Juvenile salmon use of estuaries: investigating food web ecology, growth, and residency

by
Michael Arbeider

B.Sc., Simon Fraser University, 2015

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

in the
Department of Biological Sciences
Faculty of Science

SIMON FRASER UNIVERSITY
Fall 2018

Approval

Name: **Michael Arbeider**

Degree: **Master of Science**

Title: **Juvenile salmon use of estuaries: investigating food web ecology, growth, and residency**

Examining Committee: **Chair:** Michael Hart
Professor

Jonathan W. Moore
Senior Supervisor
Associate Professor

John D. Reynolds
Supervisor
Professor

David Patterson
Examiner
Adjunct Professor
School of Resource and Environmental Management

Date Defended/Approved: September 7th, 2018

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 valuable nursery and stopover habitats that support mobile consumers during their ontogenetic migrations such as juvenile anadromous salmon. My first data chapter was an extensive field study that examined how two salmon and two small pelagic fish integrate with key prey across the estuary of the Skeena River. The different fishes selected different prey that were unevenly distributed across the estuary seascape in time and space; however, some prey were associated with biophysical factors like salinity and eelgrass. My next chapter compiled empirical published data on five species of juvenile salmon growth rates and residency durations. Several species had poor coverage of these aspects, but it was evident that different salmon species and life history strategies have different growth rates and residency durations in estuaries. Collectively, this work adds and organizes empirical support for valuing estuaries as important habitat for juvenile salmon.

Keywords: estuary; Oncorhynchus; ontogenetic diet; nursery; growth; residency

Acknowledgements

There are many individuals and organizations who contributed to this research and supported me in various ways. First, I must thank Jon Moore, who made this entire work possible by providing me with the opportunity to join his lab and being the centrepin that connected all the people I worked with. Thank you for your guidance, patience, and adaptability. John Reynolds, thank you for being on my committee, your consistent insight and suggestions made my thesis better and more rounded. Also thanks for employing me directly before this and keeping me connected with the E2O!

This work is the product of a collaboration with Skeena Fisheries Commission and Lax Kw’alaams Fisheries of the Lax Kw’alaams First Nation. Without their support, this project would not have been possible, and I am forever thankful to them. Thank you, Charmaine Carr-Harris, you paved the way for this research through your years of research and collaboration in the area. Your drive and passion for understanding this system is inspiring and your guidance on the ground was key to making all subsequent projects (including mine) a success. You are also the reason I got into zoops, so that deserves a shout out! I sincerely thank Bill Shepert and Jen Gordon for their logistical support and time. The field crew, Harvey James Russell, Wade Helin, Jim Henry Jr., Devin Helin, Katelyn Cooper, and Brandon Ryan from Lax Kw’alaams Fisheries Department along with David Doolan from Metlakatla Fisheries Program, thank you so much for your badassery on the water. Your skills and teamwork made catching thousands of fish both possible and fun. And thank you, John Latimer, for your continued contributions on mapping and GIS for these projects.

I have to thank the wonderful people in the Salmon Watersheds Lab who supported me throughout this journey. Particularly, Ciara Sharpe, my fisher-in-arms, my confidant and roomie in Rupert, my in-house estuary expert. You truly set the tone (in a good way, aha) of my experience up there. Your chipper attitude, determination, and flexibility have always been an inspiration. Thank you for all your help and guidance on my project. Thank you, Sam Wilson, our other Skeena estuary team member, for your upbeat attitude in the field and sharing so much of your knowledge and experience with me (and with lots of other people all the time!!). Colin Bailey, thanks for taking me under your crazy fly-fishing wings and making me feel like family. And thank you Karl, Kyle, Kara, Courtney, Elissa, Will and Luke for all the awesome times we had at lab parties,

retreats, meetings, and around the office. And finally, a special thank you to Emma Hodgson for saving my butt and providing the ground-work for my second chapter, it has been a pleasure working with you.

I have also been a part of the Earth2Oceans lab group since my days in undergraduate and they have shaped the scientist I am today. Thank you to my direct supervisors over the years, David Scott, Rylee Murray, Kirsten Wilcox, and Jeremiah Kennedy, you have all helped me grow and learn. Thank you, Drs. Wendy Palen, Nick Dulvy, Isabelle Côté, and of course the Jo(h)ns, for facilitating such an amazing scientific community and for teaching and guiding me throughout my entire journey. And thank you to all the members of E2O and the greater community in the Department of Biology, there are too many of you to list here, but thanks for all the good times and emotional support.

Research also costs a lot of money, and there were many organizations that supported both me and the resources I used whom I am grateful to. Thank you Natural Sciences and Engineering Research Council of Canada, Simon Fraser University, Liber Ero Foundation, Skeena Wild, and Coast Opportunities for funding this research.

Finally, to my friends and family, the biggest thank you goes out to you. There were many times when it felt like too much, but you were all there to keep me going. I feel truly blessed to have so many wonderful people in my life. I hope you all know who you are, thank you. And a special thank you to my parents, you have helped shape me into who I am today and your support and attitudes throughout the past two years of difficult times is truly inspiring.

Table of Contents

List of Tables

List of Figures

Chapter 1.

Introduction

Estuaries are important nurseries for many mobile species because they provide a productive, protected, and connected mosaic of habitats (Beck et al. 2001, Sheaves et al. 2015). Estuaries are considered some of the most productive areas on earth (Cloern et al. 2014), and their productivity creates a prey base (Jones et al. 1990, Griffin & Rippingale 2001, Marques et al. 2007) that underpins their function as nurseries (Sheaves et al. 2015). They also provide an environment that can have relatively fewer predators than most ocean areas (McCabe et al. 1983, Willette 2001). Perhaps most importantly, they provide connectivity between refugia and foraging grounds at a small spatial and temporal scales, and between habitats used during ontogenetic migrations on a longer scale (Sheaves et al. 2015).

Anadromous salmon are an example group of species that benefit from estuaries during their ontogenetic migration from fresh water to the ocean (Thorpe 1994). Several studies show enhanced growing opportunities in estuaries compared to fresh water (Tschaplinski 1987, Murphy et al. 1997, Wallace & Allen 2007, Hoem Neher et al. 2013), which can lead to increased survival in subsequent life stages (Healey 1982b, Holtby et al. 1990, Beamish et al. 2004, Moss et al. 2005, Duffy & Beauchamp 2011). There is mixed evidence of the amount of direct predation on juvenile salmon in estuaries (Johnston 1982, McCabe et al. 1983, Bottom & Jones 1990, Evans et al. 2016) but it is typically thought to be lower than in ocean environments (Willette 2001). Finally, in addition to connecting anadromous salmon between their fresh- and saltwater ontogenetic stages, estuaries provide a salinity gradient that may ease their required osmoregulatory transition (Taylor 1921) that can result in physiological stress (Tschaplinski 1987, Healey 1991a) or reduced swimming capabilities (Weitkamp 2008). Accordingly, there is evidence that the condition of estuaries can influence survival of salmon and influence their population productivity (Magnusson & Hilborn 2003, Meador 2014).

Estuaries are incredibly dynamic environments that mobile consumers must integrate over. Dynamic gradients and variability in estuary conditions can create variable distributions of predation pressures (Gregory 1993, Gregory & Levings 1998), foraging efficiencies (Griffiths 1973, 1975, Gregory & Northcote 1993), and prey (Marques et al. 2007, David, Selleslagh, et al. 2016), A prey's abundance affects its availability to mobile consumers (Griffiths 1975). The trade-offs between foraging opportunity and predation risk influence both within-habitat movement (Halpin 2000) and the decision to move to new habitats (Werner & Hall 1988, Willette 2001). Individuals who make successful behavioural decisions based on foraging and predation pressures optimize their survival and eventually contribute back to the population (Walters & Juanes 1993). Additionally, a juvenile salmon's foraging capabilities are limited by the physiology of their ontogenetic stage, such as gape or burst speed limitations (Lazzaro 1987), with different life histories of juvenile salmon having variable abilities (Thorpe 1994, Bollens et al. 2010). Various antipredator mechanisms of prey (Buskey et al. 2002, Clarke et al. 2005) interact with foraging ability to affect the availability of prey (Griffiths 1973). Given that estuaries are just one step in a salmon's life cycle, their growth and condition in this phase can also influence the survival in next life-history stage (Duffy & Beauchamp 2011). Thus, juvenile salmon in estuaries provide a system in which to consider complex life-cycles and how they interact with complex environments.

Estuaries are changing quickly and there are variable knowledge gaps in juvenile salmon estuary ecology across different species and life-history stages. Climate change and anthropogenic development in estuaries is changing their quality and quantity at a rapid rate (McClelland & Valiela 1998, Lotze et al. 2006, Thorne et al. 2018). There is evidence that habitat loss in wetlands negatively affects juvenile salmon foraging efficiency (David, Simenstad, et al. 2016). However, baseline information is lacking on juvenile salmon behaviour across many species and life-histories in estuaries (Brodeur et al. 2000, Pickard et al. 2015, Levings 2016). This thesis addresses specific knowledge gaps, synthesizes existing knowledge, and identifies knowledge gaps for future research to investigate. Specifically, I investigated juvenile salmon food web ecology in an estuary under increasing anthropogenic development threat, the Skeena River estuary, and synthesized the current state of knowledge on growth and residency across life-histories of anadromous Pacific salmon in North American estuaries.

My first data chapter (Chapter 2) is an extensive field study that examined how two juvenile salmon species and two small pelagic fish species integrate with key prey across the estuary of the Skeena River. I asked i) how are prey distributed in the estuary across space and time, ii) what are the most important and selected prey of these four fish species, iii) do biophysical factors of the estuary co-vary or predict diet variability, and iv) can variability in prey abundance be predicted by biophysical factors? I collected fish from purse seining and plankton from concurrent vertical plankton tows to allow comparisons between diets and prey in the environment. I found that different fish species selected different prey that were unevenly distributed across the estuary seascape in time and space. I also found that some prey abundances in either diets or the environment were associated with biophysical factors like salinity, eelgrass, or catch per unit effort. I discuss these results through the lens of landscape ecology, as previously suggested (Nagelkerken et al. 2015), and explore differences in diets using ontogenetic niche theory (Werner & Gilliam 1984) and species-level differences in physiology and behaviour (Lazzaro 1987).

My next chapter compiled empirical published data on five species of juvenile salmon growth rates and residency durations. Growth rates and residency are two key variables that reflect the relationship between juvenile salmon and estuaries. I asked i) what is the spatial and biological (i.e. species and life histories) coverage of information on growth rates and residency durations? ii) what methods are used to quantify estuary residence and growth and do different methods yield different estimates? and iii) how does the mean and variability between species and life-histories differ? I conducted a rigorous literature review to compile empirical estimates. Coverage of these aspects varied greatly across species' life-histories, but it was evident that different salmon species and life-history strategies have different growth rates and residency durations in estuaries. I conclude by introducing several hypotheses that could explain the variation in average estuary growth rates and residency durations within species.

I conclude my thesis by overviewing the key findings of these studies and discuss implications to management and future directions. Overall, my research provides a case-study that enhances the local knowledge of a single complex system, highlights differences in eco-evolutionary drivers between co-occurring estuarine fishes, and synthesizes the state of knowledge and trends in juvenile salmon estuary use.

Chapter 2.

Integrating prey dynamics, diet, and biophysical factors across an estuary seascape for four fish species

2.1. Abstract

Estuary food webs support many fishes whose habitat preferences and population dynamics may be controlled by prey abundance and distribution. Yet the identity and dynamics of important estuarine prey of many species are either unknown or highly variable between regions. As anthropogenic development in estuarine areas increases, so does the need to understand how these environments may be supporting economically, culturally, and ecologically important fishes. Here, we surveyed juvenile coho salmon *Oncorhynchus kisutch*, juvenile sockeye salmon *O. nerka*, Pacific herring *Clupea pallasii*, and surf smelt *Hypomesus pretiosus* diets along with zooplankton abundance in the estuary of the Skeena River (British Columbia, Canada). We examine how these predators integrate with their prey across the seascape and what may influence prey dynamics. We found diets were highly variable, even within a species, but one or two prey comprised the majority of diet contents per species. Juvenile coho salmon primarily consumed terrestrial insects and larval fish, whereas sockeye salmon primarily consumed Harpacticoid copepods, which increased in both coho and sockeye diets over the season. In contrast, small pelagic fish (Pacific herring and surf smelt) primarily consumed Calanoid copepods, which were the most abundant prey in the environment. We found that certain prey groups were correlated with biophysical factors. For example, Calanoid copepod abundance was positively correlated with salinity while Harpacticoid copepod abundance was highest over eelgrass sites. Identifying key prey species and how they distribute within the estuary seascape is an integral link in understanding the food-web foundation of fish habitat use in areas under pressure from anthropogenic development.

Keywords: juvenile salmon, small pelagic fish, diet, prey, estuary, *Oncorhynchus*, *Clupea*, *Hypomesus*

2.2. Introduction

Marine prey are highly heterogenous across space and time (Hutchinson 1961, Hunt Jr. 1990, Barry & Dayton 1991), creating both challenges and opportunities for mobile consumers. For example, infrequent pulses of prey due to stochastic processes or seasonal dynamics and prey phenology can create temporary prey hotspots for predators (Croll et al. 2005, Yang et al. 2008). Further variation of prey abundance across space and time may be driven by major habitat transitions, abiotic preferences of prey, environmental dynamics, and top down effects of predators (Telesh & Khlebovich 2010, Lannin & Hovel 2011, David, Selleslagh, et al. 2016). Studying these aspects in marine environments is difficult, but increased application of landscape ecology approaches to seas (or seascapes) has improved our understanding of faunal-seascape relationships (Boström et al. 2011). The dynamics and heterogeneity of prey across seascapes, which are dynamic and heterogeneous themselves (Boström et al. 2011, Nagelkerken et al. 2015), can increase risks of starvation and predation to mobile consumers (Frank & Leggett 1986, Letcher & Rice 1997, Pitchford 2001, Chittenden et al. 2010). To cope with this spatio-temporal variation in prey, predators respond behaviourally by modifying their distributions (e.g. migration) and search patterns (e.g. Lévy walk) to increase encounter rates with prey patches (Viswanathan et al. 1996, Croll et al. 2005, Sims et al. 2008). Alternatively, mobile predators may integrate across staggered, smaller pulses of prey that occur over the variable seascape (e.g. prey waves instead of hot spots) to achieve more extended and consistent feeding opportunities (Armstrong et al. 2016). Different species of predators have different prey preferences, foraging abilities, and employ different search movements to survive and thrive in heterogeneous prey seascapes (Deudero & Morales-Nin 2001, Graeb et al. 2005). Thus, understanding the prey dynamics of seascapes is a key component of understanding the ecology of their consumers.

Estuaries can be prey-rich places for planktivorous fishes (St. John et al. 1992, Thorpe 1994, Selleslagh et al. 2012, Levings 2016), but they are driven by multiple biophysical processes that produce particularly dynamic prey fields. Here, we refer to estuaries as the tidally-influenced portions of rivers that have saltwater influence and the constituent bays that have freshwater influence (Perillo 1995). Productivity in estuaries is derived from the combination of riverine inputs and upwelled ocean nutrients, as well as local production from sea grasses, salt marshes, benthic and epiphytic algae, and microbes (Cloern et al. 2014). Each of these sources have seasonal patterns, often creating large phytoplankton blooms followed by zooplankton blooms (Cloern 1996, Mackas et al. 2012). In addition, zooplankton within an estuary must compete with a hydrodynamic hurricane of tides and currents that interfaces with a variety of habitats to remain in their optimal environment (Palmer 1988, Lucas, Koseff, Monismith, et al. 1999, Menendez et al. 2012, David, Selleslagh, et al. 2016). For example, rising tides over intertidal areas can push pelagic zooplankton into high density patches (David, Selleslagh, et al. 2016). In contrast, benthic and epibenthic zooplankton are known to have higher site fidelity than pelagic species because they can bury or attach themselves to their substrate and avoid this redistribution (Palmer 1988). Temperature and turbidity are also strong drivers of zooplankton habitat preference and are linked with their growth and reproductive development (Huntley & Lopez 1992, Morgan et al. 1997). Thus, a dynamic mosaic of zooplankton prey provide the resource base for planktivorous fishes that may rely on estuaries for staging or important nursery habitats (Beck et al. 2001, Sheaves et al. 2015, Nagelkerken et al. 2015).

Multiple economically, culturally, and ecologically important small fishes such as juvenile coho salmon *Oncorhynchus kisutch,* juvenile sockeye salmon *O. nerka*, adult Pacific herring *Clupea pallasii*, and adult surf smelt *Hypomesus pretiosus* are supported by zooplankton and other food sources in estuaries along the West Coast of North America (Table A1). Food webs supporting juvenile coho salmon are well researched, though many studies are from systems in the California Current System like the Columbia estuary or Puget Sound (Table A1). These studies found large regional, seasonal, annual, and ontogenetic variability in juvenile coho salmon diets (Brodeur, Daly, Sturdevant, et al. 2007, Daly et al. 2009, Bollens et al. 2010, Levings 2016). Juvenile coho are considered generalists, eating decapod larvae, amphipods, pteropods, copepods, euphausiids, eggs, and various other larval crustaceans but are predominantly piscivorous and insectivorous (Brodeur 1991). Studies on sockeye diets in estuaries reported that they consumed euphausiids, cirripeds, mysids, larval fish, and calanoid copepods as well as other crustaceans in minor amounts (Simenstad et al. 1982, Birtwell et al. 1987, Ajmani 2011). In contrast, Pacific herring and surf smelt can have variable diets but generally consume copepods and other crustaceans in coastal environments (Miller & Brodeur 2007, Hill et al. 2015). To the best of our knowledge, few published reports on the estuarine diets of adult Pacific herring exist and none for adult surf smelt (Table A1). Interestingly, two studies on Pacific herring found that large herring can consume juvenile salmon entering estuaries (Thorsteinson 1962, Ito & Parker 1971). Overall, there is variable scientific understanding of the estuary diets of juvenile coho and sockeye salmon, Pacific herring, and surf smelt in Northeast Pacific estuaries. There are even fewer studies linking diets and prey distribution patterns (Bollens et al. 2010) or understanding the role of estuaries as staging and nursery habitats (Sheaves et al. 2015, Nagelkerken et al. 2015, McDevitt-Irwin et al. 2016).

Here, we quantify the spatial and temporal dynamics of estuarine prey for four fish species and their relationships with biophysical aspects of their seascape. Specifically, we studied juvenile coho salmon, juvenile sockeye salmon, adult Pacific herring, and adult surf smelt in the estuary of the Skeena River in northern British Columbia, Canada's second most productive salmon watershed. We asked: i) how are prey distributed in the estuary across space and time, ii) what are the most important and selected prey of these four fish species, iii) do biophysical factors of the estuary co-vary or predict diet variability, and iv) can variability in prey abundance be predicted by biophysical factors? We discovered that diets varied greatly across the small spatial and temporal scale of our study for each species, particularly salmon, and that a few prey had consistently high abundances across the seascape while other prey were associated with different biophysical factors such as salinity or the presence of eelgrass. These findings provide insight into important prey dynamics and identifies biophysical factors through which potential change could impact food webs supporting key fish species —a recognized knowledge gap in on-going decision-making and planning processes in the Skeena River watershed (Pickard et al. 2015).

2.3. Methods

We investigated the spatio-temporal dynamics of zooplankton prey, along with the diets of four fish species in estuary of the Skeena River, British Columbia, Canada. We mapped important prey abundance across our sampling sites and tested for trends in abundance between sites and sampling periods. Next, we ranked prey importance and selectivity with two common metrics and scored diet overlap across individuals within species to measure small scale diet variability. Subsequently, we assessed whether variation in important prey abundance in diet samples and in the seascape could be predicted by biophysical factors through generalized linear regression.

2.3.1. Field sampling and laboratory methods

Our study was in the Skeena River estuary. The Skeena River is the second largest watershed entirely in British Columbia, Canada, draining an area of 55 000 km^2. The Skeena mixes with the ocean in Chatham Sound, a semi-enclosed basin approximately 1500 km^2 (Ocean Ecology 2014), by travelling through three major passages. Our study area is situated at the end of the northern-most passage, Inverness, which directs approximately 25% of the total flow of the Skeena River (Trites 1956). The study region (Fig 2.1) is in the traditional territory of the Tsimshian First Nations and is a focus of a research program developed in collaboration with Lax Kw'alaams Fisheries and Skeena Fisheries Commission to improve understanding of estuarine use by juvenile salmon and the broader estuarine food web. This study focusses on an estuary region previously demonstrated to be used in high abundances by juvenile salmon during their migration, up to 2-8 times greater than other regions (Carr-Harris et al. 2015). This region also supports juvenile salmon from throughout the Skeena watershed with at least 40 different populations identified in the estuary (Carr-Harris et al. 2015, Moore et al. 2015) that enter at different times (Carr-Harris et al. 2018), most likely forage there, and reside for variable amounts of time (Moore et al. 2016). The average estimated residencies for sockeye and coho were 2 and 14 days, respectively (Moore et al. 2016). Further work within this region identified that different fish abundances were associated with abiotic aspects of estuary habitat (Sharpe 2017), however, how the estuarine zooplankton community support salmon and other small pelagic fish in the Skeena remains unknown.

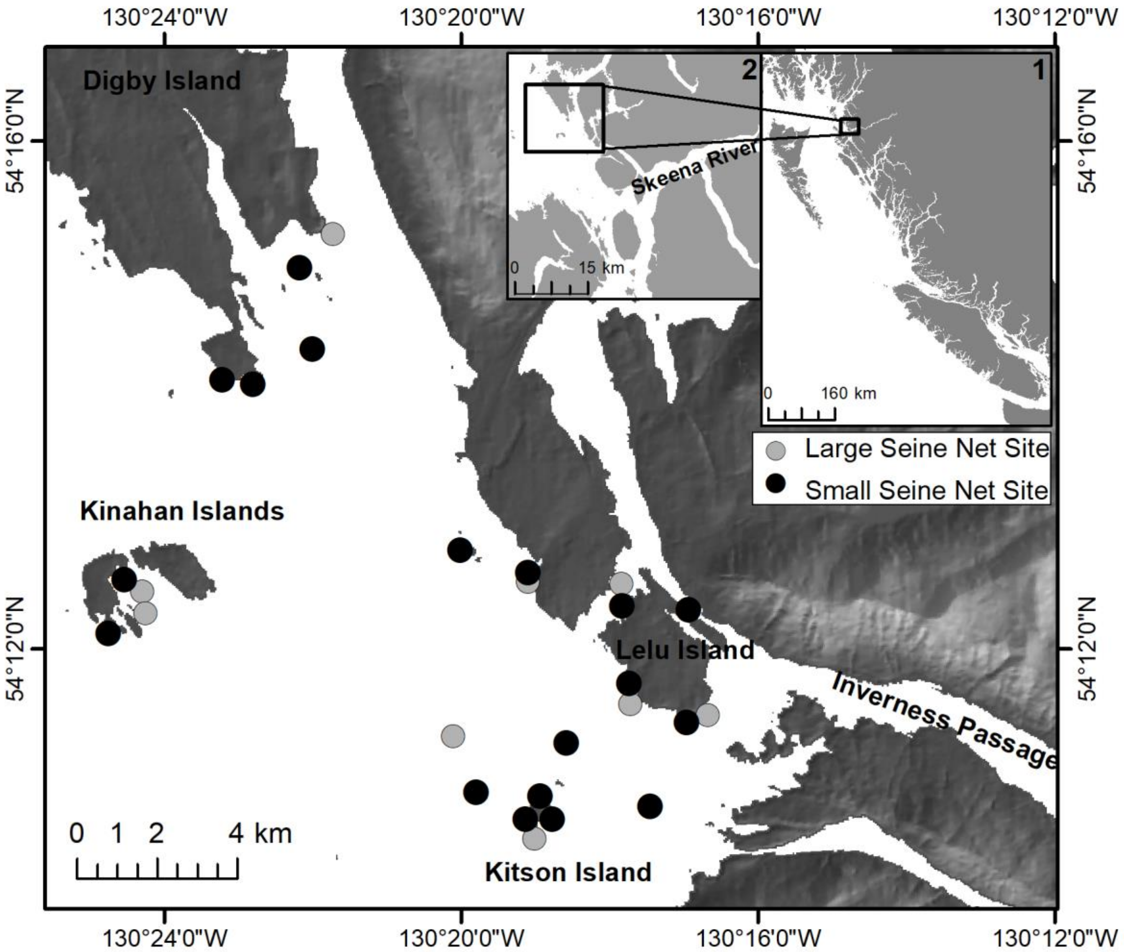


Figure 2.1 **Map of sampling locations according to net type used to capture fish across the Skeena River estuary. Note that vertical zooplankton tows were done concurrently at small seine net sampling events.**
Map inserts indicate location of sampling region in relation to: 1) the coastline of British Columbia, 2) the mouth of the Skeena River. Source: Sharpe 2017. Reproduced with permission.

For diet analysis, we lethally sampled (Simon Fraser University Animal Care 1107B-11; Fisheries and Oceans Canada licence XR 82 2016) 111 sockeye salmon, 57 coho salmon, 57 Pacific herring, and 35 surf smelt across 17 sampling occasions (from here on, referred to as "sets"). The 17 sets occurred across 10 sites that were from a subset of 25 sites from the ongoing research program. Sites were chosen to represent four main habitat types available in the estuary, eelgrass, sandy bay, rocky shoreline, and open water (Sharpe 2017), or were part of the long-term monitoring project (Carr-Harris et al. 2015). We collected fish with two sizes of purse seine; the larger net measured 73.2 m long by 9.1 m deep with 5.1 cm webbing at the tow end and 1.3 cm webbing at the bunt, and the smaller net measured 45.7 m long by 5.5 m deep with 1.3 cm webbing at the tow end and 0.64 cm webbing at the bunt end. The two sizes of net were used so we could target the entire water column of sites with varying depths without catching the estuary substrate. We enumerated each species of fish and calculated a catch per unit effort (CPUE) as a measurement of salmon abundance. Relative abundances from the smaller purse seine were standardized to the larger purse seine by multiplying the small net catches by the large net area (length by width) and net tow duration, and then dividing by the area and tow duration of the small net. Fish samples were retained when there were at least five individuals of a species from any given set available for collection. We collected fish between May 10th and June 21st, 2016, to capture juvenile salmon around the peak of their outmigration, immediately storing lethal samples in seawater buffered 5% formalin solution.

