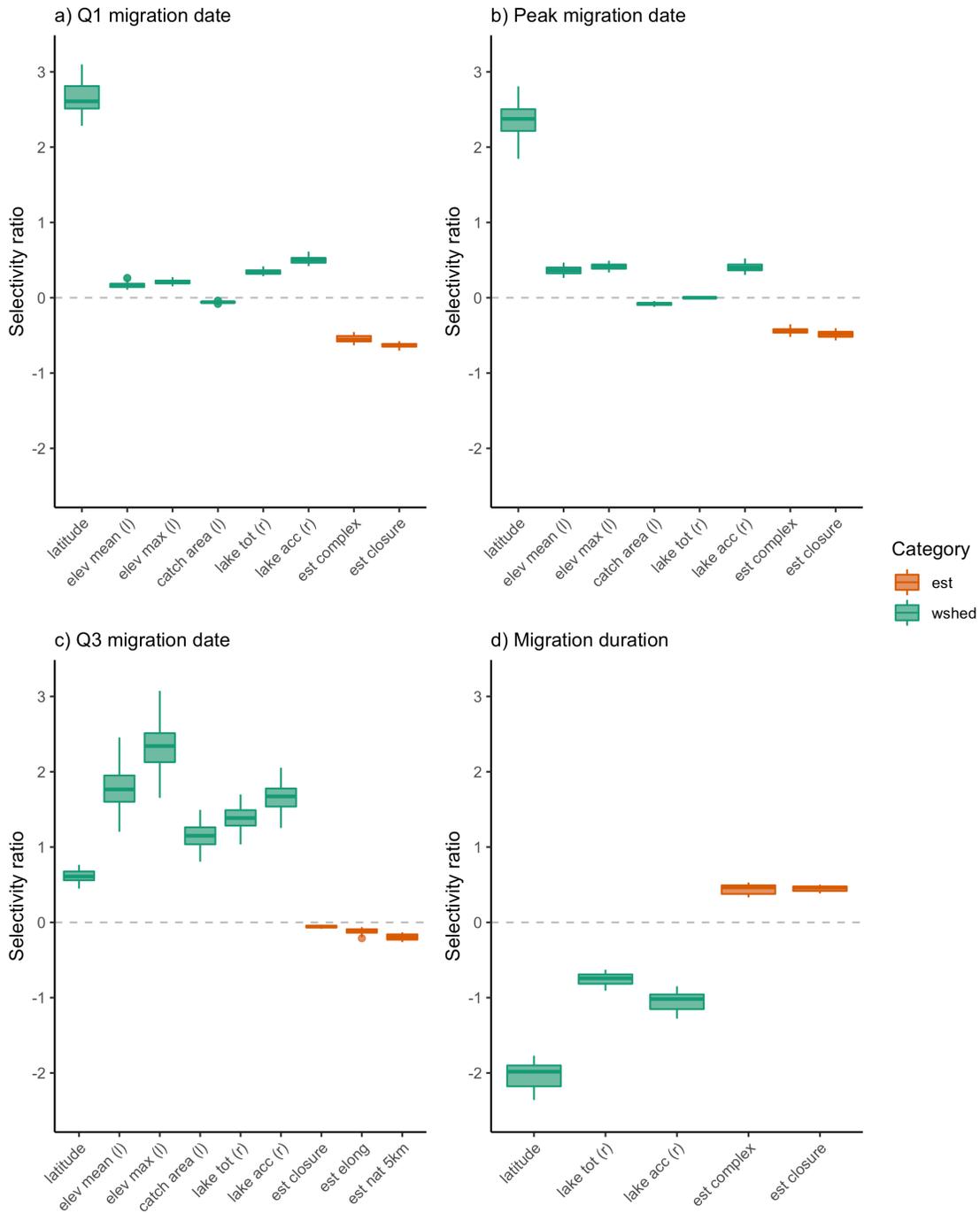


Figure A.2. Selectivity ratio boxplots for each of the four migration timing response variables, representing model outputs from 108 non-pseudoreplicated data subsets.

Note: Selectivity ratios indicate the most influential predictor variables in a partial least-squares regression model, and are defined as the variance explained by each predictor divided by its residual (unexplained) variance. To depict relationship directionality between each response and predictor variable, selectivity ratios for negatively correlated variables have been multiplied by -1.

Appendix B. Supplemental Material for Chapter 3

Comparative methods for quantifying estuary residence

We compared estuary residence estimates derived from the negative binomial GLM described in *Methods* to those produced by two alternative approaches: 1) log-linear quantile regression and 2) a Cormack-Jolly-Seber (CJS) mark-recapture model. We conducted this comparison as a means of assessing the validity of the negative binomial GLM. Our reasons for doing so were twofold: our estuary recapture rate was relatively low, and the negative binomial GLM was limited to the subset of recapture data collected at Reach 1 sites. Due to site characteristics, it was not possible to recapture juvenile salmon at the precise point of marine entry; Reach 1 sites were located near, but not precisely at, the transition from the estuary to the marine environment. Both alternative methods enabled incorporation of recapture data from the Koeye River estuary in its entirety. Results generally corroborate the estuary residence estimates derived from the negative binomial GLM.

First, we used log-linear quantile regression to relate duration of estuary residence to size at freshwater exit. Quantile regression fits a regression line to a defined quantile of data, defined by the percentage of residual error that falls below the regression line (τ) and above the regression line ($1 - \tau$). Here, we were interested in identifying a best-fit regression line to represent the upper tranche of estuary residence values observed, as a proxy for the upper limit of stopover duration exhibited by individuals of a given size at freshwater exit. Based on the results of GLM model selection, we assumed that individuals of a given size spend similar amounts of time rearing in the estuary, regardless of recapture location. Therefore, this model considered all individuals recaptured throughout the estuary, not just those recaptured at marine entry. Goodness-of-fit testing performed on quantiles representing the upper 25% of observed estuary residence values ($\tau = 0.75, 0.8, 0.85, 0.9, 0.95, 1.0$) indicated that a 0.75 quantile regression line best fit the data. This method provides a conservative estimate of estuary residence duration.

Second, we developed a CJS mark-recapture model to estimate estuary stopover duration relative to length at freshwater exit. For a given group of marked individuals (i.e., individuals of a given fork length), CJS mark-recapture models estimate

two parameters: probability of detection p and probability of survival ϕ . Recapture data were pooled across years and by three-day increments to enable model convergence. We fixed the probability of detection p at 0 for days in a given year when estuary sampling did not occur and allowed the model to estimate a constant p only for sampled dates. In CJS models, the survival parameter ϕ may describe either true survival (i.e., whether an animal is still alive), continued presence (i.e., whether an animal is still in the study area), or both (Schaub et al. 2001). Because the population of juvenile salmon in our study was open (i.e., immigration and emigration occurred throughout the sampling period), here ϕ represents apparent survival, which incorporates both emigration from the estuary and death in the estuary. Per methodology outlined by Schaub et al. (2001) and clarified by Efford (2005), we used the ϕ to estimate stopover duration S for individuals of a given length at freshwater exit FL_{RST} whereby:

$$S_i = \frac{-1}{\ln(\phi_{FL_{RST}})}$$

Our data met the four underlying assumptions required for use in CJS mark-recapture models: for individuals of a given size at freshwater exit, 1) every marked animal present in the population at a given sampling occasion (t_i) has the same probability of detection p , 2) every marked animal in the population immediately after t_i has the same probability of survival ϕ to t_{i+1} , 3) marks are not lost or missed, and 4) all samples are instantaneous relative to the interval between t_i and t_{i+1} , and each release is made immediately after the sample. Our data also met three additional assumptions required to derive stopover duration S from apparent survival ϕ for individuals of a given size at freshwater exit: 1) apparent survival ϕ for a given group is constant across sampling events, 2) the day of tagging is the first day of residence, and 3) stopover duration is Poisson distributed (Schaub et al. 2001, Efford 2005).

Quantile regression and goodness-of-fit testing were performed using the packages ‘quantreg’ (Koenker 2020) and ‘QTools’ (Geraci 2016). CJS mark-recapture analysis was performed using the package ‘marked’ (Laake et al. 2013).

Results of comparative estuary residence analyses

Residence analyses revealed that small juveniles exhibited longer estuary stopovers than their larger counterparts. Each of the alternative residence approaches we tested corroborated the negative relationship between size at freshwater exit and duration of estuary stopover indicated by the negative binomial GLM (Figure B.1). Apparent survival ϕ , the probability of continued presence in the estuary, decreased with fish size. Median estuary stopover duration estimates were similar across all residence models: median stopover was 14.5 days (95% CI 11.1-19.1 days) for the negative binomial model, 15.6 days (95% CI 12.0-20.4 days) for the 75% quantile regression model, and 12.5 days for the CJS mark-recapture model. We were unable to calculate 95% confidence intervals for the CJS mark-recapture model due to poor error convergence caused by a low recapture rate. The effect of size at freshwater exit was strongest in the negative binomial model ($\beta = -0.034$, $p = 0.004$), and somewhat more moderate in the 75% quantile regression model ($\beta = -0.020$, $p = 0.174$) and CJS mark-recapture model ($\beta = -0.011$; Table S1). All three analytical approaches revealed that juvenile salmon that were small at freshwater exit reared in the estuary for longer than those that were comparatively large.