Fish and diet samples were further processed in the laboratory. We measured fork length and wet weight (outside pat dried with paper towel) of all fish before excising their stomachs. Stomach contents were analyzed by identifying prey to the lowest possible taxonomic level. Abundance, total wet weight, and state of digestion was reported for each prey taxa in each stomach. Prey that was too digested to be identified was removed from the subsequent analysis. When diet contents could be identified to taxonomic group but were broken into parts, preventing an accurate count of individuals, we estimated abundance by using prey specific linear regressions of known abundance on weight from our diet samples (Table A2). One sockeye salmon, four coho salmon, and one Pacific herring had empty stomachs, leaving 110 sockeye salmon, 53 coho salmon, 56 Pacific herring, and 35 surf smelt in the analysis (Table A3).

We concurrently sampled for zooplankton in the environment at the 18 small-purse seine sites as when fish were sampled (Fig 2.1). Zooplankton were collected over four time periods, May 13 - 20, May 24 - Jun 1, Jun 6 - 10, and Jun 20 – 24 (n = 71, one sampling occasion was missed due to safety concerns from ocean conditions). We used a 250 µm WP2 plankton net towed by hand vertically from a boat from 5 m below the surface to standardize the volume of water that was sampled. Samples were stored in a seawater buffered 5% formalin solution. We stained zooplankton with Rose Bengal to make them more visible, partitioned them with a Folsom plankton splitter, and sorted them until at least 400 individuals or the entire sample had been identified. We used a taxonomic level that was comparable to zooplankton identified within the diet samples and enumerated each group. We used abundance, corrected by the size of partition, as the final variable because all samples were from the same depth (5 m) and, therefore, volume of water (3900 L).

2.3.2. Prey abundance across the seascape

We identified six fish prey groups to investigate their spatial and temporal trends based on their common occurrence in diets of our study fish in other studies. Harpacticoid and Calanoid copepods, Cirripedia cyprids, decapod zoea, pteropods, and oikopleurans were chosen based on their prevalence in prior diet research that we compiled (Table A1) and representation in the zooplankton tows (i.e. we did not investigate prey groups such as larval fish that could avoid the plankton net nor terrestrially derived insects who would be concentrated at surface waters). We tested for differences in zooplankton abundance between sites and periods, for each species, using the non-parametric Kruskal-Wallis test by ranks. If there was a significant difference (alpha = 0.05 level) between groups, we used Dunn’s test to determine which sites or periods were different. We determined the direction of any differences in abundance graphically.

2.3.3. Importance, selectivity, and variability of prey in diets

We used two indices that calculate consumption and selectivity of different prey by predators to determine what prey are most important and selected for by the study fish. First, we quantified prey consumption by the amount and frequency it was consumed for every individual fish as a metric of prey importance to each fish species using a modified Index of Relative Importance (IRI) (Bottom & Jones 1990):

$$IRI_{ij} = \left(A_{ij} + B_{ij}\right) \times (FO_j) \tag{1}$$

We calculated an IRI score for each prey taxa (*j*) for each individual fish (*i*). *A* represents the percent abundance of prey *j* in fish *i*. *B* represents the percent wet weight biomass of prey *j* in fish *i*. *FO* is the percent frequency of occurrence of prey *j* across all individuals of a given species. The IRI metric considers prey “importance” as best described by both its percent abundance and percent wet weight biomass within a diet because abundance and weight relationships are not equivalent across taxa (e.g. one fish larvae may account for a high percentage of prey biomass but a low percent of abundance while many small copepods may do the opposite). Multiplying the cumulative percent of prey abundance and biomass by its percent frequency of occurrence scores rare prey lower than common prey and helps standardize IRI scores across varying individuals. Thus, individuals who did not consume a certain prey were not a 0 but an NA for this analysis and subsequent calculation of standard error around the mean IRI for each prey per predator species.

Second, we quantified prey electivity to investigate which food resources were appearing more often in the diets than expected by chance. Electivity indices are commonly used to provide inference on realized selectivity within a given prey seascape. We used Chesson's α-electivity index (Chesson 1978; Robert et al. 2008) to rank the electivity of fish for each prey taxa (j):

$$\alpha_j = \frac{d_j}{p_j} / \sum\left(\frac{d_i}{p_i}\right), \text{ for } i = 1, \ldots N, \tag{2}$$

where N is the number of prey taxa considered (N = 7, 9, 11, and 13 for coho, sockeye, herring, and smelt, respectively), d_j/p_j is the relative frequency ratio of the proportion of prey j in the diet (d) of an individual fish and in the plankton (p) of its associated site, and $\sum(d_i/p_i)$ is the sum of this ratio for all prey taxa included in the analysis. The neutral electivity threshold, which suggests that a prey is being eaten in an equivalent proportion to what it would be encountered at by random in the environment, is defined for each predator as $1/N$. We removed some species from analysis including prey that could readily avoid capture in the plankton net (e.g. larval fish, crab megalopa, cumaceans, isopods) or occurred in less than 5% of tow samples (e.g. terrestrial insects) because they artificially inflated the electivity denominator (p) due to systemic sampling error or general rarity (Brodeur et al. 2011). Prey that were not eliminated from this process but were still not present at some sites were assigned a p that was one order of magnitude smaller than the smallest measured p so that there were no zeros in the denominator. Since zooplankton samples were only taken at the 18 small purse seine sites during concurrent fish sampling, diet samples of fish caught from large purse seine sets were matched with the nearest plankton sample in time and space. If multiple plankton samples were taken within 250 m of the diet sample, we selected the sample closer in time.

We quantified the amount of variability in diet samples across all individuals within a fish species by using Schoener's (1970) percent similarity index (PSI):

$$(3) \qquad PSI_{x,y} = 100\left(1 - 0.5\left(\sum_{j}^{n} |P_{x,j} - P_{y,j}|\right)\right)$$

where $P_{x,j}$ = percent wet weight of prey j in the stomach of individual x; and

$P_{y,j}$ = percent wet weight of prey j in the stomach of individual y; and

n = the total richness of prey consumed of the fish species concerned.

A PSI of 100 represents complete diet overlap and zero represents complete dissimilarity.

We also quantified gut fullness across all individuals within each fish species. Gut fullness is also referred to as stomach fullness, an index of feeding intensity (Bottom & Jones 1990), or feeding index (Price et al. 2013), and is commonly calculated as a percent of body weight (%BW) (Brodeur et al. 2015):

$$(4) \qquad \%BW = 100 \times (M_P/(M_T - M_P))$$

where M_T = total wet weight of the fish prior stomach removal; and

M_P = total wet weight of prey contents.

2.3.4. Predicting prey in diets and across the seascape

We subsequently investigated patterns that could predict variability of important or selected prey across individuals. We chose prey (Table A4) with higher than average IRI and α scores per fish species and regressing their abundance across individual diets (including zeros) against a suite of covariates using generalized linear models with mixed effects (GLMM). The covariates included: fish fork length, turbidity (Secchi disk depth), water temperature, distance from shore, number of conspecifics in set (in CPUE), total number of fish in set (in CPUE), and day of year. We formulated several hypotheses about the relationships between each of these variables, with explanations and examples for why they could be negative or positive (Table A5). We included a random effect for set in each model because individuals caught in the same net are considered non-independent.

We used a similar approach to the diet variability analysis to investigate relationships between variation in prey abundance with biophysical covariates of the estuary seascape. We used the same six prey from the prior prey analysis: Harpacticoid and Calanoid copepods, Cirripedia cyprids, decapod zoea, pteropods, and oikopleurans. We used GLMMs to regress prey abundance counts from zooplankton tows against temperature, salinity, time of tow, main habitat type (eelgrass, sandy bay, rocky shore, open water), and site distance from shore. We did not include turbidity because it had a Pearson correlation coefficient of 0.7 with salinity, which is known to be a strong determinant of zooplankton distributions. We explored hypotheses about the relationships between each of these variables, with explanations for why they could be negative or positive (Table A6). We included site as a random effect in all models to account for the expected covariation (non-independence) within sites that may be present across sampling time periods.

2.3.5. Generalized linear model specifications

Generalized linear mixed effects models were used to provide information for our third and fourth questions (predicting prey in diets and the seascape). For both the diet variability and prey variability analysis, we fit single fixed-effect GLMMs with their respective random effect due to the limited amount of data and risk of overfitting (Babyak 2004, Hitchcock & Sober 2004). We compared model fits of Poisson, negative binomial 1, and negative binomial 2, with log links using Akaike Information Criterion corrected for small sample size (Burnham & Anderson 2002) to determine which distribution family was appropriate for each response-predictor variable combination. We fit models in R (R Core Team 2017) using the package glmmTMB (Magnusson et al. 2017), which estimates parameters by maximizing likelihood. We tested the likelihood that covariates had a significant effect on improving model fit against an intercept only model with a likelihood ratio test at the $\alpha = 0.05$ level. However, because we did multiple comparisons using single covariate models for each response variable, we increased the probability of committing a type I error (i.e. rejecting H_0 when H_0 is true) (Cabin & Mitchell 2000). Thus we applied a Bonferroni correction (Bonferroni 1936, Dunn 1961) to α of α/m, where m is the number of likelihood ratio tests per response variable. However, we discuss all results even if they were subsequently rejected by the Bonferroni correction because statistical power to detect effects in behavioural research can often be low (Jennions 2003, Nakagawa 2004). All covariates were centered and scaled (subtracted the mean from each observation and divided by one standard deviation) so that their effects could be comparable and to improve model convergence. If a covariate had a significant effect, we visually inspected their fit by examining the Pearson's and standardized residuals plotted against fitted values and checked for patterns. Subsequently, we graphically inspected the trends against real data for biological significance and confidence around the average prediction.

2.4. Results

2.4.1. Prey abundance across the seascape

We found differences in abundance between prey groups, across sampling locations, and between time periods within several prey species. Calanoid copepods had the highest average abundance and were present in every sample (Table 2.1), making them the numerically dominant and most ubiquitous prey. Pteropods were the only other prey present in every sample but occurred at considerably lower average abundance than Calanoid copepods. Cirripedia cyprids and oikopleurans had the next highest average abundances and frequencies of occurrence, followed by the more sporadically distributed Harpacticoid copepods and decapod zoea. Three of the six species we tested for variability in abundance (Calanoid copepods, pteropods, and decapod zoea) had statistically different medians at the alpha = 0.05 level between sites (Fig 2.2). Differences between sites could suggest that they are not entirely independent and that some sites are possibly hotspots within the seascape for these species (Fig 2.2,2.3). No single site appeared to have consistently higher abundance of all species, but some sites had consistently below average abundance, which could represent an area with low prey availability. Two prey species, Cirripedia cyprids and oikopleurnas, had statistically different medians between periods (Fig 2.2). Only period two had a higher median than the other periods for Cirripedia cyprids, whereas periods two and four had higher medians than one and three for oikopleurns (Fig 2.2). Because only two of six prey showed differences between sampling periods and not in a consistent manner, we suggest that period may not have as an important effect as site and thus we did not include it as a random effect in subsequent models. Harpacticoid copepods did not have either temporal nor site-specific differences in their abundance.

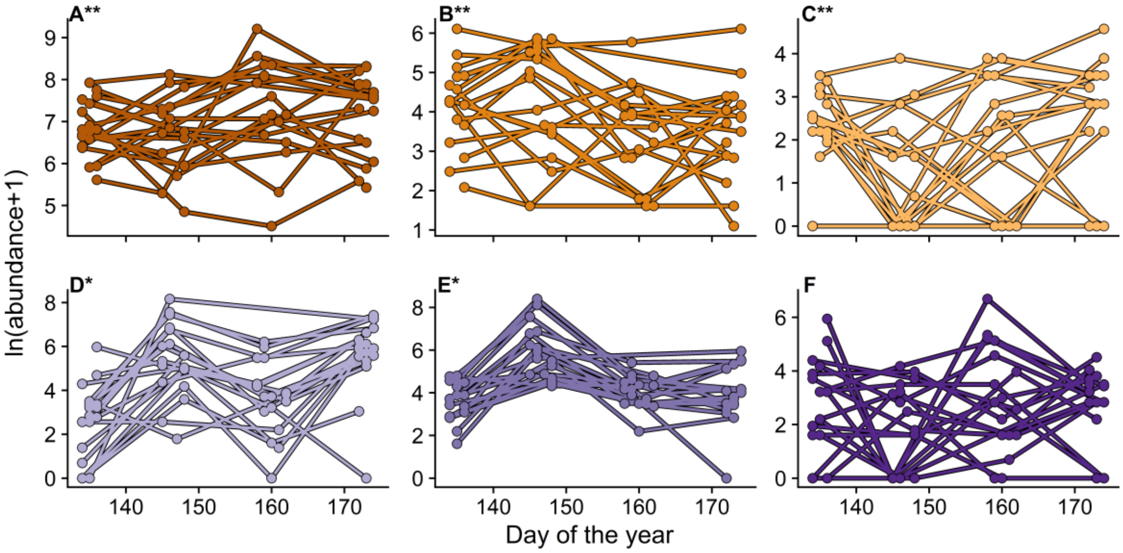


Figure 2.2 Spatial and temporal patterns of abundance of a) Calanoida, b) Pteropoda, c) Decapoda zoea, d) Oikopleura, e) Cirripedia cypris, and f) Harpacticoida. Points connected by lines are samples from the same site within the Skeena estuary.

Note the that not all y axes are equivalent and contain broken axes. Letters denoted by ** and * had significant site or sampling period differences, respectively, as detected by a Kruskal Wallis tests at α level = 0.05.

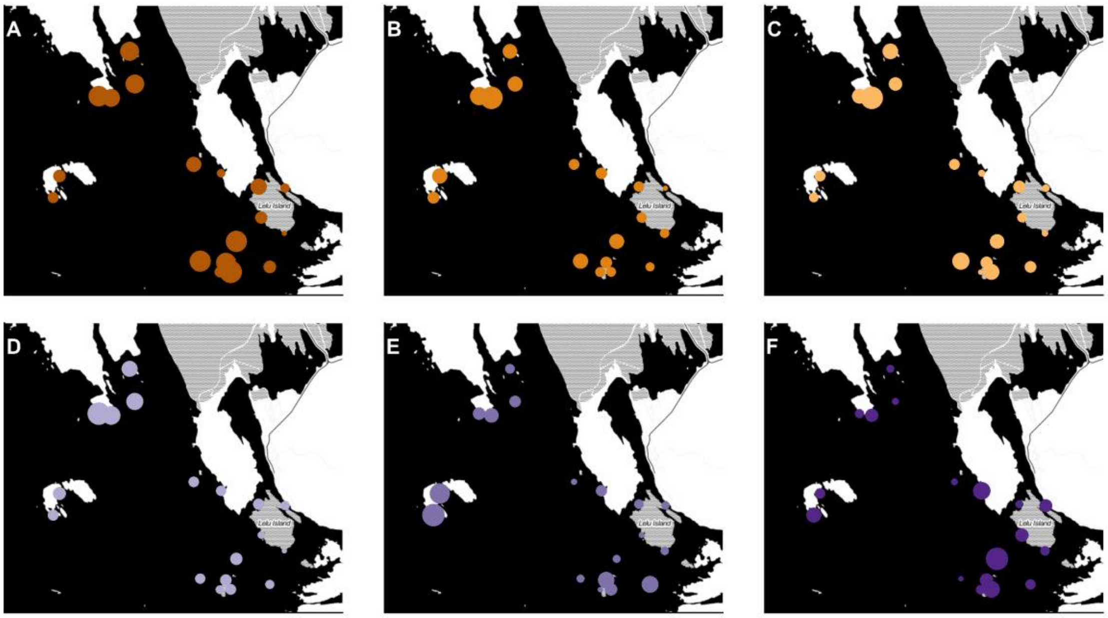


Figure 2.3 **The spatial distribution and relative mean abundance across all time periods of a) Calanoida, b) Pteropoda, c) Decapoda zoea, d) Oikopleura, e) Cirripedia cypris, and f) Harpacticoida across sampling sites in the Skeena River estuary.**

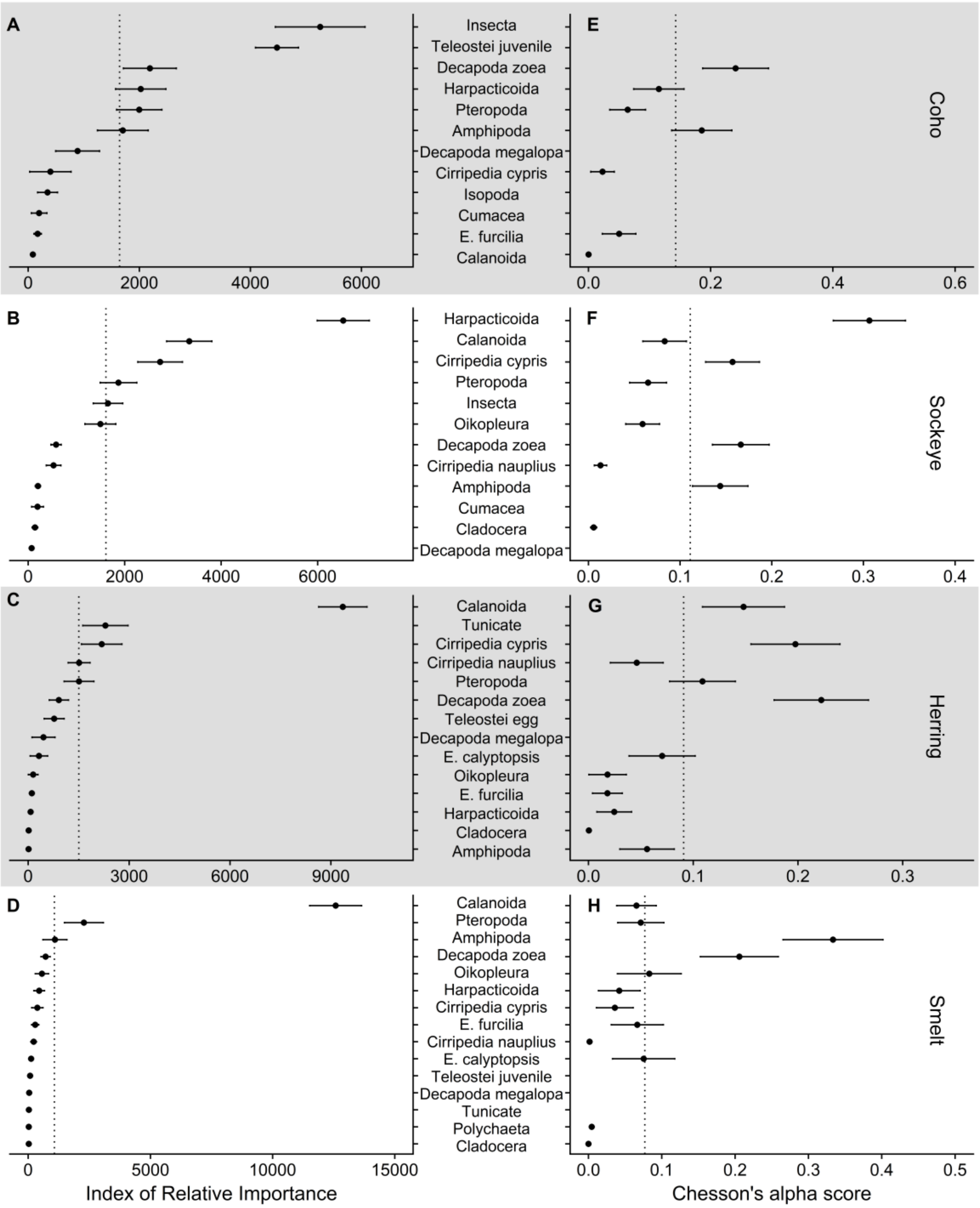
Bubble size is scaled by the relative abundance within a species, i.e. the size of bubbles is not comparable between species, only within. Large bubbles of species that had site level differences (top row) could represent hotspots for those prey. Black is water, white and grey are land.

Table 2.1 **Average abundance per sample (3.9 L) of select prey species and their frequency of occurrence across samples (n = 71).**

Prey species	Mean abundance SD	Occurrence
Calanoid copepods	1630 1563	1.00
Pteropoda	92 109	1.00
Decapoda zoea	14 17	0.72
Oikopleura	333 582	0.92
Cirripedia cyprids	282 715	0.99
Harpacticoid copepods	45 109	0.76

2.4.2. Importance, selectivity, and variability of prey in diets

We observed large variation in importance (IRI) and electivity (α) scores across individual fish within a species. There was considerable variability within the highest mean IRI scoring prey items for each fish species, with the values often ranging from ~0 to one order of magnitude larger than the mean. In the discussion, we refer to prey that have more than twice the average IRI score as primary prey and those around the average as secondary prey.



(Previous page)

Figure 2.4 Index of Relative Importance and Chesson's electivity scores of each prey species with standard error for coho salmon (A,E), sockeye salmon (B,F), Pacific herring (C,G), and surf smelt (D,H). The dashed line represents the overall average IRI score and the neutral alpha selectivity threshold for each fish species. Alpha scores above the neutral selectivity threshold suggest that a species is represented in the diet more than it is represented in the environment (i.e. proportionally higher in the diet), whereas below the line suggests that the prey is proportionally higher in the environment. Note the reduced diversity of prey presented with Chesson's alpha because poorly sampled prey were removed. Only the prey that occurred in more than 5% of diets is presented for both indices for coho salmon, sockeye salmon, and Pacific herring, with a 10% occurrence cut-off for surf smelt because of the higher diversity of prey consumed in small amounts.

For juvenile coho salmon, terrestrial-based insects and larval/juvenile fishes had the highest mean IRI scores, 2.4 and 2.1 times higher than the third highest prey, respectively (Fig 2.4a). Insects were primarily Diptera (64% by abundance), followed by Hemiptera (26%), Coleoptera (6%), and others (Collembola, Hymenoptera, Trichoptera, and Ephemeroptera). Only 23% of juvenile and larval fish were identified to family or lower, which were either Pleuronectidae (86%) or Pacific herring (14%). Decapod zoea (primarily from infraorder Brachyura), Harpacticoid copepods, gastropods (*Limancina* pteropods when identifiable to genera), and amphipods also had higher than average mean IRI scores. Amphipods were primarily Gammaridea (83%) with a notable 47% of Gammaridea being a high-intertidal family, Talitridae. The remaining amphipods (17% by abundance) were Hyperiidae. Coho had the highest electivity for decapod zoea followed by amphipods (Fig 2.4e). The mean Harpacticoid copepod electivity score was slightly below the neutral selectivity threshold. All other prey groups were consumed in lower abundances than their relative abundance in the environment.

In juvenile sockeye salmon, Harpacticoid copepods had the highest mean IRI score, 2 times higher than their next highest ranked prey (Fig 2.4b). Calanoid copepods, Cirripedia cyprids, gastropods (*Limancina* pteropods when identifiable to genera), and terrestrial-based insects (majority Diptera and Hemiptera), also had higher than average mean IRI scores. It is interesting to note that five individuals also consumed adult stages of the salmonid parasite from the family Caligidae, which has also been observed in southern British Columbia (Price et al. 2013). Juvenile sockeye salmon had the highest electivity for Harpacticoid copepods followed by decapod zoea, Cirripedia cyprids, and amphipods (Fig 2.4f).

Calanoid copepods had the highest mean IRI scores for both adult Pacific herring and adult surf smelt, 4 and 5.5 times higher than their next highest ranked prey, respectively, for each fish species (Fig 2.4c, d). Ascidian tunicates and Cirripedia cypriids were the only other Pacific herring prey whose mean IRI scores were higher than the overall mean IRI. Herring had the highest electivity for decapod zoea followed by Cirripedia cyprids, Calanoid copepods, and gastropods with nearly neutrally electivity for euphausiid calyptopsis (Fig 2.4g). Gastropods, all of which were unidentifiable beyond *Gastropoda*, were the only other surf smelt prey whose mean IRI score was above average. Smelt had the highest electivity for *Hyperiidea* amphipods followed by decapod zoea and had neutrally electivity for oikopleurans, ephausiid calyptopsis and furcilia, gastropods, and Calanoid copepods (Fig 2.4h). Although both herring and smelt had a high electivity value for decapod zoea, it was only found in 47% and 51% of individuals, respectively, and zoea were not consumed in large quantities. High electivity and generally low presence in the diet could mean that when zoea were encountered, despite their rarity, they were opportunistically targeted by both predators.

We found that diets and gut fullness within each species were highly variable with low diet overlap between individuals. The mean PSI values across all individuals within a species were all below 50 on average (Table 2.2), meaning that diets were frequently more than 50% different across individuals of the same species. When we examined PSI pair-wise comparisons that were done between individuals from the same set (still of the same species), we found that the average PSI values increased but were still below 50% for all species except for surf smelt. Average percent gut fullness was comparable to other studies on coho and sockeye salmon in estuary and nearshore environments if not slightly higher (Bottom & Jones 1990, Healey 1991b, Brodeur, Daly, Schabetsberger, et al. 2007, Price et al. 2013). In contrast, surf smelt and Pacific herring had less than half the gut fullness of both salmonids (Table 2.2).

Table 2.2 Average Percent Similarity Index (PSI) values with standard error for each fish species between all individuals and between only individuals from the same sets, mean gut fullness (%BW) with standard deviation, and fork length (FL) range with mean.

Fish species	Mean PSI SE	Mean set PSI SE	Mean gut fullness SD	FL Range Mean
Coho	19.3 0.85	26.0 4.01	0.91 0.86	84-136 102
Sockeye	20.2 0.35	45.6 5.16	0.83 1.11	59-109 82
Herring	30.7 0.80	39.1 7.58	0.38 0.73	68-168 125
Smelt	48.0 1.40	52.9 6.60	0.34 0.34	106-168 134

2.4.3. Predicting prey in diets and across the seascape

We found three relationships between prey diet abundance and several biophysical factors that had parameter estimates that were statistically different than a null model by using likelihood ratio tests at the Bonferroni corrected α = 0.05 level, and eight additional relationships when α was uncorrected (Fig A1, Table A7). The abundance of Teleostei juveniles in coho salmon diets decreased with increasing distances from shore. Insect abundance in coho salmon diets decreased with temperature, possibly due to increased turnover of water from the river and increased delivery of upriver insects. Day of year was positively correlated with harpacticoid copepod abundance in sockeye diets. The following eight relationships were only significant at the uncorrected α = 0.05 level. Increased total set CPUE (total abundance) decreased the number of insects in coho salmon diets and the number of calanoid copepods in Pacific herring diets, possibly because of exploitative competition. Insect and decapod zoea abundance in coho salmon diets increased with secchi depth, possibly due to increased ability of fish to see insects stranded in surface waters and decapods within the water column in clearer water. Decapod zoea abundance in coho salmon diets also increased with coho length, but this relationship appears to be driven by outlying data points. Calanoid copepod abundance in surf smelt diets decreased with fish length, a possible indicator that larger individuals were targeting a different prey for consumption. Calanoid copepod abundance in Pacific herring diets increased with distance away from shore, but the confidence intervals on this relationship are particularly large. Water temperature was positively correlated with harpacticoid abundance in sockeye diets. However, day of year and temperature were highly correlated for sets with sockeye samples (Pearson’s correlation coefficient = 0.65) and day of year fit better upon visual inspection.