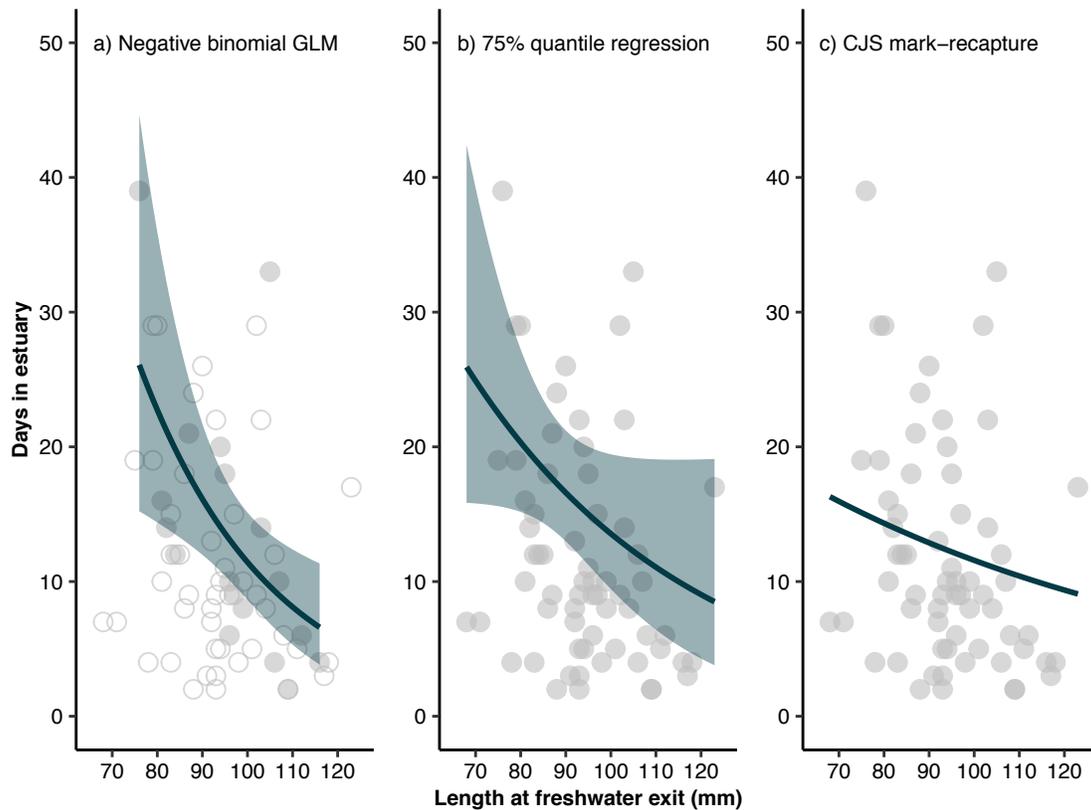


Figure B.1. Estuary residence models (with 95% CI), including a) negative binomial GLM, b) 75% quantile regression, and c) Cormack-Jolly-Seber mark-recapture model.

Note: Dark points indicate recapture data used in each model, open points indicate data not considered for a given model (i.e., for the negative binomial GLM, open points indicate individuals captured upstream of the estuary mouth).

Table B.1. Effect size of length at freshwater exit and predicted duration of estuary stopover (with 95% CI) for juvenile coho salmon comprising the 0.1, 0.5, and 0.9 size quantiles at freshwater exit (Q0.1 = 78 mm, Q0.5 = 93 mm, Q0.9 = 112 mm).

	Negative binomial GLM	75% quantile regression	CJS mark-recapture
Intercept	5.872	4.634	3.515
β_{FL}	-0.034	-0.020	-0.011
Q _{0.1} estuary stopover	24.4 days (14.8-40.0)	21.2 days (15.4-29.1)	14.6 days
Q _{0.5} estuary stopover	14.5 days (11.1-19.1)	15.6 days (12.0-20.4)	12.5 days
Q _{0.9} estuary stopover	7.6 days (4.8-12.0)	10.6 days (5.9-19.1)	10.2 days