We found three relationships between prey abundance in the environment with biophysical factors that had parameter estimates statistically different than zero at the Bonferroni corrected α = 0.05 level and three additional relationships when α was uncorrected (Fig 2.5, Fig A2, Table A8). Calanoid copepod and oikopleuran abundance were positively correlated with salinity, possibly driven by these species’ natural salinity tolerances. Pteropoda abundance was negatively correlated with temperature. The following three relationships were only significant when α was uncorrected. Pteropoda abundance was positively correlated with salinity. Harpacticoid copepods were more abundant on average at sites with eelgrass substrate compared to sites over open water or close to rocky shores and had a slight tendency to be more abundant than sites that were sandy bays. Cirripedia cyprid abundance was negatively correlated with temperature. No biophysical factors predicting decapoda zoea abundance had statistical support.

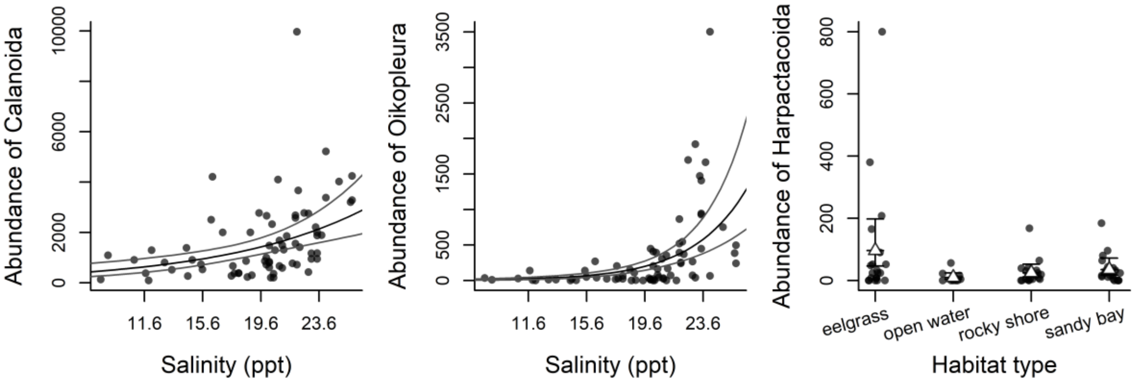


Figure 2.5 **Predicted relationships between the abundance of several important prey in the environment and biophysical aspects of the seascape within the Skeena estuary, including 95% confidence intervals calculated from their respective GLMMs.**

2.5. Discussion

The high productivity of estuaries produces a dynamic and diverse prey layer of the seascape (Jones et al. 1990, Cloern et al. 2014), which adds value to habitats for both adult and juvenile planktivorous fishes. Indeed, estuaries are particularly valued as key nursery habitats for a variety of fish species (Beck et al. 2001), where the dynamics of prey resources are an integral component of the nursery function (Sheaves et al. 2015). Here we found that four co-occurring estuary fish species relied on different prey that were dynamic across space and time. Our results also highlight high variability in diet contents within a small region, and even between fish of the same species from the same seine set, whereas prior research often contrasts diets over seasons, years, or regions (Simenstad et al. 1982, Brodeur, Daly, Sturdevant, et al. 2007, Hill et al. 2015). Biophysical factors predicted some of the variability in fish diets and prey in the environment. Thus, we provide rare empirical evidence for the spatio-temporal dynamics of prey and how predators integrate across them within a major estuary. The spatiotemporal prey mosaic has been previously suggested as a critical but under-studied dimension of the role of estuaries as important refuges and nursery habitats (Sheaves et al. 2015, Nagelkerken et al. 2015).

Our study fills recognized knowledge gaps for the Skeena River estuary (Pickard et al. 2015) by furthering our understanding about how prey are distributed during the period of highest juvenile salmon abundance (Carr-Harris et al. 2015, Sharpe 2017). Prey abundance and distribution can determine their availability to predators (Griffiths 1973, 1975), so it is important to understand these features of the prey mosaic when considering how predators integrate with prey. Calanoid copepods showed consistent differences in abundance between sites but because they were the most abundant and ubiquitous zooplankton prey, the sites with low abundance still had higher abundance than most other prey groups. Calanoid copepods' relatively high abundance has the potential make them one of the most available prey (Griffiths 1975). Cirripedia cyprids and oikopleurans were present in moderate abundance and showed different temporal patterns across sites, with Cirripedia cyprids having a single temporal peak in abundance while oikopleurans had two. Peaks in abundance could be interpreted as differing bloom phenologies between these two groups and could affect their availability by matching or mismatching predators' estuary timing (Cushing 1990, Satterthwaite et al. 2014). Decapod zoea and Harpacticoid copepods had the overall lowest average abundance and sporadic distributions, which could increase the search intervals (or decrease encounter rates) for this patchier prey (Viswanathan et al. 1996, Sims et al. 2008). We did not effectively sample for larval fish or terrestrial insects (Brodeur et al. 2011), which are also known common prey (Table A1). But overall, the prey field in the Skeena River estuary appears to be saturated by Calanoid copepods with temporally variable abundances of Cirripedia cyprids and oikopleurans, and low and patchy abundance of decapod zoea and Harpacticoid copepods.

Our study also addresses a gap in knowledge for juvenile coho and sockeye salmon diets in the Skeena River estuary (Pickard et al. 2015), as well as for the co-occurring and highly abundant small pelagic fishes in the area (Sharpe 2017), Pacific herring and surf smelt. Despite the observed diet heterogeneity within sets, each species often consumed one or two prey most often and in high abundance or weight, here referred to as primary prey, followed by a few secondary prey that were consumed at a magnitude more than all remaining prey. Primary prey for coho were insects and larval fish, which is consistent with prior research in British Columbia (Manzer 1969, Osgood 2016). Although we did not include insects and larval fish in the electivity analysis, their ubiquity in diets across other regions along the West coast of North America (Table A1) leads us to presume they were likely selected for. Coho also selected for decapod zoea and Gammarid amphipods (included in our analysis) in the estuary environment. Harpacticoid copepods were the most important and selected for prey by sockeye salmon, followed by decapod zoea, amphipods, and Cirripedia cyprids. We believe that this research is the first record of juvenile sockeye salmon primarily foraging on Harpacticoid copepods in estuaries. Harpacticoid copepods were also an important secondary prey for coho salmon in our estuary and are a known primary prey in other estuaries for coho as well as for chum (*O. keta*), pink (*O. gorbusha*), and ocean-type Chinook (*O. tshawytscha*) salmon (Healey 1979, 1980a, Godin 1981, Simenstad et al. 1982, Macdonald et al. 1987, Northcote et al. 2007). By contrast, the primary prey for both Pacific herring and surf smelt were Calanoid copepods. Whereas herring selected for Calanoid copepods, Cirripedia cypriids, and decapod zoea, surf smelt only selected for amphipods and decapod zoea, with neutral affinity for Calanoid copepods. All four species consumed pteropods as a secondary prey, selected for decapod zoea, and three out of four selected amphipods, suggesting that these prey could be an energetically desirable or easily caught prey across predator taxa (Emlen 1966).

The drivers of the difference in the primary copepod prey between salmonid and small pelagic fish in this study can be examined in the context of ontogenetic niche theory (Werner & Gilliam 1984) and by how prey activity can affect its availability to predators (Griffiths 1973, Ware 1973). Small pelagic fish fed heavily on Calanoid copepods whereas juvenile salmonids relied more on Harpacticoid copepods. Harpacticoid copepods are generally more sedentary than Calanoid species because they are epibenthic and phytal, primarily feeding on epiphytic and macroalgae as well as detritus, bacteria, and fungi (Chandler & Fleeger 1987, Steinarsdóttir et al. 2010), whereas Calanoid copepods primarily feed actively in the water column (Mauchline 1998). In addition, Harpacticoid copepods have slower burst speeds, relative to species of Calanoid copepods who are known for their evasive behaviour (Leising & Yen 1997, Buskey et al. 2002). Juvenile sockeye salmon are facultative planktivores, primarily targeting and consuming one prey item at a time (Lazzaro 1987) and are known to select for slower, larger prey in lakes when it is available (Eggers 1982). This is consistent with our observation that juvenile sockeye salmon selected for the slower Harpacticoid copepods while consuming Calanoid copepods less than their relative availability (with regards to abundance) in the environment. Even in coastal environments where Harpacticoid copepods are often not found in the water column as an alternative prey, juvenile sockeye salmon eat Calanoid copepods at proportions near or less than their availability in the environment (Price et al. 2013); possibly because of the difficulty to capture them. In contrast, Pacific herring consumed Calanoid copepods more than they were available in the environment and surf smelt consumed them equivalently. Pacific herring and surf smelt may be better adapted to handle the quick, abundant, and pelagic Calanoid copepods because they can create strong suction using their round mouths and buccal cavities, and even filter-feed at high prey densities (Gibson & Ezzi 1985, Lazzaro 1987, Brachvogel et al. 2013). The physiological adaptations of small pelagic fish are likely highly selected for because they spend much of their ontogeny at sizes relatively close to their full size whereas juvenile salmon quickly grow to larger sizes and can use different foraging tactics on different types of prey (Werner & Gilliam 1984, Daly et al. 2009, Duffy et al. 2010). This contrast in foraging patterns between juvenile salmon and small pelagic species illuminates key differences in how these fish species may integrate with the prey layer of estuarine seascapes.

Differences within the diets of small pelagic fish may suggest subtle behavioural differences that drive how they integrate with their prey in estuaries too. We found Pacific herring selected Cirripedia cyprids and barely consumed Hyperiid amphipods, whereas surf smelt highly selected for Hyperiid amphipods and consumed Cirripedia cyprids at relatively low quantities. Hyperiid amphipods and Cirripedia cyprids could be distinguishable to herring and smelt as they have considerably different morphologies, colour and refraction, and swimming patterns (Giske et al. 1994). The subtle differences in foraging patterns between these two pelagic fish could be the result of differences in visual capabilities or light attenuation of prey that makes one more discernable than the other (Giske et al. 1994), or the distribution of predators and prey in the water column is such that they overlap/encounter the prey more frequently (Eggers 1977), or small differences in feeding morphology (Labropoulou & Eleftheriou 1997), or some type of other learned preference (Culum & Laland 2003).

Variability of prey abundance in diet samples for each predator was linked to some biophysical factors. We suggest that abiotic environmental factors could affect how predators integrate with their prey across the seascape in addition to inherent physiological constraints of the predators. We found that increasing secchi depth, our index for water clarity, increased the abundance of two important prey in coho diet samples, decapod zoea and terrestrial insects. Less turbid conditions may increase capture success of live decapod zoea (Berg & Northcote 1985, Gregory & Northcote 1993) or increased line of sight to surface waters where expired or non-evasive terrestrial insects concentrate (Tschaplinski 1987). Insect prey in coho diets also increased with colder water temperatures. As river temperatures were cooler than ocean temperatures during our sampling period, cool surface temperatures may correlate with increased riverine prey subsidies that are flushed down from upstream into certain areas (Tschaplinski 1987). Finally, Calanoid copepod abundance decreased in Pacific herring diets as the set total CPUE of all fish increased. Since Calanoid copepods were eaten by herring, smelt, and sockeye in this study, this inverse relationship may suggest per capita Calanoid copepod consumption rates decreases when the combined abundance of these multiple predators is high (Arditi & Ginzburg 1989, Sih et al. 1998). We found that biophysical characteristics did not explain variation in Calanoid copepod abundance in surf smelt diets nor Cirripedia cyprids in sockeye and Pacific herring diets. The lack of statistical or biologically relevant relationships between these predator-prey pairs suggests that they are not affected by biophysical processes or that we did not identify the correct process. We also must acknowledge the possibilities that processes such as stochastic variation and insufficient sample size could affect our observed results. Furthermore, prey may have been consumed elsewhere and thus not directly related to the biophysical factors from the site. However, the effects from biophysical factors we detected, as well as others, influence how different predators integrate with their prey across the estuary seascape in time and space.

We found an additional seasonal pattern of Harpacticoid copepod abundance in juvenile salmon diets that was not linked directly to any biophysical variables. The abundance of Harpacticoid copepods in sockeye diet samples increased with day of year. In theory, zooplankton production and abundance may increase over time in the spring and summer towards a seasonal maxima (Mackas et al. 2012), however, we did not find a relationship with Harpacticoid abundance across time in our study. The lack of an increasing trend of Harpacticoid abundance in the environment could be explained by top-down control of predators in areas with high production of prey (Rudstam et al. 1994, Menge 2000, Yang et al. 2008). Therefore, Harpacticoid copepod production may have been increasing but their abundance did not because of high predation rates by juvenile sockeye salmon (Sibert 1979). Interestingly, prevalence of Harpacticoid copepods increased across time within coho diet samples also, (relationship not statistically significant) and were consumed above average compared to other prey types. Thus, it may be possible for juvenile salmon to have collectively consumed Harpacticoid copepods in the environment at a rate equivalent (or even greater) to their production as a form of top down control (Healey 1979, Sibert 1979, Godin 1981, Fujiwara & Highsmith 1997).

Although we found no biophysical predictors of Harpacticoid copepods abundance in diets, we did find that they were more abundant over eelgrass habitats than other habitats in the seascape. Site specific hotspots of Harpacticoid abundance were not discernable across time. Yet at sites where eelgrass was present, mean abundance in the water column was higher than sites beside rocky shoreline or over open water. Eelgrass is known to support higher densities of Harpacticoid copepods and it is likely a population source (Hosack et al. 2006, Kennedy et al. 2018). Multiple studies have shown that juvenile salmon are capable of consuming large proportions of total Harpacticoid production (Healey 1979, Godin 1981, Fujiwara & Highsmith 1997). Therefore, degradation of eelgrass may affect prey productivity and could affect salmon foraging behaviour and potentially survival. In our system, sockeye and coho salmon abundances were consistently highest in the region of a particularly large eelgrass bed, Flora Bank (Carr-Harris et al. 2015, Sharpe 2017). We speculate that the Flora Bank eelgrass habitat may be an important source of Harpacticoid copepods for these young salmon. Eelgrass habitat has previously been identified as a conservation priority because of its role as a productive food source for multiple juvenile fish species in other estuaries (McDevitt-Irwin et al. 2016). The Flora Bank region in our study estuary was the proposed location of major industrial developments (Moore et al. 2015, CEAA 2016) and previous assessment reports identified information on food web-habitat connections as “high prioritization” data gaps (Pickard et al. 2015). Founding these food-web habitat connections in areas posed for development is an important step in identifying the potential habitat value of estuarine seascapes to species of interest. The next steps are to identify species specific predator-prey responses to possible impacts on habitats involved in supporting the estuary prey mosaic, such as eelgrass bed fragmentation or reductions in shoot density (Lannin & Hovel 2011, Ljungberg et al. 2013, Chacin & Stallings 2016).

The abundances of other zooplankton prey within the estuarine seascape were related to biophysical processes through space and time in multiple ways. Calanoid copepods, Pteropods and decapod larvae showed site level consistencies in their abundance over time which could indicate that certain locations are acting prey hotspots. The best fit predictor of variability in Calanoid copepod's abundance was salinity, a common gradient in estuaries and driver of zooplankton distributions (Telesh & Khlebovich 2010). Increasing salinity was correlated with increases in pteropods, a secondary prey for all of our predators, and oikopleurans, a prey that was marginally consumed by sockeye salmon in this study but is often found in the diets of other juvenile salmon (Manzer 1969, Landigham et al. 1998, Brodeur, Daly, Sturdevant, et al. 2007). Although the salinity gradient and abundance patterns of Calanoid copepods and pteropods were associated with sites, there was still variability within the salinity gradient at sites across time. Oikopleurans did not show any site-level persistence in abundance patterns despite being correlated with salinity. We suggest that this prey group is responding to dynamic environment forcing rather than being statically abundant in a specific location. Learning how prey are influenced by biophysical processes, like salinity (Telesh & Khlebovich 2010, Mendes et al. 2014), or habitat features like eelgrass patches (Lannin & Hovel 2011, Ljungberg et al. 2013), are an integral layer of understanding the prey mosaic of estuaries.

Here we integrated understanding of the spatial and temporal dynamics of zooplankton and their consumption by four species of fishes, but it is important to consider potential limitations of our study. We discovered that juvenile coho salmon primarily consumed terrestrial insects and fish, however, because these prey items are not adequately sampled by vertical plankton tows with the mesh size we used (Brodeur et al. 2011), we could not assess the abundance of these important prey sources across space or time. Our inference on Harpacticoid copepods abundance is also based on what we sampled in the water column, yet they are associated with meiobenthic and epiphytic habitat (Alheit & Scheibel 1982, Steinarsdóttir et al. 2010). Juvenile salmon are more likely feeding in the water column (Clark & Levy 1988) and less so directly from substrate or blades of eelgrass. Thus, we believe that our zooplankton sampling likely represented relative densities that these fish might be encountering but lacks the ability to properly identify epibenthic zooplankton population sources, like that of Harpacticoid copepods. With the example of Harpacticoid copepod abundance in the environment, it is also difficult to tease apart the effects of bottom-up biophysical processes or phenology of zooplankton and top-down effects from predation. Furthermore, diet samples only represent a snapshot of what an individual fish was eating and only from locations where fish were present at the time of sampling. Isotope and fatty acid analyses could provide additional longer-term perspectives on diet trends (Daly et al. 2010, Selleslagh et al. 2015) but we believe that our study captures variability in diets and provides a picture of primary and secondary prey types consumed in the Skeena River estuary. Last, when calculating Chesson's alpha, we assumed that diet snapshots were representative of the site where samples were taken from, but the duration required to travel between sites by fish is less than that of egestion rates (Brett & Glass 1973, Brodeur & Pearcy 1987). However, we compared Chesson's alpha results from spatially averaged zooplankton abundances and found only minor differences. Thus, our study has important limitations, but also contributes to the relatively understudied fields of the prey basis of nursery function in estuaries (Sheaves et al. 2015).

Collectively, our study highlights how four culturally, economically, and ecologically important fish species integrate with prey differently across the dynamic seascape of a major estuary. For example, ontogenetically driven physiological constraints on foraging ability of juvenile sockeye salmon are not the same as those on adult small pelagic fish (Werner & Gilliam 1984), thus the realized availability of prey like Calanoid copepods to sockeye salmon may be low across the seascape despite their ubiquity and abundance (Griffiths 1973, 1975). Small pelagic fishes' strong schooling behaviour (Eggers 1976, Pitcher & Parrish 1993) may bias them towards dense prey fields that are visually more apparent and can be seen by multiple individuals that then influence the direction of the school (Romey 1996, Viscido et al. 2004), which may be an additional reason that the small pelagic fish in our study primarily consumed Calanoid copepods. We also found that few biophysical factors covaried with herring and smelt diets other than total CPUE, suggesting that their diets may be influenced most by the number of fish present and less so by abiotic conditions. In contrast, multiple abiotic variables covaried with the abundance of certain prey in juvenile coho salmon diets, suggesting that there might be stronger impacts on their foraging success with abiotic changes. The productivity of the primary prey of sockeye salmon, Harpacticoid copepods, may be connected to eelgrass habitat, whose uneven distribution in the estuary may affect the distribution of sockeye salmon. In addition to integrating with prey across the biophysical dynamics of the seascape, populations of juvenile salmon enter the Skeena River estuary at a diversity of times and may interact with different peaks of zooplankton abundance in different seascape conditions (Carr-Harris et al. 2018). Thus, different populations' diets may be affected differently depending on when they enter the estuary.

The spatial and temporal asynchronies in different prey abundances and the ubiquity and abundance of others within the Skeena River estuary may provide extended and buffered foraging opportunities for co-occuring mobile consumers. Juvenile salmon diets may benefit from a diverse prey portfolio that buffers them from fluctuations in a single prey item or allows them to capitalize on easily captured prey (Armstrong et al. 2016). Harpacticoid copepods are one example of a non-evasive prey and could occur in adequate abundances in patches, such as over eelgrass habitats (Kennedy et al. 2018), to support salmon. Pacific herring and surf smelt appear more adapted to forage on the most abundant prey group (Hill et al. 2015), the highly evasive but ubiquitous Calanoid copepods in this system. However, Calanoid copepod abundance is correlated with salinity and its distribution may change if river flow changes the salinity gradient with climate change or anthropogenic development (Sherwood et al. 1990, Nohara et al. 2006). Our work adds to the growing appreciation that estuary seascapes have dynamic and complex prey mosaics that underpin their function as nursery and foraging habitats (Sheaves et al. 2015, Nagelkerken et al. 2015) and may be affected through multiple biophysical processes.

2.6. Acknowledgements

This research is part of a collaboration between Lax Kw'alaams First Nation, Skeena Fisheries Commission, and Simon Fraser University. Any opinions, findings, conclusions, or recommendations expressed in this paper are those of the authors and do not necessarily reflect the views of the partner organizations. Charmaine Carr-Harris, Ciara Sharpe, and Jonathan Moore are all co-authors of this work for the time and effort they devoted into project design, data collection, edits, and support for this chapter. We sincerely thank Bill Shepert, Jen Gordon, Harvey James Russell, Wade Helin, Jim Henry Jr., Devin Helin, Katelyn Cooper, and Brandon Ryan from Lax Kw’alaams Fisheries Department along with David Doolan from Metlakatla Fisheries Program for providing field and logistical support. We are grateful to many members of the Earth to Oceans Research Group and Salmon Watersheds Lab for advice and inspiration. This research was supported by Liber Ero Foundation, Natural Sciences and Engineering Research Council, and the Coast Opportunities Fund.

Chapter 3.

The estuarine growth and residency of juvenile Pacific salmon in North America: a compilation of empirical data

3.1. Abstract

The value of estuaries as stopover or nursery habitat to juvenile anadromous salmon is likely variable across estuaries and across the diversity of life-history strategies employed within and across species. Here, we compiled published empirical data on two key metrics of juvenile salmon estuary use – growth rate and residency duration. This study aimed to quantify the range and variability of these aspects for Chinook, coho, sockeye, pink, and chum salmon across and within their populations; asking, i) What is the spatial and biological coverage of this information, ii) Do different methodologies used to quantify estuary growth and residency generate different results, and iii) How do estuary growth and residency vary across life histories? We found that species that are often described as having little estuary dependency – pink, chum, and yearling sockeye – had the least amount of coverage and research was distributed towards the north. Most articles were distributed in the southern range over Chinook and coho life histories. Studies used a variety of methodologies, ranging from cohort-based approaches to individual marking. Acoustic tagging studies consistently produced the shortest and least variable residency estimates but, in general, variation within studies was higher than variation between methods. Growth estimates were done using many differing methods and metrics, such that trends were difficult to identify. A unification of methodology could strengthen future research in growth rates. Importantly, there was variation in residency durations across salmon life histories and species; for example, natural-origin 0+ Chinook and 0+ coho often reared in estuaries for one to several months whereas their older counterparts averaged around one month. In comparison, there was a trend for hatchery-origin Chinook and coho to spend less than a week in estuaries, except for hatchery 0+ Chinook. Pink and chum resided in estuaries for 1-2 weeks on average. In addition, there was much variation in estimates of residency across studies, which suggests that different estuaries likely play different roles for outmigrating juvenile salmon. Collectively, compilation of this information highlights key patterns emerging in salmon estuary ecology, knowledge gaps, and lays the foundation for future analysis to quantify the importance of estuaries for specific salmon stocks in the context of conservation goals and life-history theory.

Keywords: estuary, *Oncorhynchus sp*., growth, residency

3.2. Introduction

Estuaries are thought to be important nursery and stopover habitat for juvenile salmon (Healey 1982a, Simenstad et al. 1982, Groot & Margolis 1991, Thorpe 1994, Quinn 2005, Levings 2016, Beamish 2018). However, how important estuaries are may vary greatly across species and life histories of salmon, and across estuaries. Some species of salmon emigrate immediately out of freshwater systems after emerging from the gravel, whereas others have flexible life histories and may emigrate after zero, one, or two years of rearing in fresh water (Thorpe 1989, Groot & Margolis 1991). Salmon life-history diversity such as this can be fostered by abiotic characteristics and variation of the upriver watershed, such as lakes, glacier or rain runoff, gradient, and temperature (Thorpe 1989, Taylor 1990, Quinn 2005, Crozier et al. 2008, Walsworth et al. 2015). Estuaries also exhibit great diversity in their form and dynamics; estuaries are created through various processes (e.g. drowned river or glacial fjord) and create diverse features as different types of rivers reach into the variable coastline (Perillo 1995, Elliott & McLusky 2002). Accordingly, the value of estuaries to juvenile salmon may depend on estuary size, the amounts of different habitats and their connectivity, productivity (Sheaves et al. 2015), as well as the system-specific biology of the salmon. Understanding the potential different roles of different estuaries to salmon could facilitate conservation planning or guide restoration activities, which is increasingly important because estuaries are being altered by anthropogenic factors at a rapid pace (McClelland & Valiela 1998, Lotze et al. 2006, Thorne et al. 2018).

Estuaries may support juvenile salmon through three main processes: productive foraging opportunities, refuge from predation, and physiological transition (Thorpe 1994). Estuaries are highly productive habitats and produce seasonal blooms of phytoplankton followed by increased abundances of zooplankton and larval fish (Lucas, Koseff, Cloern, et al. 1999, Griffin & Rippingale 2001, Tommasi et al. 2014), which form the basis of juvenile salmon estuarine diets (Healey 1979, Simenstad et al. 1982, Bollens et al. 2010, Chapter 2 *this thesis*). Prey may be more abundant in in estuaries than river habitats (Tschaplinski 1987). Thus, estuaries can provide productive foraging opportunities for juvenile salmon and thus high growth potential (Healey 1982a, Thorpe 1994), which can result in increased future survival (Werner & Gilliam 1984). Additionally, estuaries may provide refuge from predators. It is proposed that predation rates are generally low in estuaries because of high turbidity or low predator abundance (Quinn 2005). Although few examples of direct observation of estuary predation rates exists, they show somewhat contrasting results, both relatively low predation (Armstrong & Morrow 1980, McCabe et al. 1983, Bottom & Jones 1990) and high predation (Johnston 1982, Evans et al. 2016). Finally, to physiologically transition between salt and fresh water, juvenile salmon need to adjust their osmoregulatory function and swim bladders to maintain proper buoyancy (Taylor 1921). For example, Healey (1991) found that some populations of subyearling (0+) Chinook could survive an immediate transport into 30 ppm salinity (ocean level), whereas others had high mortality rates, suggesting that there is variability in osmoregulatory stress responses even within a species. Estuaries provide a salinity gradient and may ease juvenile salmon's physiological transition. Thorpe (1994) found strong to indeterminate support for each of these aspects depending on the life history of any given salmon species across multiple systems and used growth and residency in estuaries as key metrics to compare the degree to which estuaries support these three processes.

Quantifying growth rates of juvenile salmon in estuaries is a direct way to elucidate how much estuaries support growth. Growth rates directly relate to both the quality and quantity of food available (Griffiths 1975) in estuaries and their growing conditions (Nicieza & Metcalfe 1997), which may be affected by estuary temperature and the density of competitors (Brett et al. 1969, David, Simenstad, et al. 2016). Further, growth rates in fish can be non-linearly related to size and age, thus juvenile salmon in different life-history stages or of different sizes may have intrinsically different absolute growth rates (Von Bertalanffy 1938, Lugert et al. 2016). If the high seasonal estuary productivity (Cloern et al. 2014) matches the timing of juvenile residency, it may provide juvenile fish opportunities for increased growth rates relative to previous habitats and increase their survival in subsequent habitats (Werner & Gilliam 1984, Cushing 1990) because generally larger fish have lower mortality (Sogard 1997). Most studies have found growth rate or size-selected mortality of juvenile salmon in the early ocean period

(Healey 1982b, Holtby et al. 1990, Beamish et al. 2004, Moss et al. 2005, Duffy & Beauchamp 2011, Gamble et al. 2018). Multiple studies have also found larger juvenile salmon of the same age in estuaries compared to rivers (Murphy et al. 1997, Hoem Neher et al. 2013, Wallace et al. 2015). However, whether these are large fish that migrated early, or fish that grew faster in the estuary is not always clear. Therefore, studies that directly measure growth rates of juvenile salmon in estuaries are valuable for enhancing understanding of how growth can vary in different estuaries for different salmon populations.

Estuary residency, the amount of time that juvenile salmon spend in the estuary prior to migrating to the ocean, is another key trait that can provide insight into the estuary ecology of salmon (Levings 2016). Residency may be selected to optimize a balance between growth potential and refuge from predation relative to other habitats across a salmon's life-cycle (Walters & Juanes 1993, Willette 2001). Therefore, residency in transitory habitat such as estuaries should be determined not only by current conditions, but also growth and survival in previous (freshwater) and subsequent (marine) habitats (Willette 2001). For instance, the duration a juvenile fish grows in an estuary influences its size before it enters the next phase of its life, and thus affects its subsequent size-selective survival (Sogard 1997). Additionally, if predation is lower in the estuary than adjacent habitats, selection during the ocean phase may favor juveniles that reside and grow for longer in estuaries even if growth potential is greater in ocean waters (Walters & Juanes 1993). Predation pressure may also interact with a juvenile salmon's osmoregulatory ability and swim bladder control during its physiological transition (Taylor 1921, Weitkamp 2008). Weitkamp (2008) found hatchery coho juveniles had more lipids than wild fish and may have more difficulty transitioning to increased salinities along with increased vulnerability to surface predators. The requirement of fish to modify their physiology when migrating between salinities (Taylor 1921) may influence the minimum amount of time juvenile salmon reside in estuaries, while trade-offs between growth and predation may influence the upper bound of residency.

Previous narrative reviews on the extent estuaries are used by salmon species have suggested that different species have varying patterns of growth and residency. Thus, different species and life histories of salmon have apparently evolved different strategies in response to the tradeoffs in freshwater, estuary, and marine selective pressures. Previously, Thorpe (1994) hypothesized that species with shorter freshwater residency, such as pink and chum salmon, had fewer freshwater adaptations and were more “prepared” for salt water, therefore less reliant on estuaries for this transition. Thorpe (1994) also surmised that life histories of species that spend more than a year in freshwater, such as yearling coho, Chinook, and sockeye, begin smoltification prior migration (McCormick & Saunders 1987, Bassett et al. 2018) and may also be prepared for salt water and less reliant on estuaries. However, the evolutionary mechanisms connecting freshwater and estuary residency durations is still a topic of debate (McDowall 2002). Despite an incomplete understanding of how these trends evolved, literature syntheses generally state that ocean-type or subyearling Chinook and coho have longer residencies while pink, chum, sockeye, and stream-type or yearling Chinook and coho have shorter residencies (Healey 1980b, 1982a, Simenstad et al. 1982, Quinn 2005, Weitkamp et al. 2014, Levings 2016). Few syntheses have generalized on growth other than that larger (and older) life histories have higher incremental growth rates (Levings 2016). There is an opportunity to build on these previous reviews with a more quantitative compilation of residency and growth data across species, life histories, and estuaries.

Here, we summarize empirical data compiled on two aspects of anadromous Pacific salmon estuary use across their North American range that can be used as indexes of importance of estuaries for juvenile salmon: growth rate and residency duration. The aim of this study is to quantify the range and variability of these two aspects for Chinook, coho, sockeye, pink, and chum salmon across and within their populations. We ask i) what is the spatial and biological (i.e. species and life histories) coverage of this information across species? Additionally, given the diversity of empirical methods, we also ask ii) what methods are used to quantify estuary residence and growth and do different methods yield different estimates? Last, iii) how does the mean and variability between species and life histories differ? We predict that life histories that are described in the literature as more estuary dependent will have more articles (a rough unit of research effort), that different methodologies may lead to different estimates of estuary residency and growth, that older life histories will have higher growth rates, and that life histories that are more “prepared” for salt water (Thorpe 1994) will have shorter residency estimates, whereas species that have generally more variable freshwater life histories will have more variation in their estuary residencies.

3.3. Methods

We conducted a rigorous literature review to create an updatable database of juvenile salmon estuary growth and residency literature and results, subsequently referred to as *the database*. We started by conducting a literature search in *Web of Science Core Collection* through Simon Fraser Universities library proxy on April 24th, 2018, using the search parameters (salmon, Oncorhynchus) AND (estuary*) AND (residen* OR growth OR survival OR mortality), which returned 681 results. We subsequently sorted the results, first by if they discussed Pacific salmonids, and then by a more thorough read to extract any information on growth and residency into the database (Table B1). We only included articles whose study estuary was in North America because there were few articles that were found by our search from elsewhere (n<5). We included papers that estimated growth from marked cohorts or individuals and from changes in unmarked population size over time, provided there was some evidence that most growth was done in the estuary and not from later migration of larger individuals. We did not include estimates of residency based purely on abundance or presence of fish in the estuary as they do not represent individual residency but rather population residency (Levings 2016), which is the accumulation of individual residencies over time. We also confined our definition of estuary (Perillo 1995) to the tidally-influenced portion of the river and bay that still had saltwater influence. We did not include tidally-influenced freshwater sections because they do not provide the same environmental transition and change in prey fields associated with brackish water (Simenstad & Cordell 2000). We also did not include studies that focused on what is defined as a river plume or estuary plume (e.g. John et al. 1992, Brodeur et al. 2015) because most of these sections of "estuary" lack the habitat features of other estuaries. Finally, we made note of prior literature summaries and citations and crossed checked them with entries in the database, which produced additional peer reviewed and non-peer reviewed references (n = 10) that were missed by the initial search.

We grouped species' life histories by how old they were when they first entered the estuary. Therefore, if an article referred to the life-history stage it was analyzing that entered the estuary as fry, subyearling, or occasionally parr that was specified as less than a year old, we categorized these fish as "0+". If an article's cohort was referred to as a yearling, or smolt or parr that was migrating after spending one year in fresh water, we categorized these fish as “1+”. Only one article analyzed fish that resided in fresh water for the first two years of their life; we refer to these fish as “2+”. Subsequently, when we compare across life histories, it is implied that we are comparing across all combinations of species’ life-histories unless specified that it is within a species or stage; i.e. not just between 0+ and 1+ salmon but 0+ coho, 0+ Chinook, 1+ coho, and 1+ Chinook, etc.

We used mean and median growth rate and individual residency estimates because they were the most comparable metric reported across articles. In the database, we recorded information on the type of metric reported, mean, median, percentile, range, as well as the type of error reported if there was any. Some articles reported multiple means or medians because of biological, temporal, or spatial segregations they made in their data; we refer to individual means or medians as average estimates. Therefore, there are more estimates than there are articles. Articles mostly reported results as a mean or median--86% of growth rate estimates and 81% of residency duration estimates. If an article only reported a range (maximum range, mean range, interquartile range, other qualitative ranges), the mean between the two values was taken to make estimates more comparable with other article’s average estimates. All growth rate ranges were transformed in this way. Only three percent (6 estimates) of residency estimates were unable to be transformed because they were reported as a single percentile or maximum only and thus were left as such in the analysis because they also did not represent outliers. We did not generally include study specific variability or error terms in the analysis, except in specific within-article comparisons, because the sample size and error were not always reported across studies, and error was reported in many ways that were not convertible such as confidence intervals or standard error compared to r^2 values. Thus, we only report descriptive statistics, such as the mean, median, and maximum range of average estimates from articles.

We described the distribution of average estimates of growth rate and residency duration across life histories and study types but did not perform formal statistical analyses. We did not perform formal statistical analyses for several reasons. First, a formal meta-analysis that considered study variation was not possible because within-study variation and sample size was haphazardly and inconsistently reported. Second, statistics were difficult to justify because the data was reported in various units, on differing spatial scales, and between natural and hatchery origin populations. Growth rates were reported across seven different units, including mm/day, g/day, log10(g)/day, ln(g)/day, %mm/day, %g/day, and g/g/day. We did not transform between these units because they either require a life-history relationship between length and weight that is species and system specific or because the calculation approach assumed a linear (e.g. mm/day, g/day) versus exponential (e.g. log10(g)/day, %mm/day) relationship between size and time. All residency duration estimates were transformed into days. In addition, both growth rates and residency estimates were reported on various spatial scales. Estimates were either inferred to be for the whole estuary scale or for one of its constituent parts such as a single salt marsh or channel within the estuary that was more easily sampled. Although there is additional spatial variation within partial estuary estimates, we have generalized estimates as either being from the “whole estuary” or an “estuary part” to reduce the further splitting of data. Furthermore, we also note that there may be a difference in the behavior of hatchery- and natural-origin fish because literature that has directly compared them has found differences in estuary use (Myers & Horton 1982, Levings et al. 1986, Weitkamp 2008, Reese et al. 2009). Therefore, we reserve our analysis to descriptive statistics because the sample sizes per life history were too small to account for possible effects of spatial coverage and fish origin as well as other variables that may explain variation in growth rates and residency durations.

3.4. Results

3.4.1. Biological and spatial coverage of empirical estimates of growth and residency

We compiled 173 and 177 empirical estimates of growth rate or residency duration, respectively, from 40 articles, which are now stored in the database (Table B1). Twenty articles reported estimates of growth rates and 31 articles reported residency durations, with 14 of the 40 reporting an estimate for both aspects. Articles were distributed across 9 different life histories: 0+ and 1+ Chinook; 0+, 1+, and 2+ coho; 0+ chum; 0+ pink; and 0+ and 1+ sockeye (Fig 3.1). Research was also distributed across estuaries that ranged in latitude from Alaska (59^{o}47’) to California (37^{o}51’; Fig 3.1 A). Some articles contained estimates on multiple life histories or estuaries, but few estuaries had more than one article (max 3 articles in one estuary; Fig 3.1 C, E). Overall, no life history had coverage of either growth rates or residency durations across their entire natural home range along western North America.

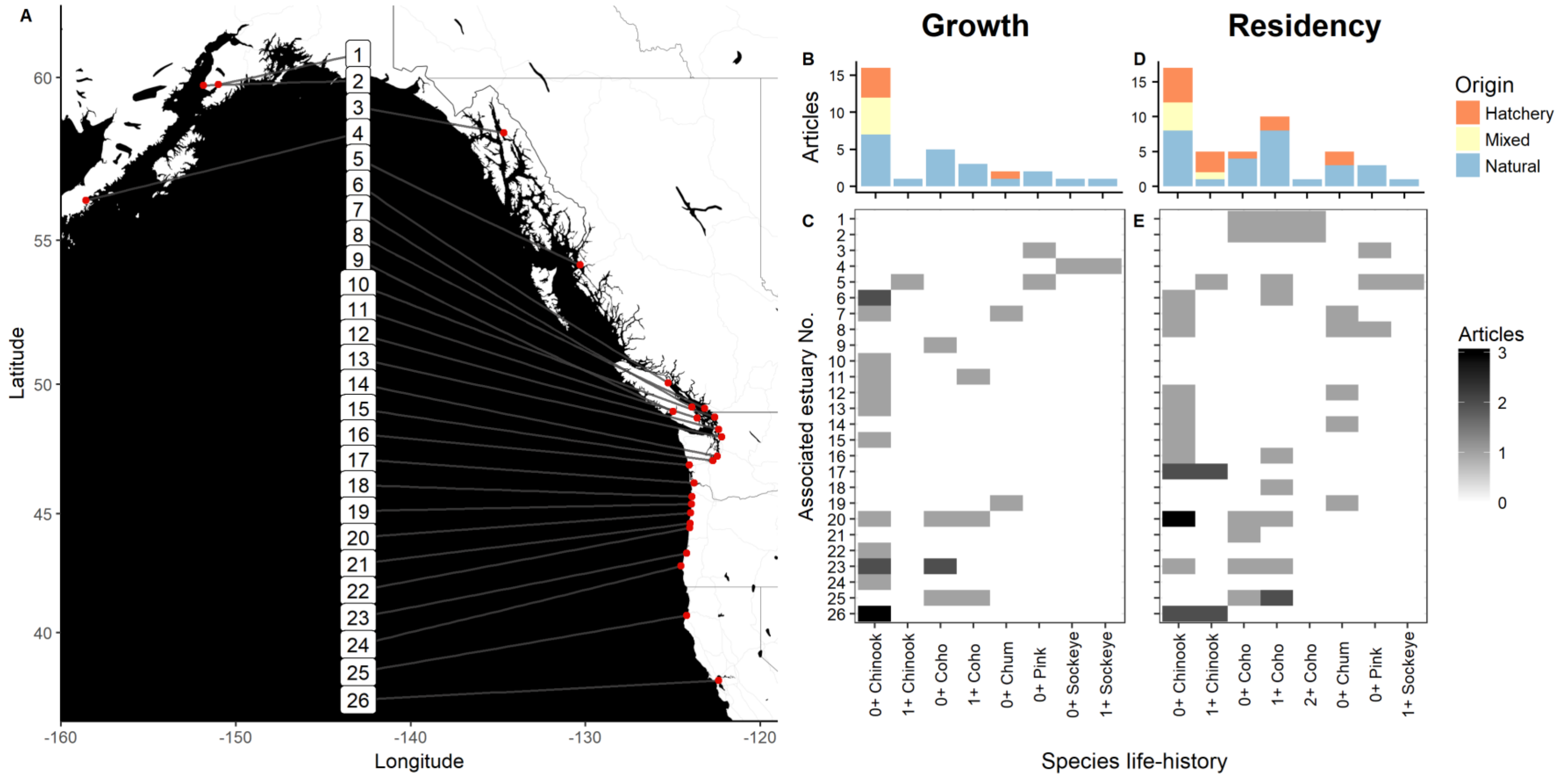


Figure 3.1 **Biological and spatial coverage of articles that provide empirical estimates of anadromous North American Pacific juvenile salmon growth rates or residency across estuaries in their North American range.**

A) The geographical location of study's estuaries. B) The total number of articles that reported growth rates for each species' life-history, separated by origin. C) The number of articles on growth for each species' life-history in each estuary that had an associated study. D) The total number of articles that reported residency duration for each species' life-history, separated by origin. E) The number of articles on residency for each species' life-history in each estuary that had an associated study. Estuary names associated with each number can be found in Table B2.

Articles had uneven coverage of both growth rates and residency across life histories (Fig 3.1 B, D). There were by far the most studies on growth rates of 0+ Chinook, with 16 articles, whereas 0+ coho had the next best coverage with 5. Other life histories had even fewer articles: 1+ coho had 3; 0+ pink and chum had 2 each; and 0+ sockeye, 1+ sockeye, and 1+ Chinook each had one. 0+ Chinook also had the most articles on residency, 16, followed by 1+ coho with 10. There was generally more even coverage of residency as 1+ Chinook, 0+ coho, and 0+ chum each had 5 articles. 0+ pink, 2+ coho, and 1+ sockeye had fewer than 5 articles, with 3, 1, and 1, article(s), respectively. Only two life histories had an estimate in one aspect and not the other; 0+ sockeye with only a growth estimate and 2+ coho with only a residency estimate. Generally, 0+ Chinook had the highest coverage in both aspects, followed by coho life histories.

Within life histories, articles were also distributed between natural and hatchery origin fish (Fig 3.1 B, D). Natural-origin cohorts comprised 60% and 51.5% of growth rate and residency duration articles, respectively, with 20% and 36.4% of articles from hatchery cohorts and the rest (20%, 12.1%) from mixed or unknown origins. 0+ Chinook were the focus of most articles that researched hatchery- or mixed-origin fish in both aspects. Chum were the only other species to have growth rate research on hatchery-origin fish, whereas all other life-histories' growth rate research was on natural-origin fish. There were more life histories that had both natural-origin and hatchery- or mixed-origin fish in residency research than growth research, which included 0+ and 1+ Chinook and coho, as well as 0+ chum.

Spatial coverage within life histories were also typically skewed towards the south or north, depending on the life history (Fig 3.1). Half of the life histories did not have estimates for neither growth nor residency north of the Skeena River estuary (54^{o}11') and 70% of all articles' research occurred in the southern half (<48^{o}) of the total range. Most life histories that had the fewest associated articles were primarily distributed in the northern estuaries and life histories that had more articles were primarily distributed in the southern estuaries.

The spatial coverage within each life history was also split between studies that estimated growth and residency at varying estuary scales. Studies differed by whether they studied the whole estuary or a constituent part, e.g. a single marsh or channel habitat within a larger estuary. 86% and 65% of articles estimated growth rates and residency over the whole estuary, respectively, whereas the remainder sampled an estuary part. Therefore, in the subsequent section when we compare across methodologies within a life history, we distinguish between estuary spatial extent (whole estuary or estuary part) when comparing methodological categories.

3.4.2. Methodology used for estimating estuary growth and residency

A variety of field methodologies were used to estimate growth rates and residency durations across studies (Table 3.1). The major difference in methods used to estimate growth rates and residency was the separation between those that averaged across individuals or those that examined cohorts. Individuals were identified through coded wires and passive integrated transponder (PIT) or acoustic tags through the estuary. Otolith growth increments and microchemistry or tissue isotopes from an individual were also used to infer growth or residency on a per individual basis. Cohort estimates of growth rate were done with both unmarked and batch-marked groups and comprised 70% of approaches that articles employed. Fin clips, coloured or ultraviolet paint, and otolith stress marks, were all used as different batch marking techniques. In addition, one study that employed a method for estimating residency with individual's tissue isotopes (Moore et al. 2016) used a regression of individual fish lengths over their estimated residence time, which we grouped under the cohort section ("Tissue Isotopes", Table 3.1) because it is more analogous to cohort methods of estimating growth. Typically, when residency was estimated using cohorts, which was in 45% of articles, it was done with batch-marked groups. However, the analytical methodology used to estimate residency varied among papers (Table 3.1): the mean number of days since release per marked individual (Levy 1990, Shreffler et al. 1990, Miller & Sadro 2003); a weighted mean of recaptured individuals since release, weighted by the number of fish initially marked per cohort (Fisher & Pearcy 1990, Mortensen et al. 2000); or a half-life of a rate of decay of abundances of marked fish (Congleton et al. 1981, Myers & Horton 1982, Pearcy et al. 1989). Two articles (Healey 1980a, Levings et al. 1986) also inferred residency using an estimated growth rate to determine the duration it would require to produce individuals of the observed size difference from earlier to later in the season. These different methodologies may be capturing different perspective on these metrics of estuary usage and may rely on different assumptions.

Table 3.1 A count of different approaches used to estimate growth and residency across and within papers. Estimates are separated generally by if they are derived from either averaging across individuals or a cohort. Subsequently, the type of calculation was sometimes employed over different tagging techniques. “Batch Marked” includes multiple techniques of marking groups of fish in either time or space of initial capture but with no way to distinguish individuals.

Aspect	Individual or Cohort	Calculation specifics	Tagging specifics	Number of Estimates
Growth	Individual	Change in fork length since time of release and last capture	PIT Tagged	2
			Coded Wire	1
		Average change in fork length between all capture intervals	PIT Tagged	1
		Change in fork length from 14 days prior using proportional back calculation method of year specific fork length to otolith regressions	Otolith	2
		Change in fork length from 50 days prior using proportional back calculation method of year specific fork length to otolith regressions	Otolith	1
		Change in fork length from otolith determined estuary entry using proportional back calculation method of year specific fork length to otolith regressions	Otolith	1
		Semi-experimental. Released into an enclosed section and recaptured. Slope of otolith growth increments.	Otolith	1
	Cohort	Regression of average length or weight of catch over time	Unmarked	7
			Batch Marked	1
		Regression between length and residency estimate	Tissue Isotopes	1
		Change in average fork length from time of release	Batch Marked	4
		Difference between two averages divided by the time interval	Unmarked	2
Residency	Individual	Time elapsed from first detection to last	Acoustic tagged	6
			Acoustic tagged (transit time)	3
			PIT Tagged	3
			Coded Wire	1

Aspect	Individual or Cohort	Calculation specifics	Tagging specifics	Number of Estimates
		Number of daily increments after Sr:Ca increase	Otolith	6
		Difference in isotopic signatures in tissues with different turnover rates	Tissue Isotopes	1
	Cohort	Time elapsed from first detection to last	Batch Marked	5
		Semi-experimental. Released directly into estuary. Time elapsed from first detection to last	Batch Marked	1
		Weighted average time elapsed from release to recapture	Batch Marked	3
		Half-life disappearance/emigration rate decay curve	Batch Marked	6
		Based on growth rates and estimated time interval to produce observed size	Batch Marked, Unmarked	3

The natural variation in average growth rate estimates within studies was greater than variation across different field methodologies. This indicates that different methods do not introduce large and systematic error or biases. There were only enough articles and estimates to compare average growth rates in mm/day between methodological approaches within the database for 0+ Chinook (Table B3). The average 0+ Chinook growth rates from individual otoliths for both mixed- and natural-origin fish were marginally lower than their unmarked and batch-marked cohort counterparts (i.e. comparing between fish from the same origin) for whole estuary estimates. There was a single natural-origin batch-marked estimate that appeared to be an outlier (Fig B1). The second highest estimate, another possible outlier, was in 0+ Chinook growth rates from a natural-origin, whole estuary, unmarked cohort method study. If we removed this outlier, it made the median of natural-origin, whole estuary estimates close to the otolith method of equivalent category (0.49 and 0.40 mm/day, respectively). The removal of a single study's estimate shows that there may be more natural variation between estuaries than biases introduced by methodology in estimating growth rates. Additionally, the variability in estimates within studies with the highest numbers of estimates from a single estuary nearly encompassed the entire range of all varying methodologically derived estimates from other studies, except the outliers, which again may be because natural variation is greater than methodological bias.

There was also evidence that the variation in average residency durations within studies was greater than possible methodological bias in general, but one method did produce consistently different estimates of residency than others. Articles that used acoustic tagging to estimate residency duration consistently produced the lowest estimates and often the least amount of variability across methodologies, spatial scales, and life histories, even when there was a high number of estimates (Fig B3-B5). The comparison of methodologies for residency was possible within 0+ and 1+ life histories for both coho and Chinook (Table B4). Like the growth rate results, the variation in residency estimates from article's that reported the highest numbers of estimates in any given approach was greater than the variation between methods across papers (Fig B2-B4). Typically, the less costly individual-based mark-recapture methods like PIT and coded wire tagging allowed for such numerous averages within a single study. Overall, otolith, PIT tagging, and batch marking methodologies did not show any bias in estimates. There also did not appear to be generally lower estimates produced by studies focused on a single estuary part compared to the whole estuary within an origin category. Thus, we conclude that there is likely more natural variation among estuaries and article's estimates for both growth and residency than introduced methodological bias except for studies that use acoustic tags.

3.4.3. Variability in average growth rates and residency durations

There were differences in estimated average incremental growth rates across several salmon life histories. We only compared mean growth rates between species and life histories using mm/day because it had the highest coverage (Fig 3.2; Table B3). Of the life histories with multiple estimates, growth rates of 0+ Chinook and 1+ coho were the highest and most variable, whereas 0+ coho had generally much lower estimates. It is important to note that since these growth rates are not relative growth rates it is important to consider size when comparing them. Not all studies included size information, but we did not observe a trend in growth rate with size for those that did. There was a slightly increasing trend in median growth rate estimates from hatchery-origin to mixed-origin to natural-origin groups within 0+ Chinook. Only one estimate was available for 1+ Chinook, 0+ pink, and 0+ sockeye, and 1+ sockeye, which made it difficult to draw conclusions between these life histories and others.

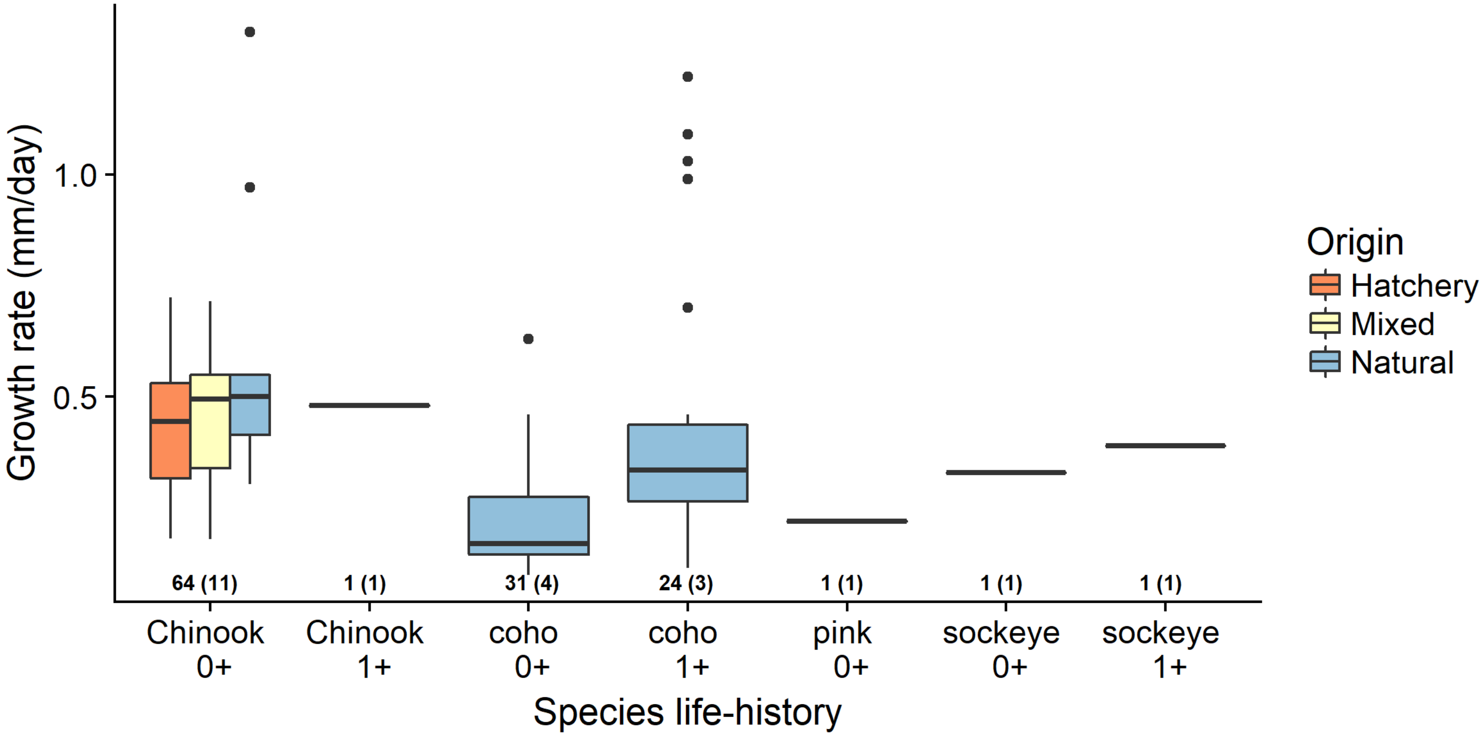


Figure 3.2 . Distribution of average (means & medians) growth rate estimates reported in mm/day for multiple juvenile salmon in different life history categories separated by origin (hatchery, mixed, or natural).
The number outside of the brackets is the number of estimates in each species life-history category and the number inside the brackets is the number of articles they are from.

Average estuary residency duration estimates also varied across origin, life histories, and species (Fig 3.3). Overall, for wild origin salmon species, we found that their estuary residency approximated the following rank, from longest to shortest residency: 0+ coho, 0+ Chinook, 1+ Chinook, 1+ coho, 0+ pink, 2+ coho, 0+ chum, and 1+ sockeye salmon.

Hatchery-origin fish resided for shorter durations in some life histories. Hatchery-origin 0+ and 1+ coho had short residency durations that were more than 10 and 3.5 times less than natural-origin estimates, respectively. Hatchery-origin 1+ Chinook resided for 26 times less on average than their natural-origin counterparts, however, natural-origin 1+ Chinook had only one residency estimate and from a much more northern estuary. The means and variability in natural-origin 0+ Chinook and 0+ chum residency estimates highly overlapped their hatchery-origin estimates. Thus, there is mixed evidence for a trend in reduced hatchery-origin fish residency.

Younger life histories tended to reside for shorter durations than older ones in some species. This trend is most apparent in natural-origin coho, who had representation from 0+, 1+, and 2+ life histories. We observed the same trend in hatchery- and mixed-origin 0+ and 1+ Chinook. The single natural-origin 1+ Chinook estimate did not follow the trend, but again, it is from a much more northern estuary than the 0+ Chinook estimates. Residency in hatchery-origin coho also did not follow the trend. Thus, there is mixed evidence across species and origin for the trend that younger life histories tended to reside for shorter durations.

Like growth rate estimates, there was a lot of variation in the average residency estimates, particularly in natural-origin fish. The largest ranges (difference) between the lowest and highest average residency estimates were 277, 144, 65, 65, 43, and 29, days for natural-origin 0+ coho, natural-origin 1+ coho, natural-origin 0+ Chinook, hatchery-origin 0+ Chinook, mixed-origin 0+ Chinook, and natural-origin 0+ pink, respectively. These are differences of up to 1, 2, 5, and 9 months, which can have major implications for how these life histories are behaving across or within estuaries. It also should be noted that these ranges are the ranges of median or mean estimates across articles, there was often even higher variation within studies around these average estimates. Estimates also came from multiple methodologies, estuaries, and years.

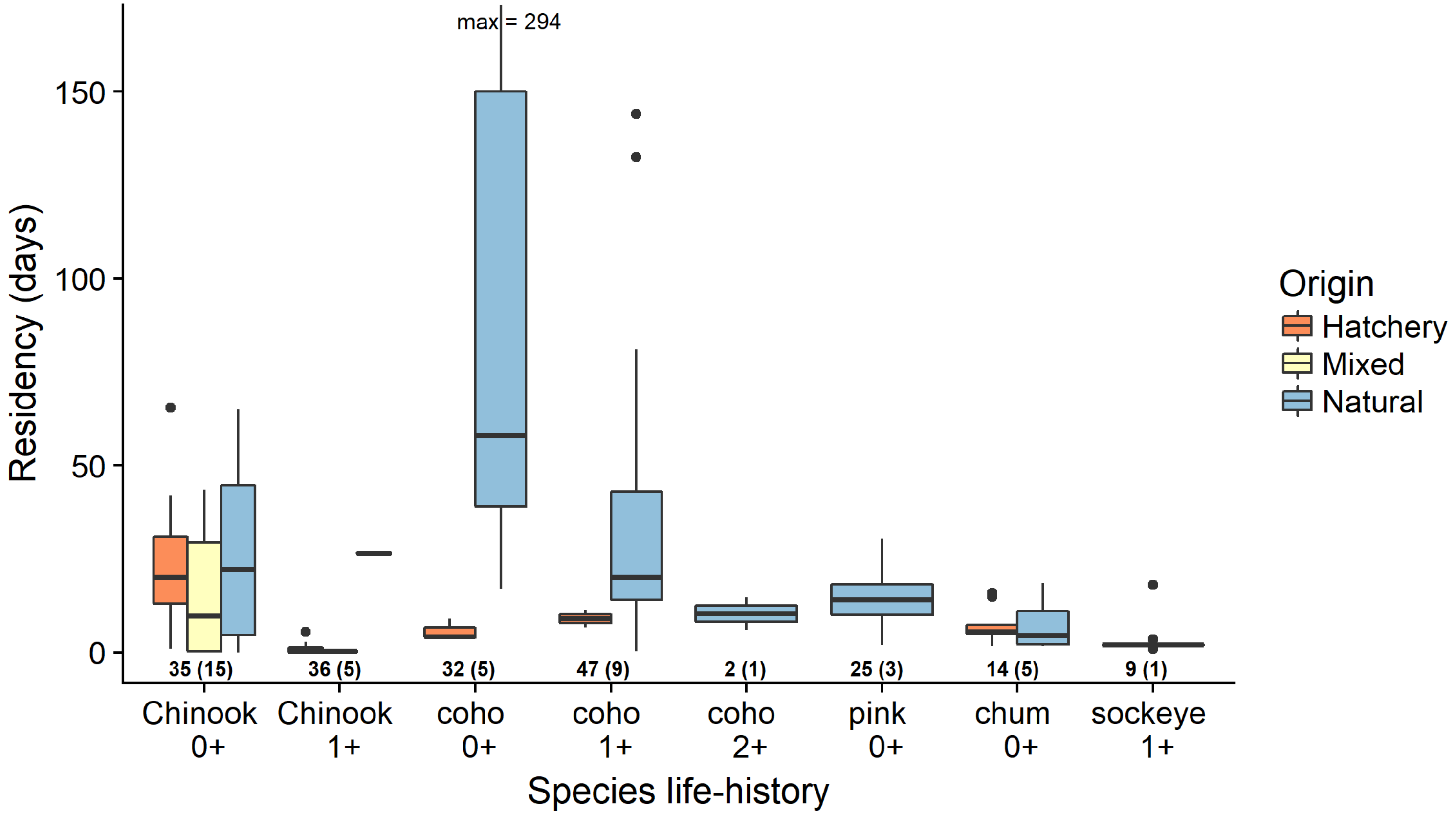


Figure 3.3 Distribution of average (means & medians) residency duration estimates reported in days for multiple juvenile salmon in different life history categories separated by origin (hatchery, mixed, or natural).

The number outside of the brackets is the number of estimates in each species life-history category and the number inside the brackets is the number of articles they are from.

3.5. Discussion

Here, we compiled and explored a wealth of published estimates of juvenile salmon estuary growth and residency to summarize current estimates across life histories, identify spatial and biological gaps in knowledge, and determine possible methodological biases. We found that life histories with the most published literature were primarily researched in their southern range while poorly covered life histories were researched in more northerly latitudes. Our general overview of methodologies suggested that variation within studies may be greater than bias introduced by methodology. Variability in growth-rate analytical methodology made it difficult to compare across species and represents an aspect that could benefit from unifying methods. The inter-quartile range of all growth rates was 0.23-0.51 mm/day. In comparison, residency estimates were more comparable across species. Natural-origin 0+ Chinook and 0+ coho reared in estuaries for the longest durations, one to several months. Their older counterparts averaged a residency around one month and their hatchery-origin counterparts often only resided in estuaries for a week or less. Pink and chum tended to reside in estuaries 1-2 weeks and sockeye resided for less than a week. In addition, there was much variation in residency durations across estuaries, which suggests that different estuaries may vary in the roles and importance for migrating juvenile salmon populations. The compilation of this data allows us to test prior predictions of estuary use, hypothesize on factors that may influence the relative importance of estuaries to juvenile salmon, and provides a basis for future research directions.

There was an uneven distribution of science on estuary growth and residency of juvenile salmon across space and species in North America (Fig 3.1). There was better biological and spatial coverage of residency than growth, perhaps because most methodologies used to estimate growth require recapture of marked fish (Levings 2016). Scientific effort (as measured by number of articles) across species and life-stages was extremely disparate—there were numerous studies of 0+ Chinook and coho, but other life histories had two or less articles on either growth or residency. Furthermore, the vast majority of research on estuary growth and ecology of juvenile salmon occurred south of Vancouver Island, BC (Fig 3.1), where human density and accessible is greater, and where more salmon biodiversity has been lost (Gustafson et al. 2007, Griffiths et al.

2014). While there is an enormous amount of research on salmon, our compilation reveals important gaps in knowledge. Future research could target data poor areas to contribute to understanding the estuary ecology of salmon.

Multiple possibilities likely contribute to an uneven distribution of scientific effort across species and life histories. The distribution of research across life histories generally followed our expectation that those described as more estuary dependent would have more research, but there were exceptions. 0+ Chinook and coho had the 1st and 3rd most articles on them, which we expected because they are typically described as being the most estuary dependent (Thorpe 1994, Koski 2009). Unexpectedly, 1+ coho had the 2nd most research over the largest range of latitudes, primarily from estimates of residency, despite expectation that they migrate quickly through the estuary (Thorpe 1994, Levings 2016). The quantity of research on yearling coho is possibly due to their listing as endangered in several systems (NOAA 2018) and the ability to fit them with PIT and acoustic tags. Three species that are described as having some of the least estuarine dependency, 0+ pink and chum and 1+ Chinook, were the 5th and tied for 4th most researched life histories, respectively. 1+ sockeye, also a species not expected to have much estuary dependency, were researched the 6th most. Contrary to our prediction, 0+ sockeye, which Thorpe (1994) described as one of the hypothetically most estuarine dependent life histories, had only one study on growth rate. However, 0+ sockeye life histories are also relatively rare (Groot & Margolis 1991), which may explain this discrepancy. Overall, research efforts appeared to be distributed in correlation with previous expectations of the reliance of different species and life histories on estuaries. Our ability to understand the full range of functions that estuaries play for juvenile salmon could be strengthened by increasing research on less estuary-dependent life histories that could provide us with a comparative baseline within salmon.

Studies used a diversity of methodologies to quantify estuary growth and residency that could introduce bias, but our results suggest that this bias was generally not greater than natural variation. It is important to recognized the different assumptions and inferences that accompany varying methods (Levings 2016). One of the key divisions in methods from studies we compiled was cohort-based approaches versus individual-based approaches. However, the only apparent difference we observed was between acoustic-tagging studies and other studies, regardless of whether they also used individual-based approaches or cohort-based. Studies that used acoustic-tagged fish to estimate residency consistently produced the lowest estimates and had the least amount of variation, even when there were many estimates within a study. These estimates may be lower because acoustic tags can only be inserted into larger fish that may naturally have shorter residency times; it is also possible that there may be a tagging effect that increases transit rates. Importantly, a case-study that used both PIT and acoustic tags also found that acoustic tagged fish transited more rapidly than PIT tagged fish in the estuary (Miller & Sadro 2003). Several other case-studies that used multiple methods showed additional sources of potential methodological bias [(Healey 1980a, Levings et al. 1986, Shreffler et al. 1990, Miller & Sadro 2003, Jones et al. 2014); see Text B1 for summary], but when we compared estimates across studies we did not find a trend in any methods estimates other than with acoustic tags. Instead of trends resulting from methods, we found the variation in studies with many estimates within a single estuary were greater than any differences in the averages across studies that used different methodologies. Thus, natural variation may be generally greater than any introduced systematic error, but caution is still warranted when comparing estimates of residency from certain methods such as acoustic tagging.

The largest trend in growth rates was that older life histories of coho tended to have greater incremental growth rates. The average 1+ coho had double the average 0+ coho growth rate as measured in mm/day. However, incremental increases in length of fish can be an allometric function of age and size (Von Bertalanffy 1938, Lugert et al. 2016). The inconsistent reporting of length data with growth rates makes it difficult for us to determine whether the increased growth rates are due to size, age, or other environmental factors because size-at-age relationships are determined by a systems growing degree-days and the relative abundance of food (Parker & Larkin 1959, Neuheimer & Taggart 2007). The lack of growth data that used the same units across multiple life histories made it difficult to identify any other trends or rank which species may benefit most from residing in estuaries for longer. Overall, juvenile salmon growth rate research represents a large opportunity for future study and it is a key part of the equation to understanding the value of estuaries as nursery habitats (Sheaves et al. 2015).

The average residencies from studies of natural-origin fish provide us with a quantitative test of previous hypothesis that predict patterns of estuary residency across species and life histories. Thorpe (1994) suggested that 0+ Chinook and sockeye were most dependent on the estuary, whereas 0+ pink and chum, and all 1+ life histories were less so. The empirical data supported some of these suggestions, but not others. 1+ Chinook and sockeye, and 0+ pink and chum had shorter residencies on average than 0+ Chinook. However, natural-origin 0+ pink, which were described as the least estuary dependent life history (Thorpe 1994), had a higher mean residency (2 weeks) than 0+ Chum (1 week) and 1+ sockeye (~4 days). Another life history that is expected to migrate quickly through estuaries, 2+ coho (Thorpe 1994), had an average residency of 10 days. Further, while some historical studies suggested that 0+ coho did not survive once they were flushed downstream (Quinn 2005), more recent studies have found that indeed 0+ coho can survive the marine phase (Koski 2009, Bennett et al. 2015). In this review, we illustrate that natural-origin 0+ coho had the highest average residency estimates with a mean of 3 months and a maximum average over 9 months, suggesting that estuaries might be particularly important for this life history. There were no estimates for 0+ sockeye residency, which is surprising for a life history that was thought to be one of the most estuary dependent (Thorpe 1994). While 0+ Chinook, the other hypothetically most estuary dependent (Thorpe 1994), had the most amount of research and a high average residency, 27 days, it was only a week longer than the average of 1+ coho who were expected to migrate through the estuary relatively quickly (Thorpe 1994). Thus, like other authors (McDowall 2002), we suggest that the evolutionary legacy hypothesis postulated by Thorpe (1994) does not fully explain patterns of estuary residency in salmon. Instead, estuary residency is likely the product of trade-offs between estuary conditions (growth and survival) and previous freshwater conditions as well as future marine conditions.

The differences in estuary residencies across life histories may illuminate the extent that different estuary functions may play in determining juvenile salmon behavior. These different roles are: productive foraging opportunities, refuge from predation, and physiological transition (Thorpe 1994), with the latter predicting the minimum amount of time species need to hold in estuaries. The durations of residencies that we observed, even in pink and chum, are beyond those needed for juvenile salmon to undergo physiological shifts without mortality induced stress (Tschaplinski 1987, Healey 1991a, Weitkamp 2008). Relatively long residencies suggest that most species and life histories of juvenile salmon are also benefiting from the remaining roles that estuaries can play. Within a species, life histories that entered estuaries younger (and smaller) tended to reside longer. In this case, increased residency may be from selective pressure on them to grow bigger to reduce predation risk in subsequent habitats (Sogard 1997, Beamish & Mahnken 2001). However, across species, there were no consistent patterns with regards to residency and the size/age of estuary entry. For instance, pink and chum salmon enter the ocean at similarly small sizes at 0+ age but only tended to rear for a week or two. In contrast, 0+ Chinook and coho resided in estuaries for one to several months, entering the estuary at more variable sizes. There was also high variability in 0+ coho average residencies which ranged from 17-294 days, which is presumably the result of employing multiple life-history strategies after initial estuary entry (Jones et al. 2014), though the selective pressures driving this variability are unclear. Thus, there are within species trends between age-classes that follow what theory would predict, but the across species and within life-history variability suggests that different species are interacting with and deriving benefits from estuaries in different ways.

Hatchery-origin juvenile salmon had different patterns of estuary residency than natural-origin fish. Both hatchery-origin coho life histories and 1+ Chinook had consistently lower estuary residencies, with their average estimates either not overlapping at all with natural-origin estimates or only overlapping with the lowest quartile. This differential use in estuaries could occur for multiple reasons. First, hatcheries may have selected for life histories with short residency; the loss of genetic diversity in hatchery stocks is widespread (Verspoor 1988, Waples & Teel 1990, Allendorf & Phelps 2011). Genetic-stock differences are known to be connected with different behaviours and habitat use (Swain & Riddell 1990, Roegner et al. 2016). Another possibility is that hatchery fish may be more likely to be present in systems with more degraded habitat (Griffiths et al. 2014), including in estuaries. However, several studies have observed divergent behavior in natural- and hatchery-origin fish within shared estuaries (Myers & Horton 1982, Levings et al. 1986, Weitkamp 2008, Gamble et al. 2018). Alternatively, phenotypes of hatchery-origin fish that enter estuaries may be different than wild due to hatchery practices (Huntingford 2004) such as feeding parr at high rates and densities (Fenderson et al. 1968), and releasing larger individuals (Miller et al. 2010) or at specific times of the year. Regardless of the mechanism driving the difference, the fact that some hatchery fish are behaving differently in estuaries means that they may respond differently to habitat alterations and may not correlate with the responses of wild fish to similar changes in estuarine environments. Previous studies of hatchery-origin fish have found that their survival can be lower in more degraded and contaminated estuaries (Magnusson & Hilborn 2003, Meador 2014). If wild populations are residing in estuaries longer, as suggested by this synthesis, they may be even more sensitive to estuary degradation than previously thought.

We presented the results from the compilation of articles on juvenile salmon growth rates and residency, however there are limitations to how comprehensive our database is. We did not perform a systematic search of reports ("grey literature"). Reports are not cited as often as peer-reviewed literature but may contain more data that could be added to this research. The database is also limited by a lack of comparability between the reporting of results. This could be remedied by a coordinated collaboration and consisting reporting standards, which could also address additional questions on the biases that are introduced using different analytical methods (Healey 1980a, Levings et al. 1986). We also found several articles that included tidally freshwater areas in their definition of "estuary" (Kjelson et al. 1982, Ledgerwood et al. 2004, Henery et al. 2010, McNatt et al. 2016, Weybright & Giannico 2018) but did not include those results in this research. Tidally-influenced freshwater habitats are often considered a part of estuaries (Perillo 1995, Hume et al. 2007), particularly for land management reasons (Simenstad et al. 2011), which may have impacts of juvenile salmon use of these habitats (Scott et al. 2016). However, the lack of saltwater influence means that these habitats likely play different roles for juvenile salmon (Thorpe 1994). Finally, many studies acknowledged that they were not able to estimate mortality rates, which may affect estimates of residency. Mortality can be confused with early estuary emigration. Smaller fish often have higher mortality (Sogard 1996) but also may reside in estuaries longer (Healey 1979, *this chapter*). Thus, many of the residency estimates here may be conservative average estimates (underestimates). However, by making this compilation open access, we hope that this research will continue and progress to allow even more complex analysis on the dynamics of juvenile salmon use of estuaries.

Behaviours in different life history stages, such as residency of migratory juvenile salmon in estuaries, can have cascading affects from survival to individual fecundity to overall population growth. There is already evidence of growth rate and size-selective mortality in juvenile salmon in the early marine period (Healey 1982b, Holtby et al. 1990, Beamish et al. 2004, Moss et al. 2005, Duffy & Beauchamp 2011), which is also considered a critical mortality period (Pearcy 1992, Beamish & Mahnken 2001). Our ability to directly measure growth rates and residency of specific populations and life histories over their entire range and a swath of biophysical conditions will increase our understanding of estuaries as nursery habitat (Beck et al. 2001, Sheaves et al. 2015) and how estuaries contribute to the population dynamics of these important fishes.

The large range of variation in average estimates of residency and growth within a given species or life history suggests that different estuaries provide different functions for juvenile salmon. For example, average residency estimates in 0+ coho ranged from 17-294 days and from 2-30 days in 0+ pink. In addition, there is even more variation around each average residency estimate, which means that variation across individual fish would be even greater. Some key characteristics of estuaries that may affect residency duration include water temperature, estuary size, estuary habitat, mortality rates, and density-dependent pressures. Water temperature is a major contributor to the growth potential (Brett 1995) of a given estuary and thus may shift the selective benefits of habitats across the temperature regime of a system (Armstrong et al. 2013). The trade-off between growth rate and mortality rate is also a major determinant of how long an individual may reside in a habitat (Werner & Gilliam 1984, Werner & Hall 1988). Estimates of juvenile salmon mortality across estuaries is likely a key predictor of variation in residency. Additionally, the density of juvenile salmon relative to the size or productivity of optimal foraging habitat may also affect individual growth and residency duration through competition (Walters & Juanes 1993, David, Simenstad, et al. 2016). Density could be either a function of a systems natural geology or anthropogenic factors. For example, if a large basin has a small estuary (e.g. a fjord type with no bar), then there is the potential for fish to inhabit that estuary at much higher densities and thus have lower growth capacity than a system with a small basin and large estuary (e.g. a bar built or drowned river mouth). Evidence of density-dependence effects on foraging efficiency in anthropogenically impacted estuaries already exists (David, Simenstad, et al. 2016). There is an opportunity and need for future research to explore whether differences in residency or growth across estuaries are explained by simple processes such as mentioned above. Indeed, understanding the degree to which different estuaries represent critical habitat to juvenile salmon is a vital research frontier that could help evaluate conservation priorities and guide restoration activities.

3.6. Acknowledgements

The conceptual basis for this research was driven by a collaboration with Emma Hodgson and Jonathan Moore, whom I would like to thank and acknowledge because they made this research a possibility.

Chapter 4.

Conclusion

In this thesis, I used a combination of an intensive field study as well as a thorough literature review to examine the estuary ecology of ecologically, economically, and culturally important fishes. In my second chapter, I quantified the dynamic prey mosaic of juvenile salmon and small pelagic fishes in the estuary of a major salmon watershed, the Skeena River. In my third chapter, I illuminated the knowledge gaps and trends in growth and residency across life histories of anadromous Pacific salmon in North America. In this chapter, I overview key findings of these studies and discuss implications and future directions.

I found that each fish species in my second chapter consumed different estuarine prey whose abundance had different dynamics. Juvenile coho salmon were highly piscivorous and insectivorous, and water clarity and temperature affected the abundance of several important prey items in their diets. Juvenile sockeye salmon primarily consumed Harpacticoid copepods, whose abundance in their diets increased over the duration of the summer in correlation with no biophysical factors I identified but whose natural abundances were higher over eelgrass habitats. Pacific herring and surf smelt primarily consumed Calanoid copepods, whose abundance in Pacific herring diets decreased with the density of planktivorous fish caught in the same area (CPUE). All four species consumed pteropods as a secondary prey, selected for decapod zoea, and all but herring selected amphipods. In addition, diets across individuals within each species were incredibly diverse, particularly in the juvenile salmon, with no prey species occurring in every diet sample. The ability to forage on a diversity of prey can buffer individuals and populations from starvation across spatially and temporally heterogeneous landscapes (Armstrong et al. 2016) or seascapes such as estuaries (Nagelkerken et al. 2015).

It was also evident that there was a distinct difference in how juvenile salmon and the small pelagic fishes integrated with the prey field. The small pelagic fishes heavily exploited the most abundant prey in the water column, Calanoid copepods, while the juvenile salmon disproportionately consumed the lower abundance prey, Harpacticoid copepods. I suggest that there is an intrinsic difference in the foraging abilities of these groups of fish that has been selected for or impeded by evolutionary processes. In the case of small pelagic fish, the ability to forage on the most abundant prey despite its evasiveness may have been selected for because they do not reach relatively larger sizes like salmon do, thus those who could exploit a ubiquitous prey possibly had higher fitness (survived to reproduce). Whereas unlike small pelagic fish, the more diverse ontogenetic stages (with regards to size) of salmon may undergo variable selective pressures that impede the selection on juveniles to become specialist planktivours of highly evasive prey. As salmon become larger they move offshore, apply different foraging tactics to different prey fields, and are exposed to different selective pressures.

I believe that the findings in Chapter 2 are important for several reasons. First, these findings are relevant to general conceptual understanding of how biophysical estuary dynamics link to prey and to their fish consumers. While it is generally accepted that the prey basis of estuaries is one of the key dimensions of their role as nursery habitat (Beck et al. 2001, Sheaves et al. 2015), relatively few studies have actually quantified fish diets and then examined the dynamics of their key prey across space and time (Nagelkerken et al. 2015). This chapter adds an important empirical example of how small mobile fishes integrate across a dynamic prey field in an estuarine seascape. Second, this chapter addresses a previously-identified knowledge gap in juvenile salmon food web ecology in an estuary under increasing anthropogenic development threat, the Skeena River estuary (Pickard et al. 2015). I am hopeful that this work may provide some insight into potential mechanisms by which stressors could impact fish through modification of their food webs.

In my third chapter, I compiled empirical estimates through a rigorous literature review of two key dimensions of juvenile salmon estuary ecology—growth and residency. There were not systematic differences in growth across species or life-histories, likely because methods for measuring and reporting growth rates were so variable. A harmonization of growth research methods represents a large opportunity for future research. One of the main results of this synthesis was that different life histories and species of juvenile salmon resided in estuaries for different lengths of time—some life-histories tended to rear for a few days, while others reared for many weeks if not months. This synthesis provides an empirical test of previous narrative statements about patterns of residency across species. As typically cited (Healey 1982a, Simenstad et al.

1982, Thorpe 1994, Quinn 2005), 1+ Chinook and sockeye, and 0+ pink and chum had shorter residencies on average than 0+ Chinook, the “most estuary dependent” life history. However, counter to some narratives that say 0+ pink have the least estuary dependency (Healey 1982a, Thorpe 1994, Quinn 2005), this species had a higher mean residency (2 weeks) than 0+ Chum (1 week) and 1+ sockeye (~4 days). While 0+ Chinook had a high average residency, 27 days, it was only a week higher than the average of 1+ coho who were expected to migrate through the estuary relatively quickly (Thorpe 1994, Quinn 2005). 0+ coho had the highest mean residency (3 months), which is surprising because at the time of Quinn’s (2005) summary they were still believed to simply perish at sea. 0+ coho are now known to contribute to the spawning population (Koski 2009, Bennett et al. 2015) and their estuary use appears to be the most extensive of any species’ life history.

The review chapter also revealed a high degree of variation in residency within species and life-histories. The average residency estimates of several well researched species’ life histories, including 0+ Chinook, 0+ coho, and 1+ coho, ranged from hours to months across estuaries. This high diversity in juvenile salmon estuary use has presumably arisen from different eco-evolutionary processes including local adaptation in life histories (Taylor 1991). Juvenile Pacific salmon experience variable biophysical conditions across their North American range in both fresh, estuarine, and marine waters. Each habitat provides different trade-offs, such as between growth and predation (Willette 2001), and may affect the decisions of fish to reside in one relative to the other (Werner et al. 1983, Werner & Hall 1988). I was unable to compile enough data on each system over my master’s to test the relationships between residency and relative freshwater-estuarine-marine complexes, but I recommend further study of this avenue to link life-history theory with estuary and watershed characteristics towards understanding the relative dependency of juvenile salmon populations on estuaries.

Another important trend that emerged from my synthesis of residency estimates in chapter 3 was that hatchery fish tended to have lower residency than their wild counterparts. Lower hatchery-origin residencies may be the result of two processes. First, genetically-linked behaviours and phenotypes in juvenile salmon may influence their estuary use. Hatchery and wild populations are known to often have differing genetics and phenotypes (Verspoor 1988, Waples & Teel 1990, Allendorf & Phelps 2011). Evidence from wild and hatchery populations within single systems shows that they differ in agonistic behaviour (Swain & Riddell 1990), habitat use (Roegner et al. 2016), diet (Sosiak et al. 1979, Chittenden et al. 2018), and even estuary residency duration (Myers & Horton 1982, Levings et al. 1986). A second possibility is that hatchery fish are more often present in systems with more degraded habitat (Griffiths et al. 2014), including in estuaries. Thus, habitat in degraded estuaries with hatchery fish may offer fewer benefits than the adjacent marine habitat and selection favors those that migrate through quickly. Thus, while previous studies of hatchery fish have found that estuary degradation can decrease their survival (Magnusson & Hilborn 2003, Meador 2014), wild salmon populations may be even more sensitive. In addition, genetic mixing of hatchery and wild fish could shift estuary life-histories.

The ecological complexity of estuaries, such as that evidenced in this thesis, can pose challenges for environmental decision-making and planning processes. In Canada, fish habitat is protected by Section 35 of the Fisheries Act (R.S.C. 1985), however, more than single habitats are required to support the diversity of fish and stocks that use estuaries. I will use the Skeena River estuary as an example. Over 40 populations comprised of five species of salmon use the Skeena River estuary (Moore et al. 2015) that have highly overlapping entry dates and residencies (Moore et al. 2016, Carr-Harris et al. 2018), all of which have experienced generations of different freshwater selective pressures resulting in local adaptations and genetic differences (Gottesfeld & Rabnett 2008). Sharpe (2017) highlights that although some species are more associated with certain habitat types, more complex biophysical models were better at predicting smolt abundance in the estuary. My research also suggests that it is not only habitats like eelgrass that may affect prey resources but also salinity, temperature, and the abundance of other fishes. Thus, estuaries provide nursery function to important fishes through a complex and dynamic estuarine seascape that differs across populations and species (Sheaves et al. 2015, Nagelkerken et al. 2015).

One potentially application for research on estuary ecology of juvenile salmon is towards clarifying stock-specific risks of potential developments. The accumulated research in the Skeena River estuary allows me to provide a simplified example of a stock-specific assessment of estuary use and comment on its relative dependency on the estuary and specific habitats. The Sustut Lake sockeye stock is of moderate size, averaging 600-1200 spawners, and located in the high interior zone of the Skeena River watershed (Gottesfeld & Rabnett 2008). The sockeye salmon smolts from Sustut Lake in the Skeena River system enter the estuary at a later date than most stocks, which is correlated with the long distance these smolts have to travel (Carr-Harris et al. 2018). The Sustut Lake stock is also estimated to have a relatively longer estuary residency than other Skeena River populations; two weeks compared to less than one week on average (Moore et al. 2016). The period that Sustut Lake individuals arrive with highest probability is also during the period when sockeye salmon were consuming Harpacticoid copepods most (mid-late June) (this manuscript; Carr-Harris et al. 2018). Although research done after the major smolt migration showed that Harpacticoid copepods were more abundant over sandy bank habitat than eelgrass (Carr-Harris 2017), my study, which sampled at the same time salmon were foraging, found higher Harpacticoid abundance over eelgrass as did prior research in another estuary (Kennedy et al. 2018). Additionally, Sharpe (2017) found that juvenile sockeye were associated with eelgrass generally, but particularly with Flora Bank where she found them at 2-8 times higher abundances than other areas (depending on the year). Thus, degradation of eelgrass, particularly Flora Bank, may pose particularly large risks to Sustut Lake sockeye salmon relative to other Skeena River sockeye salmon stocks. This example highlights how cumulative research efforts may be required to identify stock-specific risks of potential developments in complex systems like estuaries.

As marine and freshwater ecosystems continue to transform through climate change, anthropogenic development, and fishing and aquaculture pressures (Anderson & Piatt 1999, Harley et al. 2006, Gilman et al. 2010), scientists are tasked with providing evidence for decision making and management strategies (E4D 2018). The quality and quantity of estuaries in particular are being impacted at a rapid rate (McClelland & Valiela 1998, Lotze et al. 2006, Thorne et al. 2018), which is why creating and compiling information on ecologically, economically, and culturally important species in estuaries is particularly pressing. I suggest that in-depth empirical studies as well as literature syntheses can help clarify advance our understanding of these systems. As evidence accumulates regarding the complex dynamics of estuaries as nursery habitat, there is an opportunity to take a more holistic perspective on estuary habitat function, planning, and prioritization (Nagelkerken et al. 2015).

References

Ajmani AM (2011) The growth and diet composition of sockeye salmon smolts in Rivers Inlet, British Columbia. University of British Columbia

Alheit J, Scheibel W (1982) Benthic harpacticoids as a food source for fish. Mar Biol 70:141–147

Allendorf FW, Phelps SR (2011) Loss of genetic variation in a hatchery stock of cutthroat trout. Trans Am Fish Soc 109:537–543

Anderson P, Piatt J (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. Mar Ecol Prog Ser 189:117–123

Arditi R, Ginzburg LR (1989) Coupling in predator-prey dynamics: ratio-dependence. J Theor Biol 139:311–326

Armstrong RH, Morrow JE (1980) The dolly varden charrs, *Salvelinus malma*. In: Charrs. Dr. W. Junk Publisher, The Hague, p 99–140

Armstrong J, Schindler D, Ruff C, Brooks G, Bentley K, Torgersen C (2013) Diel horizontal migration in streams: juvenile fish exploit spatial heterogeneity in thermal and trophic resources. Ecology 94:2066–75

Armstrong JB, Takimoto G, Schindler DE, Hayes MM, Kauffman MJ (2016) Resource waves: phenological diversity enhances foraging opportunities for mobile consumers. Ecology 97:1099–1112

Babyak MA (2004) What you see may not be what you get: a brief, nontechnical introduction to overfiting in regression-type models. Psychosom Med:411–421

Barry JP, Dayton PK (1991) Physical heterogeneity and the organization of marine communities. In: Kolasa J, Pickett STA (eds) Ecological Heterogeneity. Springer New York, New York, NY, p 270–320

Bassett MC, Patterson DA, Shrimpton JM (2018) Temporal and spatial differences in smolting among Oncorhynchus nerka populations throughout fresh and seawater migration. J Fish Biol:10.1111/jfb.13678

Beamish RJ (2018) The Ocean Ecology of Pacific Salmon and Trout. American Fisheries Society, Bethesda, Maryland

Beamish RJ, Mahnken C (2001) A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog Oceanogr 49:423–437

Beamish R, Mahnken C, Neville C (2004) Evidence that reduced early marine growth is associated with lower marine survival of coho salmon. Trans Am Fish Soc 133:26–33

Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. BioScience 51:633–641

Bennett TR, Roni P, Denton K, McHenry M, Moses R (2015) Nomads no more: early juvenile coho salmon migrants contribute to the adult return. Ecol Freshw Fish 24:264–275

Berg L, Northcote TG (1985) Changes in territorial, gill-flaring, and feeding behavior in juvenile coho salmon (*Oncorhynchus kisutch*) following short-term pulses of suspended sediment. Can J Fish Aquat Sci 42:1410–1417

Birtwell IK, Nassichuk MD, Beune H (1987) Underyearling sockeye salmon (*Oncorhynchus nerka*) in the estuary of the Fraser River. Sockeye Salmon:25–35

Bollens SM, Hooff R vanden, Butler M, Cordell JR, Frost BW (2010) Feeding ecology of juvenile pacific salmon (*Oncorhynchus* spp.) in a northeast pacific fjord: Diet, availability of zooplankton, selectivity for prey, and potential competition for prey resources. Fish Bull 108:393–407

Bonferroni C (1936) Teoria statistica delle classi e calcolo delle probabilita. Pubblicazioni R Ist Super Sci Econ E Commericiali Firenze 8:3–62

Boström C, Pittman S, Simenstad C, Kneib R (2011) Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. Mar Ecol Prog Ser 427:191–217

Bottom DL, Jones KK (1990) Species composition, distribution, and invertebrate prey of fish assemblages in the Columbia River estuary. Prog Ocean 25:243–270

Brachvogel R, Meskendahl L, Herrmann J-P, Temming A (2013) Functional responses of juvenile herring and sprat in relation to different prey types. Mar Biol 160:465–478

Brett JR, Glass NR (1973) Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. J Fish Res Board Can 30:379–387

Brett J, Shelbourn J, Shoop C (1969) Growth rate and body composition of fingerling sockeye salmon , *Oncorhynchus nerka* in relation to temperature and ration size. Fish Res Board Can 26:2363–2394

Brodeur RD (1991) Ontogenetic variations in the type and size of prey consumed by juvenile coho, *Oncorhynchus kisutch*, and chinook, *O. tshawytscha*, salmon. Environ Biol Fishes 30:303–315

Brodeur RD, Daly EA, Benkwitt CE, Morgan CA, Emmett RL (2011) Catching the prey: Sampling juvenile fish and invertebrate prey fields of juvenile coho and Chinook salmon during their early marine residence. Fish Res 108:65–73

Brodeur RD, Daly EA, Schabetsberger RA, Mier KL (2007) Interannual and interdecadal variability in juvenile coho salmon (*Oncorhynchus kisutch*) diets in relation to environmental changes in the northern California Current. Fish Ocean 16:395–408

Brodeur RD, Daly EA, Sturdevant MV, Miller TW, Moss JH, Thiess ME, Trudel M, Weitkamp LA, Armstrong J, Norton EC (2007) Regional comparisons of juvenile salmon feeding in coastal marine waters off the west coast of North America. 57:183–203

Brodeur RD, Morgan CA (2015) Influence of a coastal riverine plume on the cross-shelf variability in hydrography, zooplankton, and juvenile salmon diets. Estuaries Coasts 39:1183–1198

Brodeur RD, Pearcy WG (1987) Diel feeding chronology, gastric evacuation and estimated daily ration of juvenile coho salmon, *Oncorhynchus kisutch* (Walbaum), in the coastal marine environment. J Fish Biol 31:465–477

Brodeur RD, Peterson WT, Boehlert GW, Casillas E, Schiewe MH, Eldridge MB, Lindley ST, Helle JH, Heard WR (2000) A coordinated research plan for estuarine and ocean research on Pacific salmon. Fisheries 25:7–16

Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach / Kenneth P. Burnham, David R. Anderson., 2nd ed. Springer, New York

Buskey EJ, Lenz PH, Hartline DK (2002) Escape behavior of planktonic copepods in response to hydrodynamic disturbances: high speed video analysis. Mar Ecol Prog Ser 235:135–146

Cabin RJ, Mitchell RJ (2000) To Bonferroni or not to Bonferroni: when and how are the questions. Bull Ecol Soc Am 81:246–248

Carr-Harris C (2017) Fish diet and selectivity study of Flora Bank and adjacent areas. Skeena Fisheries Commission, Kispiox, BC

Carr-Harris C, Gottesfeld AS, Moore JW (2015) Juvenile Salmon Usage of the Skeena River Estuary. Plos One 10:e0118988

Carr-Harris CN, Moore JW, Gottesfeld AS, Gordon JA, Shepert WM, Henry JDJ, Russell HJ, Helin WNB, Doolan DJ, Beacham TD (2018) Phenological diversity of salmon smolt migration timing within a large watershed. Trans Am Fish Soc:10.1002/tafs.10068

CEAA (2016) Decision Statement Issued under Section 54 of the Canadian Environmental Assessment Act, 2012. Canadian Environmental Assessment Agency, Ottawa, ON

Chacin DH, Stallings CD (2016) Disentangling fine- and broad- scale effects of habitat on predator–prey interactions. J Exp Mar Biol Ecol 483:10–19

Chandler GT, Fleeger JW (1987) Facilitative and inhibitory interactions among estuarine meiobenthic Harpacticoid copepods. Ecology 68:1906–1919

Chittenden CM, Jensen JLA, Ewart D, Anderson S, Balfry S, Downey E, Eaves A, Saksida S, Smith B, Vincent S, Welch D, RScott M (2010) Recent salmon declines: a reuslt of lost feeding opportunities due to bad timing? Plos ONE 5:e12423

Chittenden CM, Sweeting R, Neville CM, Young K, Galbraith M, Carmack E, Vagle S, Dempsey M, Eert J, Beamish RJ (2018) Estuarine and marine diets of out-migrating Chinook Salmon smolts in relation to local zooplankton populations, including harmful blooms. Estuar Coast Shelf Sci 200:335–348

Clark CW, Levy DA (1988) Diel vertical migrations by juvenile sockeye salmon and the antipredation window. Am Nat 131:271–290

Clarke RD, Buskey EJ, Marsden KC (2005) Effects of water motion and prey behavior on zooplankton capture by two coral reef fishes. Mar Biol 146:1145–1155

Cloern JE (1996) Phytoplankton bloom dynamics in coastal ecosystems: A review with some general lessons from sustained investigation of San Francisco Bay, California. Rev Geophys 34:127–168

Cloern JE, Foster SQ, Kleckner AE (2014) Phytoplankton primary production in the world's estuarine-coastal ecosystems. Biogeosciences 11:2477–2501

Congleton JL, Davis SK, Foley SR (1981) Distribution, abundance and outmigration timing of chum and chinook salmon fry in the Skagit salt marsh. Proc Salmon Trout Migr Behav Symp:153–163

Croll DA, Marinovic B, Benson S, Chavez FP, Black N, Ternullo R, Tershy BR (2005) From wind to whales: tropic links in a coastal upwelling system. Mar Ecol Prog Ser 289:117–130

Crozier LG, Hendry AP, Lawson PW, Quinn TP, Mantua NJ, Battin J, Shaw RG, Huey RB (2008) Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. Evol Appl 1:252–270

Culum B, Laland KN (2003) Social learning in fishes: a review. Fish Fish 4:280–288

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. In: Advances in marine biology. Elsevier, p 249–293

Daly E, Benkwitt CE, Brodeur RD, Litz MN, Copeman L (2010) Fatty acid profiles of juvenile salmon indicate prey selection strategies in coastal marine waters. Mar Biol 157:1975–1987

Daly E, Brodeur RD, Weitkamp L (2009) Ontogenetic Shifts in Diets of Juvenile and Subadult Coho and Chinook Salmon in Coastal Marine Waters: Important for Marine Survival? Trans Am Fish Soc 138:1420–1438

David V, Selleslagh J, Nowaczyk A, Dubois S, Bachelet G, Blanchet H, Gouillieux B, Lavesque N, Leconte M, Savoye N, Sautour B, Lobry J (2016) Estuarine habitats structure zooplankton communities: Implications for the pelagic trophic pathways. Estuar Coast Shelf Sci 179:99–111

David AT, Simenstad C, Cordell J, Toft J, Ellings C, Gray A, Berge H (2016) Wetland loss, juvenile salmon foraging performance, and density dependence in Pacific Northwest estuaries. Estuaries Coasts 39:767–780

Deudero S, Morales-Nin B (2001) Prey selectivity in planktivorous juvenile fishes associated with floating objects in the western Mediterranean. Aquac Res 32:481–490

Duffy EJ, Beauchamp DA (2011) Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. Can J Fish Aquat Sci 68:232–240

Duffy EJ, Beauchamp DA, Sweeting RM, Beamish RJ, Brennan JS (2010) Ontogenetic diet shifts of juvenile Chinook salmon in nearshore and offshore habitats of Puget Sound. Trans Am Fish Soc 139:803–823

Dunn OJ (1961) Multiple Comparisons Among Means. J Am Stat Assoc 56:52

E4D (2018) https://evidencefordemocracy.ca/en/about. Evid Democr

Eggers DM (1976) Theoretical effect of scholing by planktivourous fish predators on rate of prey consumption. J Fish Res Board Can:1964–1971

Eggers DM (1977) The nature of prey selection by planktivorous fish. Ecology 58:46–59

Eggers DM (1982) Planktivore preference by prey size. Ecology 63:381–390

Elliott M, McLusky DS (2002) The need for definitions in understanding estuaries. Estuar Coast Shelf Sci 55:815–827

Emlen JM (1966) The role of time and energy in food preference. Am Nat 100:611–617

Evans AF, Payton Q, Turecek A, Cramer B, Collis K, Roby DD, Loschl PJ, Sullivan L, Skalski J, Weiland M, Dotson C (2016) Avian predation on juvenile salmonids: spatial and temporal analysis based on acoustic and passive integrated transponder tags. Trans Am Fish Soc 145:860–877

Fenderson OC, Everhart WH, Muth KM (1968) Comparative agonistic and feeding behavior of hatchery-reared and wild salmon in aquaria. J Fish Res Board Can 25:1–14

Fisher JP, Pearcy WG (1990) Distribution and residence times of juvenile fall and spring Chinook salmon in Coos Bay, Oregon. Fish Bull 88:51–58

Frank KT, Leggett WC (1986) Effect of prey abundance and size on the growth and survival of larval fish: an experimental study employing large volume enclosures. Mar Ecol Prog Ser:11–22

Fujiwara M, Highsmith RC (1997) Harpacticoid copepods: potential link between inbound adult salmon and outbound juvenile salmon. Mar Ecol Prog Ser 158:205–216

Gamble MM, Connelly KA, Gardner JR, Chamberlin JW, Warheit KI, Beauchamp DA (2018) Size, growth, and size-selective mortality of subyearling Chinook salmon during early marine residence in Puget Sound. Trans Am Fish Soc 147:370–389

Gibson RN, Ezzi IA (1985) Effect of particle concentration on filter- and particulate-feeding in the herring *Clupea harengus*. Mar Biol 88:109–116

Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD (2010) A framework for community interactions under climate change. Trends Ecol Evol 25:325–331

Giske J, Aksnes DL, Fiksen Ø (1994) Visual predators, environmental variables and zooplankton mortality risk. Vie Milieu 44:1–9

Godin J-GJ (1981) Daily patterns of feeding behaviour, daily rations, and diets of juvenile pink salmon (*Oncorhynchus gorbuscha*) in two marine bays of British Columbia. Can J Fish Aquat Sci 38:10–15

Gottesfeld A, Rabnett KA (2008) Skeena River fish and their habitat. Ecotrust

Graeb BD, Galarowicz T, Wahl DH, Dettmers JM, Simpson MJ (2005) Foraging behavior, morphology, and life history variation determine the ontogeny of piscivory in two closely related predators. Can J Fish Aquat Sci 62:2010–2020

Gregory RS (1993) Effect of turbidity on the predator avoidance behaviour of juvenile chinook salmon (*Oncorhynchus tshawytscha*). Can J Fish Aquat Sci 50:241–246

Gregory RS, Levings CD (1998) Turbidity reduces predation on migrating juvenile Pacific salmon. Trans Am Fish Soc 127:275–285

Gregory RS, Northcote TG (1993) Surface, planktonic, and benthic foraging by juvenile chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. Can J Fish Aquat Sci 50:233–240

Griffin SL, Rippingale RJ (2001) Zooplankton grazing dynamics: top-down control of phytoplankton and its relationship to an estuarine habitat. Hydrol Process 15:2453–2464

Griffiths D (1973) The food of animals in an ccid morland pond. J Anim Ecol 42:285

Griffiths D (1975) Prey availability and the food of predators. Ecology 56:1209–1214

Griffiths JR, Schindler DE, Armstrong JB, Scheuerell MD, Whited DC, Clark RA, Hilborn R, Holt CA, Lindley ST, Stanford JA, Volk EC (2014) Performance of salmon fishery portfolios across western North America (D Angeler, Ed.). J Appl Ecol 51:1554–1563

Groot C, Margolis L (1991) Pacific salmon life histories. University of British Columbia Press, Vancouver

Gustafson RG, Waples RS, Myers JM, Weitkamp LA, Bryant GJ, Johnson OW, Hard JJ (2007) Pacific salmon extinctions: Quantifying lost and remaining diversity. Conserv Biol 21:1009–1020

Halpin PM (2000) Habitat use by an intertidal salt-marsh fish: trade-offs between predation and growth. Mar Ecol Prog Ser 198:203–214

Harley CDG, Hughes AR, Hultgren KM, Miner BG, Sorte CJB, Thornber CS, Rodriguez LF, Tomanek L, Williams SL (2006) The impacts of climate change in coastal marine systems. Ecol Lett 9:228–241

Healey MC (1979) Detritus and juvenile salmon production in the nanaimo estuary: I. Production and feeding rates of juvenile chum salmon (*Oncorhynchus keta*). J Fish Res Board Can 36:488–496

Healey M (1980a) Utilization of the Nanaimo river estuary by juvenile Chinook salmon, *Oncorhynchus tshawutscha*. Fish Bull 77:653–668

Healey MC (1980b) The ecology of juvenile salmon in Georgia Strait, British Columbia. In: Salmonid ecosystems of the North Pacific. Oregon State University Press, Corvallis, Oregon, p 203–229

Healey MC (1982a) Juvenile Pacific salmon in estuaries: the life support system. In: Kennedy VS (ed) Estuarine Comparisons. Academic Press, p 315–341

Healey MC (1982b) Timing and relative intensity of size-selective mortality of juvenile chum salmon (*Oncorhynchus keta*) during early sea life. Can J Fish Aquat Sci 39:952–957

Healey MC (Ed) (1991a) Life History of Chinook Salmon (*Ocorhynchus tshawytscha*). In: Pacific salmon life histories. UBC Press, Vancouver

Healey MC (1991b) Diets and feeding rates of juvenile pink, chum, and sockeye salmon in Hecate Strait, British Columbia. Trans Am Fish Soc 120:303–318

Henery RE, Sommer TR, Goldman CR (2010) Growth and methylmercury accumulation in juvenile Chinook Salmon in the Sacramento River and its floodplain, the Yolo Bypass. Trans Am Fish Soc 139:550–563

Hill A, Daly E, Brodeur R, Hill A, Daly E, Brodeur R (2015) Diet variability of forage fishes in the Northern California Current System. J Mar Sci 146:121–130

Hitchcock C, Sober E (2004) Prediction versus Accommodation and the Risk of Overfitting. Br J Philos Sci 55:1–34

Hoem Neher TD, Rosenberger AE, Zimmerman CE, Walker CM, Baird SJ (2013) Estuarine environments as rearing habitats for juvenile coho salmon in contrasting south-central Alaska watersheds. Trans Am Fish Soc 142:1481–1494

Holtby LB, Andersen BC, Kadowaki RK (1990) Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Can J Fish Aquat Sci 47:2181–2194

Hosack GR, Dumbauld BR, Ruesink JL, Armstrong DA (2006) Habitat associations of estuarine species: Comparisons of intertidal mudflat, seagrass (*Zostera marina*), and oyster (*Crassostrea gigas*) habitats. Estuaries Coasts 29:1150–1160

Hume TM, Snelder T, Weatherhead M, Liefting R (2007) A controlling factor approach to estuary classification. Ocean Coast Manag 50:905–929

Hunt Jr. GL (1990) The pelagic distribution of marine birds in a heterogeneous environment. Polar Res 8:43–54

Huntingford FA (2004) Implications of domestication and rearing conditions for the behaviour of cultivated fishes. J Fish Biol 65:122–142

Huntley ME, Lopez MDG (1992) Temperature-Dependent Production of Marine Copepods: A Global Synthesis. Am Nat 140:201–242

Hutchinson GE (1961) The paradox of the plankton. Am Nat 95:137–145

Ito J, Parker RP (1971) A record of Pacifc herring (*Clupea harengus pallasi*) feeding on juvenile Chinook salmon (*Oncorhynchus tshawytshca*) in a British Columbia estuary. J Fish Res Board Can 28:1921

Jennions MD (2003) A survey of the statistical power of research in behavioral ecology and animal behavior. Behav Ecol 14:438–445

St. John MA, Macdonald JS, Harrison PJ, Beamish RJ, Choromanski E (1992) The Fraser River plume: some preliminary observations on the distribution of juvenile salmon, herring, and their prey. Fish Oceanogr 1:153–162

Johnston JM (1982) Life histories of anadromous cutthroat with emphasis on migratory behavior. In: Proceedings of the salmon and trout migratory behavior symposium.p 123–127

Jones KK, Cornwell TJ, Bottom DL, Campbell LA, Stein S (2014) The contribution of estuary-resident life histories to the return of adult *Oncorhynchus kisutch*. J Fish Biol 85:52–80

Jones K, Simenstad C, Higley D, Bottom D (1990) Community structure, distribution, and standing stock of benthos, epibenthos, and plankton in the Columbia River Estuary. Prog Ocean 25:211–241

Kennedy LA, Juanes F, El-Sabaawi R (2018) Eelgrass as valuable nearshore foraging habitat for juvenile Pacific salmon in the early marine period. Mar Coast Fish 10:190–203

Kjelson MA, Raquel PF, Fisher FW (1982) Life history of fall-run juvenile chinook salmon, *Oncorhynchus tshawytscha*, in the Sacramento-San Joaquin estuary, California. In: Kennedy VS (ed) Estuarine Comparisons. Academic Press, p 393–411

Koski K (2009) The fate of coho salmon nomads: The story of an estuarine-rearing strategy promoting resilience. Ecol Soc 14:1–16

Labropoulou M, Eleftheriou A (1997) The foraging ecology of two pairs of congeneric demersal fish species: importance of morphological characteristics in prey selection. J Fish Biol 50:324–340

Landigham JH, Sturdevant MV, Brodeur RD (1998) Feeding habits of juvenile Pacific salmon in marine waters of southeastern Alaska and northern British Columbia. Fish Bull 96:285–302

Lannin R, Hovel K (2011) Variable prey density modifies the effects of seagrass habitat structure on predator−prey interactions. Mar Ecol Prog Ser 442:59–70

Lazzaro X (1987) A review of planktivorous fishes: Their evolution, feeding behaviours, selectivities, and impacts. Hydrobiologia 146:97–167

Ledgerwood RD, Ryan BA, Dawley EM, Nunnallee EP, Ferguson JW (2004) A surface trawl to detect migrating juvenile salmonids tagged with passive integrated transponder tags. North Am J Fish Manag 24:440–451

Leising AW, Yen J (1997) Spacing mechanisms within light-induced copepod swarms. Mar Ecol Prog Ser:127–135

Letcher BH, Rice JA (1997) Prey patchiness and larval fish growth and survival: inferences from an individual-based model. Ecol Model 95:29–43

Levings CD (2016) Ecology of salmonids in estuaries around the world: adaptations, habitats, and conservation. UBC Press, Vancouver ; Toronto

Levings CD, McAllister CD, Chang BD (1986) Differential use of the Campbell River Estuary, British Columbia by wild and hatchery-reared juvenile Chinook salmon (*Oncorhynchus tshawytscha*). Can J Fish Aquat Sci 43:1386–1397

Levy DA (1990) Sensory mechanism and selective advantage for diel vertical migration in juvenile sockeye salmon, *Oncorhynchus nerka*. Can J Fish Aquat Sci 47:1796–1802

Ljungberg P, Hasper TB, Nilsson PA, Persson A (2013) Effects of small-scale habitat fragmentation on predator–prey interactions in a temperate sea grass system. Mar Biol 160:667–675

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JB (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806–1809

Lucas LV, Koseff JR, Cloern JE, Monismith SG, Thompson JK (1999) Processes governing phytoplankton blooms in estuaries. I: The local production-loss balance. Mar Ecol Prog Ser 187:1–15

Lucas LV, Koseff JR, Monismith SG, Cloern JE, Thompson JK (1999) Processes governing phytoplankton blooms in estuaries. II: The role of horizontal transport. Mar Ecol Prog Ser:17–30

Lugert V, Thaller G, Tetens J, Schulz C, Krieter J (2016) A review on fish growth calculation: multiple functions in fish production and their specific application. Rev Aquac 8:30–42

Macdonald JS, Birtwell IK, Kruzynski GM (1987) Food and habitat utilization of juvenile salmonids in the Campbell River estuary. Can J Fish Aquat Sci 44:1233–1246

Mackas DL, Greve W, Edwards M, Chiba S, Tadokoro K, Eloire D, Mazzocchi MG, Batten S, Richardson AJ, Johnson C, Head E, Conversi A, Peluso T (2012) Changing zooplankton seasonality in a changing ocean: Comparing time series of zooplankton phenology. Prog Ocean 97:31–62

Magnusson A, Hilborn R (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

Manzer J (1969) Stomach Contents of Juvenile Pacific Salmon in Chatham Sound and Adjacent Waters. J Fish Res Board Can 26:2219–2223

Marques S, Pardal A, Pereira M, Gonçalves F, Marques J, Azeiteiro U (2007) Zooplankton distribution and dynamics in a temperate shallow estuary. Hydrobiologia 587:213–223

Mauchline J (1998) The Biology of Calanoid Copepods. Academic Press

McCabe GT, Muir WD, Emmett R, Durkin JT (1983) Interrelationships between juvenile salmonids and nonsalmonid fish in the Columbia River estuary. Fish Bull 81:815–826

McClelland J, Valiela I (1998) Changes in food web structure under the influence of increased anthropogenic nitrogen inputs to estuaries. Mar Ecol Prog Ser 168:259–271

McCormick SD, Saunders RL (1987) Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth, and metabolism. In: American Fisheries Society Symposium.p 1–229

McDevitt-Irwin J, Iacarella J, Baum J (2016) Reassessing the nursery role of seagrass habitats from temperate to tropical regions: a meta-analysis. Mar Ecol Prog Ser 557:133–143

McDowall RM (2002) The origin of the salmonid fishes: marine, freshwater... or neither? Rev Fish Biol Fish 11:171–179

McNatt RA, Bottom DL, Hinton SA (2016) Residency and movement of juvenile Chinook salmon at multiple spatial scales in a tidal marsh of the Columbia River estuary. Trans Am Fish Soc 145:774–785

Meador JP (2014) Do chemically contaminated river estuaries in Puget Sound (Washington, USA) affect the survival rate of hatchery-reared Chinook salmon? (D MacLatchy, Ed.). Can J Fish Aquat Sci 71:162–180

Mendes C, Ramos S, Bordalo AA (2014) Feeding ecology of juvenile flounder Platichthys flesus in an estuarine nursery habitat: Influence of prey–predator interactions. J Exp Mar Biol Ecol 461:458–468

Menendez MC, Dutto MS, Piccolo MC, Hoffmeyer MS (2012) The role of the seasonal and semi-diurnal tidal cycle on mesozooplankton variability in a shallow mixed estuary (Bahia Blanca, Argentina). ICES J Mar Sci 69:389–398

Menge BA (2000) Top-down and bottom-up community regulation in marine rocky intertidal habitats. J Exp Mar Biol Ecol 250:257–289

Miller TW, Brodeur RD (2007) Diets of and trophic relationships among dominant marine nekton within the northern California Current ecosystem. Fish Bull 105:548–559

Miller J, Gray A, Merz J (2010) Quantifying the contribution of juvenile migratory phenotypes in a population of Chinook salmon *Oncorhynchus tshawytscha*. Mar Ecol Prog Ser 408:227–240

Miller BA, Sadro S (2003) Residence time and seasonal movements of juvenile coho salmon in the ecotone and lower estuary of Winchester Creek, South Slough, Oregon. Trans Am Fish Soc 132:546–559

Moore JW, Carr-Harris C, Gottesfeld AS, MacIntyre D, Radies D, Cleveland M, Barnes C, Joseph W, Williams G, Gordon J, Shepert B (2015) Selling First Nations down the river. Science 349:596–596

Moore J, Gordon J, C C-H, Gottesfeld A, Wilson S, Russell J (2016) Assessing estuaries as stopover habitats for juvenile Pacific salmon. Mar Ecol Prog Ser 559:201–215

Morgan CA, Cordell JR, Simenstad CA (1997) Sink or swim? Copepod population maintenance in the Columbia River estuarine turbidity-maxima region. Mar Biol 129:309–317

Mortensen D, Wertheimer A, Taylor S, Landigham J (2000) The relation between early marine growth of pink salmon, *Oncorhynchus gorbuscha*, and marine water temperature, secondary production, and survival to adulthood. Fish Bull 98:319–335

Moss JH, Beauchamp DA, Cross AD, Myers KW, Farley EV, Murphy JM, Helle JH (2005) Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. Trans Am Fish Soc 134:1313–1322

Murphy ML, Koski KV, Lorenz JM, Thedinga JF (1997) Downstream migrations of juvenile Pacific salmon (*Oncorhynchus* spp.) in a glacial transboundary river. Can J Fish Aquat Sci 54:2837–2846

Myers KW, Horton HF (1982) Temporal use of an Oregon estuary by hatchery and wild juvenile salmon. In: Kennedy VS (ed) Estuarine Comparisons. Academic Press, p 377–392

Nagelkerken I, Sheaves M, Baker R, Connolly RM (2015) The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. Fish Fish 16:362–371

Nakagawa S (2004) A farewell to Bonferroni: the problems of low statistical power and publication bias. Behav Ecol 15:1044–1045

Neuheimer AB, Taggart CT (2007) The growing degree-day and fish size-at-age: the overlooked metric. Can J Fish Aquat Sci 64:375–385

Nicieza AG, Metcalfe NB (1997) Growth compensation in juvenile Atlantic salmon: Responses to depressed temperature and food availability. Ecology 78:2385–2400

NOAA (2018) Coho Salmon - Protected | NOAA Fisheries.

Nohara D, Kitoh A, Hosaka M, Oki T (2006) Impact of climate change on river discharge projected by multimodel ensemble. J Hydrometeorol 7:1076–1089

Northcote T, Gregory R, Magnhagen C (2007) Contrasting space and food use among three species of juvenile Pacific salmon (*Oncorhynchus*) cohabiting tidal marsh channels of a large estuary. Fisheries and Oceans Canada

Osgood G (2016) Historical diets of forage fish and juvenile Pacific salmon in the Strait of Georgia, 1966–1968. Mar Coast Fish Dyn Manag Ecosyst Sci 8:580–594

Palmer MA (1988) Dispersal of marine meiofauna: a review and conceptual model explaining passive transport and active emergence with implications for recruitment. Mar Ecol Prog Ser 48:81–91

Parker RR, Larkin PA (1959) A concept of growth in fishes. J Fish Res Board Can 16:721–745

Pearcy WG (1992) Ocean ecology of North Pacific salmonids. University of Washington Press

Pearcy WG, Wilson CD, Chung AW, Chapman JW (1989) Residence times, distribution, and production of juvenile chum salmon, *Oncorhynchus keta*, in Netarts Bay, Oregon. Fish Bull 87:553–568

Perillo GME (1995) Definitions and geomorphologic classifications of estuaries. Dev Sedimentol 53:17–47

Pickard D, Porter M, Olson E, Connors B, Kellock K, Jones E, Connors K (2015) Skeena River Estuary Assessment: Technical Report. Pacific Salmon Foundation

Pitcher TJ, Parrish JK (1993) Functions of shoaling behaviour in teleosts. In: Pitcher TJ (ed) Behaviour of Teleost Fishes. Springer Netherlands, Dordrecht, p 363–439

Pitchford WJ (2001) Prey Patchiness, Predator Survival and Fish Recruitment. Bull Math Biol 63:527–546

Price M, Glickman B, Reynolds J (2013) Prey Selectivity of Fraser River Sockeye Salmon during Early Marine Migration in British Columbia. T Am Fish Soc 142:1126–1133

Quinn TP (2005) The behavior and ecology of Pacific salmon and trout. Bethesda, Md: American Fisheries Society

Reese C, Hillgruber N, Sturdevant M, Wertheimer A, Smoker W, Focht R (2009) Spatial and temporal distribution and the potential for estuarine interactions between wild and hatchery chum salmon (*Oncorhynchus keta*) in Taku inlet, Alaska. Fish Bull 107:433–450

Roegner G, Weitkamp L, Teel D (2016) Comparative use of shallow and deepwater habitats by juvenile Pacific salmon in the Columbia River estuary prior to ocean entry. Mar Coast Fish 8:536–552

Romey WL (1996) Individual differences make a difference in the trajectories of simulated schools of fish. Ecol Model 92:65–77

R.S.C. (1985) Fisheries Act. Government of Canada, Ottawa, ON

Rudstam LG, Aneer G, Hildén M (1994) Top-down control in the pelagic Baltic ecosystem. Dana 10:105–129

Satterthwaite W, Carlson S, Allen-Moran S, Vincenzi S, Bograd S, Wells B (2014) Match-mismatch dynamics and the relationship between ocean-entry timing and relative ocean recoveries of Central Valley fall run Chinook salmon. Mar Ecol Prog Ser 511:237–248

Scott DC, Arbeider M, Gordon J, Moore JW (2016) Flood control structures in tidal creeks associated with reduction in nursery potential for native fishes and creation of hotspots for invasive species. Can J Fish Aquat Sci 73:1138–1148

Selleslagh J, Blanchet H, Bachelet G, Lobry J (2015) Feeding habitats, connectivity and origin of organic matter supporting fish populations in an estuary with a reduced intertidal area assessed by stable isotope analysis. Estuaries Coasts:1431–1447

Selleslagh J, Lesourd S, Amara R (2012) Comparison of macrobenthic assemblages of three fish estuarine nurseries and their importance as foraging grounds. J Mar Biol Assoc U K 92:85–97

Sharpe C (2017) Abiotic and biotic dimensions of habitat for juvenile salmon and other fishes in the Skeena River estuary. Master of Science, Simon Fraser University

Sheaves M, Baker R, Nagelkerken I, Connolly RM (2015) True value of estuarine and coastal nurseries for fish: Incorporating complexity and dynamics. Estuaries Coasts 38:401–414

Sherwood CR, Jay DA, Bradford Harvey R, Hamilton P, Simenstad CA (1990) Historical changes in the Columbia River Estuary. Prog Oceanogr 25:299–352

Shreffler DK, Simenstad CA, Thom RM (1990) Temporary residence by juvenile salmon in a restored estuarine wetland. Can J Fish Aquat Sci 47:2079–2084

Sibert J (1979) Detritus and juvenile salmon produciton in the Nanaimo Estuary: II. Meiofauna available as food to juvenile chum salmon (*Oncorhynchus keta*). J Fish Res Board Can 36:497–503

Sih A, Englund G, Wooster D (1998) Emergent impacts of multiple predators on prey. Trends Ecol Evol 13:350–355

Simenstad CA, Burke JL, O’Connor JE, Cannon C, Heatwole DW, Ramirez MF, Waite IR, Counihan TD, Jones KL (2011) Columbia River Estuary Ecosystem Classification— Concept and Application. U.S. Geological Survey Open-File Report 2011-1228

Simenstad CA, Cordell JR (2000) Ecological assessment criteria for restoring anadromous salmonid habitat in Pacific Northwest estuaries. Ecol Eng 15:283–302

Simenstad CA, Fresh KL, Salo EO (1982) The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: an unappreciated function. In: Estuarine comparisons. Elsevier, p 343–364

Sims DW, Southall EJ, Humphries NE, Hays GC, Bradshaw CJA, Pitchford JW, James A, Ahmed MZ, Brierley AS, Hindell MA, Morritt D, Musyl MK, Righton D, Shepard ELC, Wearmouth VJ, Wilson RP, Witt MJ, Metcalfe JD (2008) Scaling laws of marine predator search behaviour. Nature 451:1098–1102

Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull Mar Sci 60:1129–1157

Sosiak AJ, Randall RG, McKenzie JA (1979) Feeding by hatchery-reared and wild Atlantic salmon (*Salmo salar*) parr in streams. J Fish Res Board Can 36:1408–1412

Steinarsdóttir MB, Ingólfsson A, Ólafsson E (2010) Field evidence of differential food utilization of phytal harpacticoids collected from Fucus serratus indicated by δ13C and δ15N stable isotopes. Estuar Coast Shelf Sci 88:160–164

Swain DP, Riddell BE (1990) Variation in agonistic behavior between newly emerged juveniles from hatchery and wild populations of coho salmon, *Oncorhynchus kisutch*. Can J Fish Aquat Sci 47:566–571

Taylor HF (1921) Deductions concerning the air bladder and the specific gravity of fishes. Bull US Bur Commer Fish 38:121–126

Taylor EB (1990) Environmental correlates of life-history variation in juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). J Fish Biol 37:1–17

Taylor EB (1991) A review of local adaptation in Salmonidac, with particular reference to Pacific and Atlantic salmon. Aquaculture 98:185–207

Telesh IV, Khlebovich VV (2010) Principal processes within the estuarine salinity gradient: A review. Mar Pollut Bull 61:149–155

Thorne K, MacDonald G, Guntenspergen G, Ambrose R, Buffington K, Dugger B, Freeman C, Janousek C, Brown L, Rosencranz J, Holmquist J, Smol J, Hargan K, Takekawa J (2018) U.S. Pacific coastal wetland resilience and vulnerability to sea-level rise. Sci Adv 4:1–10

Thorpe JE (1989) Developmental variation in salmonid populations. J Fish Biol 35:295–303

Thorpe J (1994) Salmonid fishes and the estuarine environment. Estuaries 17:76–93

Thorsteinson FV (1962) Herring predation on pink salmon fry in a Southeastern Alaska estuary. Trans Am Fish Soc 91:321–323

Tommasi DA, Routledge RD, Hunt BP, Pakhomov EA (2014) The seasonal development of the zooplankton community in a British Columbia (Canada) fjord during two years with different spring bloom timing. Mar Biol Res 9:129–144

Trites RW (1956) The oceanography of Chatham Sound, British Columbia. J Fish Board Can 13:385–434

Tschaplinski PJ (1987) The use of estuaries as rearing habitats by juvenile coho salmon. Department of Fisheries and Oceans Canada, Research Branch, Pacifc Biological Station, Nanaimo, British Columbia.

Verspoor E (1988) Reduced genetic variability in first-generation hatchery populations of Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci 45:1686–1690

Viscido SV, Parrish JK, Grünbaum D (2004) Individual behavior and emergent properties of fish schools: a comparison of observation and theory. Mar Ecol Prog Ser 273:239–250

Viswanathan GM, Afanasyev V, Buldyrev SV, Murphy EJ, Prince PA, Stanley HE (1996) Lévy flight search patterns of wandering albatross. Nature 381:413–415

Von Bertalanffy L (1938) A quantitative theory or organic growth (inquiries on growth laws. II). Hum Biol 10:181–213

Wallace M, Allen S (2007) Juvenile salmonid use of the tidal portions of selected tributaries to Humboldt Bay, California. Final Report for Contract P0410504. California Department of Fish and Game, Sacramento, CA

Wallace M, Ricker S, Garwood J, Frimodig A, Allen S (2015) Importance of the stream-estuary ecotone to juvenile coho salmon (*Oncorhynchus kisutch*) in Humboldt Bay, California. Calif Fish Game 101:241–266

Walsworth TE, Schindler DE, Griffiths JR, Zimmerman CE (2015) Diverse juvenile life-history behaviours contribute to the spawning stock of an anadromous fish population. Ecol Freshw Fish 24:204–213

Walters CJ, Juanes F (1993) Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. Can J Fish Aquat Sci 50:2058–2070

Waples RS, Teel DJ (1990) Conservation genetics of Pacific salmon I. temporal changes in allele frequency. Conserv Biol 4:144–156

Ware DM (1973) Risk of epibenthic prey to predation by rainbow trout (*Salmo gairdneri*). J Fish Res Board Can 30:787–797

Weitkamp LA (2008) Buoyancy regulation by hatchery and wild coho salmon during the transition from freshwater to marine environments. Trans Am Fish Soc 137:860–868

Weitkamp LA, Goulette G, Hawkes J, Michael O, Lipsky C (2014) Juvenile salmon in estuaries: comparisons between North American Atlantic and Pacific salmon populations. Rev Fish Biol Fish 24:713–736

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Annu Rev Ecol Syst 15:393–425

Werner EE, Hall DJ (1988) Ontogenetic habitat shifts in bluegill: The foraging rate-predation risk trade-off. Ecology 69:1352–1366

Werner EE, Mittelbach GG, Hall DJ, Gilliam JF (1983) Experimental tests of optimal habitat use in fish: The role of relative habitat profitability. Ecology 64:1525–1539

Weybright AD, Giannico GR (2018) Juvenile coho salmon movement, growth and survival in a coastal basin of southern Oregon. Ecol Freshw Fish 27:170–183

Willette TM (2001) Foraging behaviour of juvenile pink salmon (*Oncorhynchus gorbuscha*) and size-dependent predation risk. Fish Oceanogr 10:110–131

Yang LH, Bastow JL, Spence KO, Wright AN (2008) What Can We Learn from Resource Pulses? Ecology 89:621–634

Appendix A.

Supporting Material for Chapter 2

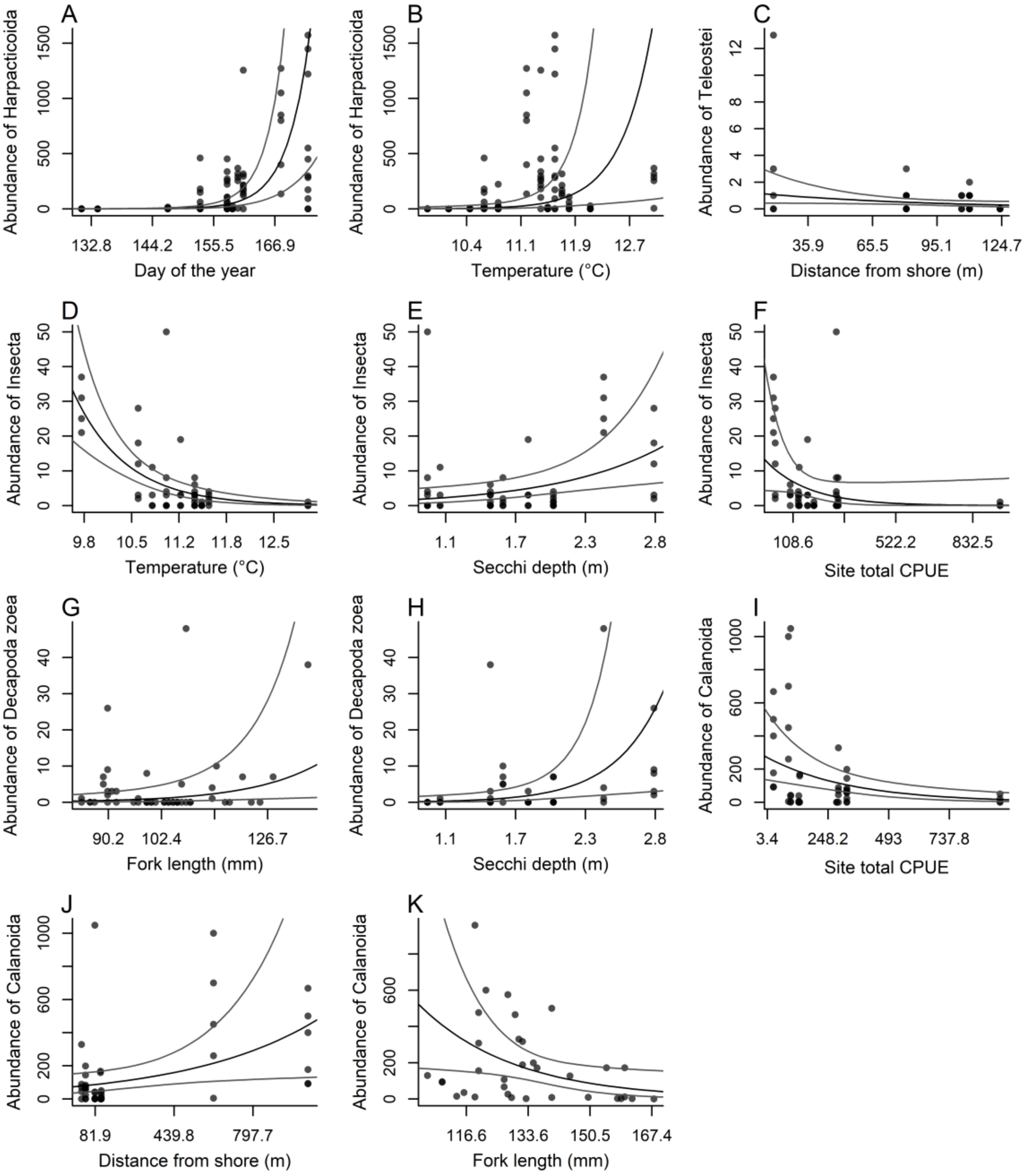


Figure A1. **Predicted relationships between the abundance of several important prey items in diet samples of sockeye salmon (A,B), coho salmon (A-H), Pacific herring, (I,J), and surf smelt (K) with biophysical aspects of the seascape or the individual fish within the Skeena estuary, including 95% confidence intervals calculated from their respective GLMMs.**

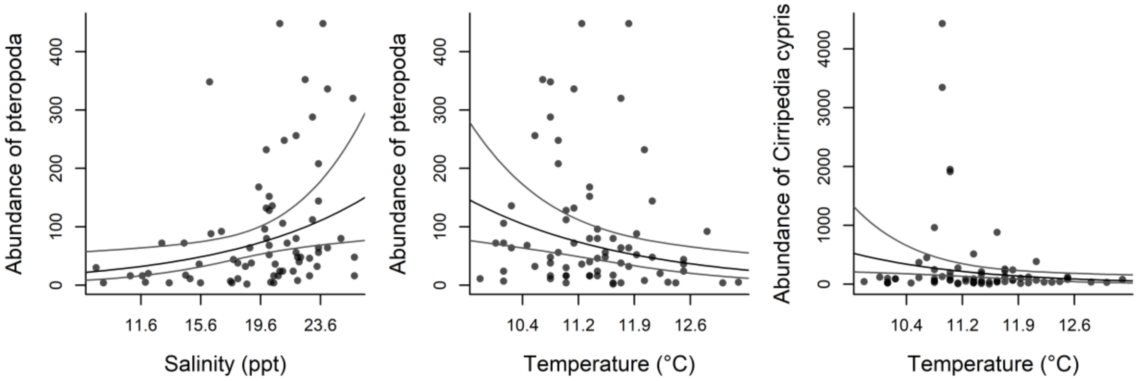


Figure A2. Predicted relationships between several important prey items in the environment and biophysical aspects of the seascape within the Skeena estuary, including 95% confidence intervals calculated from their respective GLMMs.

Table A1. **A non-exhaustive literature overview of juvenile salmon (primarily for Coho and Sockeye), Pacific herring, and surf smelt diets in estuary and coastal environments in North America.**

Estuary or Coastal	River or Region	Publication	Predator	Typical prey, reported in order of most to least consumed
Estuary	Campbell River	(Macdonald et al. 1987)	Chinook	Harpacticoida, Cumacea, Insecta
			Chum	Harpacticoida, Cumacea, Calanoida
			Coho	Cumacea, Harpacticoida
		(Bottom and Jones 1990)	Chinook	corophium (Amphipoda), Insecta, Daphnia,
		(Brodeur et al. 2015)	Chinook	Teleostei, Decapoda, Euphausiacea, Amphipoda (Hyperiidea), Pteropoda
	Fraser River	(John et al. 1992)	Pacific herring	Copepoda, Amphipoda, Cladocera, Mollusca, Euphausiia
		(Northcote et al. 2007)	Chinook	Insecta, Amphipoda, Harpacticoida
			Chum	Insecta, Amphipoda, Harpacticoida
			Pink	Harpacticoida
	Nanaimo River	(Healey 1979)	Chum	Harpacticoida, Mysida, Amphipoda (Gammaridea)
	Prince William Sound	(Foy and Norcross 1999)	Pacific herring	Oikopleura, Calanoida, Teleostei eggs, Cirripedia cyprid
	Puget Sound	(Bollens et al. 2010)	Chinook	Euphausiacea, Decapoda, Arachnida
			Chinook	Teleostei, Euphausiacea, Amphipoda (Gammaridea), Insecta, Arachnida
			Chum	Insecta, Larvacea, Arachnida, Copepoda
			Chum	Insecta, Teleostei, Amphipoda (Hyperiidea), Decapoda
			Chum	Larvacea, Amphipoda (Hyperiidea), Euphausiacea
			Coho	Decapoda, Euphausiacea, Amphipoda (Gammaridea)
			Pink	Euphausiacea, Amphipoda (Gammaridea), Copepoda, Arachnida
			Pink	Teleostei, Pteropoda, Copepoda, Insecta, Decapoda
		(Brennan et al. 2004)	Chinook	Insecta, Teleostei, Polychaeta, Amphipoda (Hyperiidea), Decapoda
			Coho	Teleostei, Decapoda, Calanoida, Amphipoda (Hyperiidea), Euphausiacea
		(Simenstad et al. 1982)	Chinook	Insecta, Decapoda, Teleostei, Amphipoda (Gammaridea), Cumacea
			Chum	Harpacticoida, Calanoida, Decapoda, Larvacea,

Estuary or Coastal	River or Region	Publication	Predator	Typical prey, reported in order of most to least consumed
			Coho	Decapoda, Amphipoda (Gammaridea), Euphausiacea, Teleostei
			Pink	Calanoida, Larvacea
			Sockeye	Euphausiacea, Mysida, Decapoda
	Rivers Inlet	(Ajmani 2011)	Sockeye	Cirripedia, Teleostei, Calanoida, Cladocera, Bivalvia
	Washington and Oregon	(David et al. 2016)	Chinook	Insecta, Amphipoda, crustaceans (Cumacea, Mysida, Copepoda)
Coastal	Auke Bay	(Coyle and Paul 1992)	Pacific herring	euphausiid eggs, barnacle nauplii, Oikopleura, calanoid Copepoda
			Sockeye	Oikopleura, Cirripedia cyprids
	Bristol Bay	(Carlson 1976)	Sockeye	Calanoida, Teleostei, Insecta
		(Farley et al. 2007)	Sockeye	Teleostei, Euphausiacea
			Sockeye	Teleostei, Euphausiacea
	Broughton Archipelago	(Gulbransen 2009)	Chum	Decapoda, Calanoida, Insecta
			Chum	Insecta, Harpacticoida, Calanoida
			Pink	Copepoda nauplii, Calanoida, Decapoda
			Pink	Calanoida, Harpacticoida, Cirripedia cyprid
	California Current System	(Brodeur et al. 2011)	Chinook	Teleostei, Decapoda, Euphausiacea, Amphipoda
			Coho	Teleostei, Decapoda, Euphausiacea, Amphipoda
		(Daly et al. 2009a)	Chinook	Teleostei, Decapoda, Copepoda,
			Coho	Teleostei, Decapoda, Euphausiacea,
			Coho	Teleostei
		(Miller and Brodeur 2007)	Chinook	Teleostei, Euphausiacea, Amphipoda (Hyperiidea), Crustacea
			Chinook	Teleostei, Euphausiacea, Crustacea
			Chum	Teleostei, Crustacea
			Coho	Teleostei, Euphausiacea
			Pacific Herring	Euphausiacea, Amphipoda (Hyperiidea), Crustacea
			Surf Smelt	Brachyura, Amphipoda (Hyperiidea), Cnidaria, Crustacea

Estuary or Coastal	River or Region	Publication	Predator	Typical prey, reported in order of most to least consumed
	Chatham Sound	(Manzer 1969)	Chum	Copepoda, Oikopleura
			Coho	Teleostei, Insecta, Decapoda, Amphipoda
			Pink	Copepoda, Oikopleura
			Sockeye	Copepoda, Teleostei, Oikopleura
	Gulf of Alaska	(Auburn and Ignell 1996)	Chum	Euphausiacea, Calanoida, Teleostei
			Coho	Teleostei, Euphausiacea
			Pink	Euphausiacea, Calanoida, Teleostei
			Sockeye	Teleostei, Euphausiacea, Amphipoda (Hyperiidea), Calanoida,
	Juan de Fuca	(Pool et al. 2008)	Coho	Teleostei, Euphausiacea, Decapoda
	Salish Sea	(Osgood 2016)	Chinook	Teleostei, Insecta, Decapoda, Calanoida
			Chum	Calanoida, Insecta, Teleostei, Larvacea, Amphipoda
			Coho	Teleostei, Decapoda, Insecta, Amphipoda, Euphausiacea
			Eulachon	Calanoida, Cladocerans
			Herring	Calanoida, Cladocerans, Teleostei, Larvacea
			Pink	Calanoida, Insecta, Amphipoda
			Sockeye	Calanoida, Insecta, Teleostei, Larvacea
	Southeast Alaska	(Jaenicke et al. 1984)	Chinook	Euphausiacea, Amphipoda (Hyperiidea)
			Chum	Euphausiacea, Amphipoda (Hyperiidea), Copepoda,
			Coho	Teleostei, Euphausiacea, Amphipoda (Hyperiidea), Decapoda
			Pink	Euphausiacea, Copepoda, Amphipoda (Hyperiidea)
			Sockeye	Euphausiacea, Copepoda, Amphipoda (Hyperiidea)
	Southeast Alaska & Northern BC	(Landigham et al. 1998)	Chinook	Teleostei, Euphausiacea
			Chum	Teleostei, Oikopleura, Amphipoda (Hyperiidea)
			Coho	Teleostei
			Pink	Amphipoda (Hyperiidea), Teleostei, Oikopleura

Estuary or Coastal	River or Region	Publication	Predator	Typical prey, reported in order of most to least consumed
			Sockeye	Teleostei, Amphipoda (Hyperiidea)
	Straight of Georgia	(Price et al. 2013)	Sockeye	Copepoda, Euphausiacea, Amphipoda, Decapoda, Teleostei
	Vancouver Island	(Godin 1981)	Pink	Harpacticoida, Copepoda nauplii, Cirripedia cyprid, Calanoida
	Whole Range	(Brodeur 1990)	Chinook	Teleostei, Euphausiacea, Amphipoda (Hyperiidea), Cephalopoda, Copepoda
			Chum	Calanoida, Euphausiacea, Amphipoda (Hyperiidea), Larvacea, Chaetognaths
			Coho	Teleostei, Euphausiacea, Decapoda, Amphipoda (Hyperiidea), Amphipoda
			Pink	Teleostei, Copepoda, Amphipoda, Euphausiacea, Pteropoda
			Sockeye	Euphausiacea, Amphipoda (Hyperiidea), Copepoda, Pteropoda, Teleostei
		(Brodeur et al. 2007)	Chinook	Teleostei, Decapoda, Amphipoda (Hyperiidea), Euphausiacea, Insecta
			Chum	Pteropoda, Tunicata, Copepoda, Teleostei,
			Coho	Teleostei, Euphausiacea, Decapoda, Amphipoda (Hyperiidea)
			Pink	Pteropoda, Teleostei, Euphausiacea, Amphipoda (Hyperiidea), Copepoda
			Sockeye	Euphausiacea, Decapoda, Copepoda, Teleostei

Table A2. **Intercept and slope (number/g) of linear regressions of known abundance on weight from our diet samples used to estimate abundance based on weight where diet contents could be identified to taxonomic group but were broken into parts.**

Prey group	Intercept	Slope
Amphipoda	1.791857	102.3156
Cirripedia Adults	3.460142	4667.708
Cirripedia Cyprid	6.061728	12229.02
Larval Fish	0.998919	5.629936
Pteropoda	6.923784	1286.676
Terrestrial Insect	2.744849	529.6775
Oikopleura	1.267107	11630.62
Decapoda Zoea	5.076472	268.0916

Table A3. **Number of non-empty diet samples for coho salmon, sockeye salmon, Pacific herring, and surf smelt**

Day of year	Site	Set #	Coho	Sockeye	Herring	Smelt
131	Porpoise Channel	1	4	4		5
134	Lelu rock	2		10	10	5
141	Flora 1	3	2	2		
141	Kitson	4		10	10	
145	Inverness Lelu	5	9		3	
147	Flora 1	6	5	6		
153	Porpoise Channel	7	5	10		
153	Kinahans West	8		10		
158	Inverness Lelu	9	5	5	5	5
158	Inverness NP	10	5	11	3	5
158	Flora 2 eg	11		5	5	
159	Kinahans Open Water	12		11	5	
160	Flora 1	13	3	5	4	5
161	Kitson	14	4	5	5	5
161	Kitson Open Water	15		5		
168	Flora 1	16	5	6		
173	Flora 1	17	5	11	5	5

Table A4. **Prey species chosen to analyze individual diet variability.**

Fish Species	Prey Species
Coho	Insects, Juvenile and larval fish, Crab Zoea
Sockeye	Harpacticoid and Calanoid Copepods, Barnacle Cyprids
Herring	Calanoid Copepods, Barnacle Cyprids
Smelt	Calanoid Copepods

Table A5. **Hypothesis between abundance of important prey in a fish's diet and biophysical covariates.**

Covariate	Positive relationship	Negative relationship	Example(s)
Length (mm)	Length has a positive relationship with gape. Bigger gape allows for more easily caught prey	Bigger gape allows to target larger prey, small prey are targeted less	(Arrhenius 1996; Moss and Beauchamp 2007; Daly et al. 2009b)
Secchi depth (cm)	Secchi depth is negatively related to turbidity. Less turbidity allows fish to see and capture prey more efficiently	More turbidity means more visible prey are easier to capture than less visible prey OR there is less predator avoidance pressure so fish are more bold	(Berg and Northcote 1985; Gregory and Northcote 1993; De Robertis et al. 2003)
Temperature (°C)	Warmer water correlates with higher metabolic demand which requires more prey consumption	Cold water can be from river waters or upwelled water. Cold river waters could bring more insects and cold upwelled waters could bring generally higher abundances of marine prey.	(Brett et al. 1969; Wang et al. 2015)
Distance from shore (m)	For pelagic species, distance from shore is correlated with depth. More available pelagic species/may have less opportunity to consume benthic species	Closer to shore, eat more benthic/epiphytic species as well as terrestrial derived species (insects).	

Covariate	Positive relationship	Negative relationship	Example(s)
Abundance of all species (CPUE site total)	Using social knowledge, i.e. a bigger school will aggregate over a bigger prey patch OR more individuals means have to invest less time into vigilance from predators	Increased competition, need to either diversify prey or prey field has been consumed so quickly that there are less of specific prey in stomach	(Pitcher et al. 1982; Morgan and Colgan 1987)
Day of year	If a prey's abundance peaks late, Could also be a proxy for some other unkown variable	If a prey's abundance peaked early.	

Table A6. Hypothesis between abundance of important prey in the environmental and biophysical covariates.

Covariate	Positive direction	Negative direction	Example(s)
-Temperature		Cooler waters often indicate more nutrient rich waters/upwelling, more zooplankton production in cooler water.	(Zhou et al. 2009; Li et al. 2014)
-Salinity	All species in our study area are more saline tolerant, i.e. abundance is typically highest in more saline water		(Telesh and Khlebovich 2010)
-Habitat type	Particular species are known to have associations with eelgrass, open water, shorelines, and sandy bays.	(Relative categorical variable)	(McDevitt-Irwin et al. 2016)

Covariate	Positive direction	Negative direction	Example(s)
-Time of day	In the GLMM framework, this is assuming a monotonic increase in abundance that is correlated with natural phenology	In the GLMM framework, this is assuming a monotonic decrease in abundance that is correlated with natural phenology	

Table A7. Results from likelihood ratio tests of single covariate models against an intercept only null model for the abundance of prey in individual diets. * denotes p-value less than 0.05, ** denotes p-value less than 0.05/6 (Bonferroni correction).

Species - prey relationship	Covariate	p-value
Sockeye - harpacticoida	day of year	0.00001374**
	temperature	0.01003*
	CPUE site total	0.5911
	length	0.7704
	distance from shore	0.8168
	secchi depth	0.8252
Sockeye - calanoida	secchi depth	0.06304
	temperature	0.452
	length	0.4926
	day of year	0.5472
	distance from shore	0.7303
	CPUE site total	0.9581
Sockeye - barnacle cyprid	temperature	0.088
	day of year	0.1645
	CPUE site total	0.3958
	distance from shore	0.5117
	length	0.5307
	secchi depth	0.9052
Coho - fish	distance from shore	0.0000987**
	secchi depth	0.1257
	temperature	0.1683
	day of year	0.1924
	CPUE site total	0.2489

Species - prey relationship	Covariate	p-value
	length	0.4352
Coho - insect	temperature	0.0004646**
	secchi depth	0.01805*
	CPUE site total	0.02687*
	day of year	0.1108
	distance from shore	0.2766
	length	0.9544
Coho - decapod zoea	secci depth	0.01037*
	length	0.01557*
	temperature	0.5988
	CPUE site total	0.709
	distance from shore	0.9302
	day of year	0.9514
Herring - calanoida	CPUE site total	0.01723*
	distance from shore	0.03283*
	secci depth	0.05249
	length	0.2313
	temperature	0.4573
	day of year	0.9503
Herring - barnacle cyprid	CPUE site total	0.07009
	day of year	0.1282
	distance from shore	0.1487
	length	0.3236
	temperature	0.3387
	secci depth	0.563
Smelt - calanoida	length	0.04454*
	secci depth	0.06201
	day of year	0.1495
	CPUE site total	0.2151
	distance from shore	0.4073
	temperature	0.8621

Table A8. **Results from likelihood ratio tests of single covariate models against an intercept only null model for the abundance of prey in the environment. * denotes p-value less than 0.05, ** denotes p-value less than 0.05/5 (Bonferroni correction).**

Prey species	Covariate	p-value
Calanoida	Salinity	0.0001**
	Distance from shore	0.215
	Habitat type	0.4444
	Time of day	0.478
	Temperature	0.9165
Harpactacoida	Habitat type	0.0131*
	Salinity	0.0786
	Distance from shore	0.4911
	Temperature	0.6053
	Time of day	0.6556
Barnacle cypriid	Temperature	0.015*
	Salinity	0.1255
	Habitat type	0.494
	Distance from shore	0.8242
	Time of day	0.9475
Oikopleura	Salinity	0.0000001**
	Time of day	0.1771
	Temperature	0.517
	Distance from shore	0.8377
	Habitat type	0.9239
Pteropoda	Temperature	0.005**
	Salinity	0.0192*
	Distance from shore	0.5675
	Time of day	0.6121
	Habitat type	0.9732

Prey species	Covariate	p-value
Decapod zoea	Distance from shore	0.1476
	Salinity	0.1492
	Temperature	0.3518
	Habitat type	0.3792
	Time of day	0.8598

Appendix A References

Ajmani AM (2011) The growth and diet composition of sockeye salmon smolts in Rivers Inlet, British Columbia. University of British Columbia

Arrhenius F (1996) Diet composition and food selectivity of 0-group herring (*Clupea harengus L.*) and sprat (*Sprattus sprattus (L.)*) in the northern Baltic Sea. 53:701–712

Auburn ME, Ignell SE (1996) Food habits of juvenile salmon in the Gulf of Alaska. N Pac Anadr Fish Comm Bull 2:89–97

Berg L, Northcote TG (1985) Changes in territorial, gill-flaring, and feeding behavior in juvenile coho salmon (*Oncorhynchus kisutch*) following short-term pulses of suspended sediment. Can J Fish Aquat Sci 42:1410–1417

Bollens SM, Hooff R vanden, Butler M, Cordell JR, Frost BW (2010) Feeding ecology of juvenile pacific salmon (*Oncorhynchus* spp.) in a northeast pacific fjord: Diet, availability of zooplankton, selectivity for prey, and potential competition for prey resources. Fish Bull 108:393–407

Bottom DL, Jones KK (1990) Species composition, distribution, and invertebrate prey of fish assemblages in the Columbia River estuary. Prog Ocean 25:243–270

Brennan JS, Higgins KF, Cordell JR, Stamatiou VA (2004) Juvenile salmon composition, timing, distribution, and diet in marine nearshore waters of central Puget Sound in 2001-2002. King County Department of Natural Resources and Parks, Seattle, WA

Brett J, Shelbourn J, Shoop C (1969) Growth rate and body composition of fingerling sockeye salmon , *Oncorhynchus nerka* in relation to temperature and ration size. Fish Res Board Can 26:2363–2394

Brodeur RD (1990) A synthesis of the food habits and feeding ecology of salmonids in marine waters of the North Pacific. Fisheries Reserch Institiute, Washington, Seattle

Brodeur RD, Daly EA, Benkwitt CE, Morgan CA, Emmett RL (2011) Catching the prey: Sampling juvenile fish and invertebrate prey fields of juvenile coho and Chinook salmon during their early marine residence. Fish Res 108:65–73

Brodeur RD, Daly EA, Sturdevant MV, Miller TW, Moss JH, Thiess ME, Trudel M, Weitkamp LA, Armstrong J, Norton EC (2007) Regional comparisons of juvenile salmon feeding in coastal marine waters off the west coast of North America. 57:183–203

Brodeur RD, Morgan CA (2015) Influence of a coastal riverine plume on the cross-shelf variability in hydrography, zooplankton, and juvenile salmon diets. Estuaries Coasts 39:1183–1198

Carlson H (1976) Foods of juvenile sockeye salmon, *Oncorhynchus nerka*, in the inshore coastal waters of Bristol Bay, Alaska 1966-67. Fish Bull 74:458–462

Coyle KO, Paul AJ (1992) Interannual differences in prey taken by capelin, herring, and red salmon relative to zooplankton abundance during the spring bloom in a southeast Alaskan embayment. Fish Oceanogr 1:294–305

Daly E, Brodeur RD, Weitkamp L (2009) Ontogenetic shifts in diets of juvenile and subadult coho and Chinook salmon in coastal marine waters: Important for marine survival? Trans Am Fish Soc 138:1420–1438

David AT, Simenstad C, Cordell J, Toft J, Ellings C, Gray A, Berge H (2016) Wetland loss, juvenile salmon foraging performance, and density dependence in Pacific Northwest estuaries. Estuaries Coasts 39:767–780

De Robertis A, Ryer CH, Veloza A, Brodeur RD (2003) Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. Can J Fish Aquat Sci 60:1517–1526

Farley EV, Murphy JM, Adkison M, Eisner L (2007) Juvenile sockeye salmon distribution, size, condition and diet during years with warm and cool spring sea temperatures along the eastern Bering Sea shelf. J Fish Biol 71:1145–1158

Foy RJ, Norcross BL (1999) Spatial and temporal variability in the diet of juvenile Pacific herring (*Clupea pallasi*) in Prince William Sound, Alaska. 77:10

Godin J-GJ (1981) Daily patterns of feeding behaviour, daily rations, and diets of juvenile pink salmon (*Oncorhynchus gorbuscha*) in two marine bays of British Columbia. Can J Fish Aquat Sci 38:10–15

Gregory RS, Northcote TG (1993) Surface, planktonic, and benthic foraging by juvenile chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. Can J Fish Aquat Sci 50:233–240

Gulbransen COM (2009) Feeding in troubled waters : a comparative diet analysis of pink (*Oncorhynchus gorbuscha*) and chum (*O . keta*) salmon British Columbia by Summer 2014 Approval. Can J Fish Aquat Sci 66:1371–1382

Healey MC (1979) Detritus and juvenile salmon production in the nanaimo estuary: I. Production and feeding rates of juvenile chum salmon (*Oncorhynchus keta*). J Fish Res Board Can 36:488–496

Jaenicke HW, Brodeur RD, Fujii T (1984) Exploratory gillnetting from the Oshoro-maru for juvenile salmonids off Southeastern Alaska, 24-25 July 1982. Bull Fac Fish Hokkaido Univ 35:154–160

Landigham JH, Sturdevant MV, Brodeur RD (1998) Feeding habits of juvenile Pacific salmon in marine waters of southeastern Alaska and northern British Columbia. Fish Bull 96:285–302

Li X, Yu H, Ma C (2014) Zooplankton community structure in relation to environmental factors and ecological assessment of water quality in the Harbin Section of the Songhua River. Chin J Oceanol Limnol 32:1344–1351

Macdonald JS, Birtwell IK, Kruzynski GM (1987) Food and habitat utilization of juvenile salmonids in the Campbell River estuary. Can J Fish Aquat Sci 44:1233–1246

Manzer J (1969) Stomach contents of juvenile Pacific salmon in Chatham Sound and adjacent waters. J Fish Res Board Can 26:2219–2223

McDevitt-Irwin J, Iacarella J, Baum J (2016) Reassessing the nursery role of seagrass habitats from temperate to tropical regions: a meta-analysis. Mar Ecol Prog Ser 557:133–143

Miller TW, Brodeur RD (2007) Diets of and trophic relationships among dominant marine nekton within the northern California Current ecosystem. Fish Bull 105:548–559

Morgan MJ, Colgan PW (1987) The effects of predator presence and shoal size on foraging in bluntnose minnows, *Pimephales notatus*. Environ Biol Fishes 20:105–111

Moss J, Beauchamp D (2007) Functional response of juvenile pink and chum salmon: Effects of consumer size and two types of zooplankton prey. J Fish Biol 70:610–622

Northcote T, Gregory R, Magnhagen C (2007) Contrasting space and food use among three species of juvenile Pacific salmon (*Oncorhynchus*) cohabiting tidal marsh channels of a large estuary. Fisheries and Oceans Canada

Osgood G (2016) Historical diets of forage fish and juvenile Pacific salmon in the Strait of Georgia, 1966–1968. Mar Coast Fish Dyn Manag Ecosyst Sci 8:580–594

Pitcher TJ, Magurran AE, Winfield IJ (1982) Fish in larger shoals find food faster. Behav Ecol Sociobiol 10:149–151

Pool SS, Brodeur RD, Goodman NI, Daly EA (2008) Abundance, distribution, and feeding patterns of juvenile coho salmon (*Oncorhynchus kisutch*) in the Juan de Fuca Eddy. Estuar Coast Shelf Sci 80:85–94

Price M, Glickman B, Reynolds J (2013) Prey selectivity of Fraser River sockeye salmon during early marine migration in British Columbia. T Am Fish Soc 142:1126–1133

Simenstad CA, Fresh KL, Salo EO (1982) The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: an unappreciated function. In: Estuarine comparisons. Elsevier, p 343–364

St. John MA, Macdonald JS, Harrison PJ, Beamish RJ, Choromanski E (1992) The Fraser River plume: some preliminary observations on the distribution of juvenile salmon, herring, and their prey. Fish Oceanogr 1:153–162

Telesh IV, Khlebovich VV (2010) Principal processes within the estuarine salinity gradient: A review. Mar Pollut Bull 61:149–155

Wang H, Chen H, Xue L, Liu N, Liu Y (2015) Zooplankton diel vertical migration and influence of upwelling on the biomass in the Chukchi Sea during summer. Acta Oceanol Sin 34:68–74

Zhou S, Jin B, Guo L, Qin H, Chu T, Wu J (2009) Spatial distribution of zooplankton in the intertidal marsh creeks of the Yangtze River Estuary, China. Estuar Coast Shelf Sci 85:399–406

Appendix B.

Supporting Material for Chapter 3

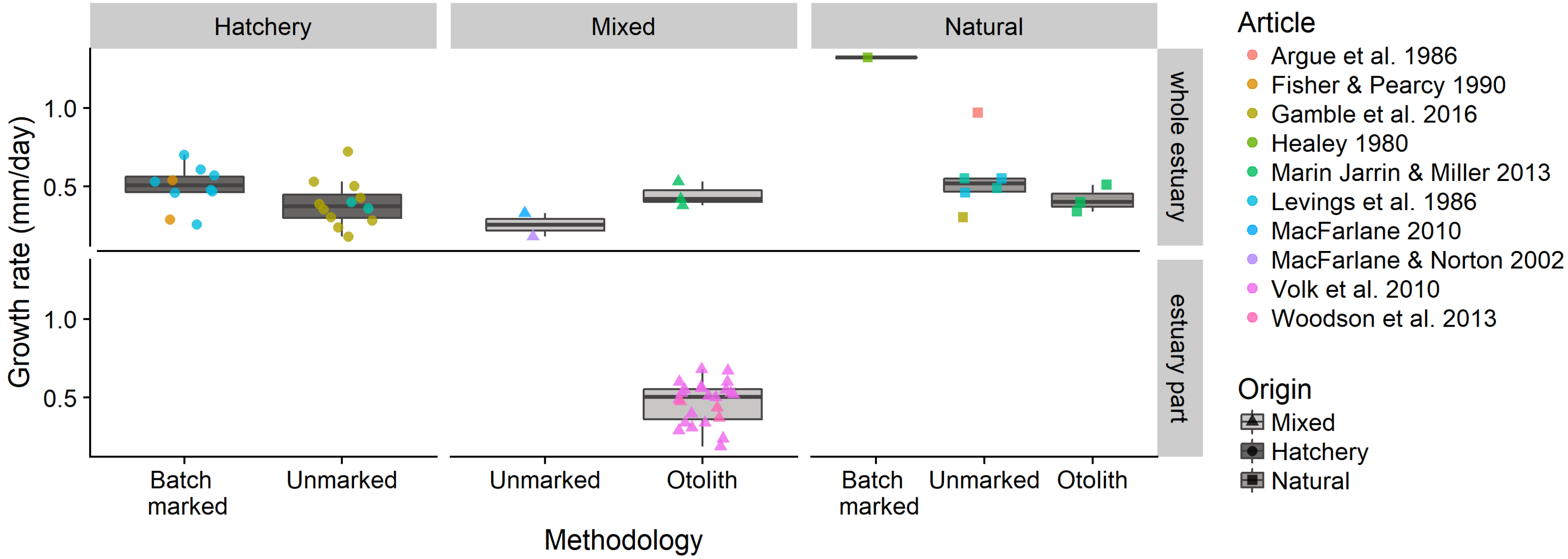


Figure B1. Average (mean or median) 0+ Chinook salmon growth rate estimates (mm/day) from different articles (colours) compared across methodology and separated by spatial extent (whole estuary or estuary part) and origin (hatchery, mixed, or natural).

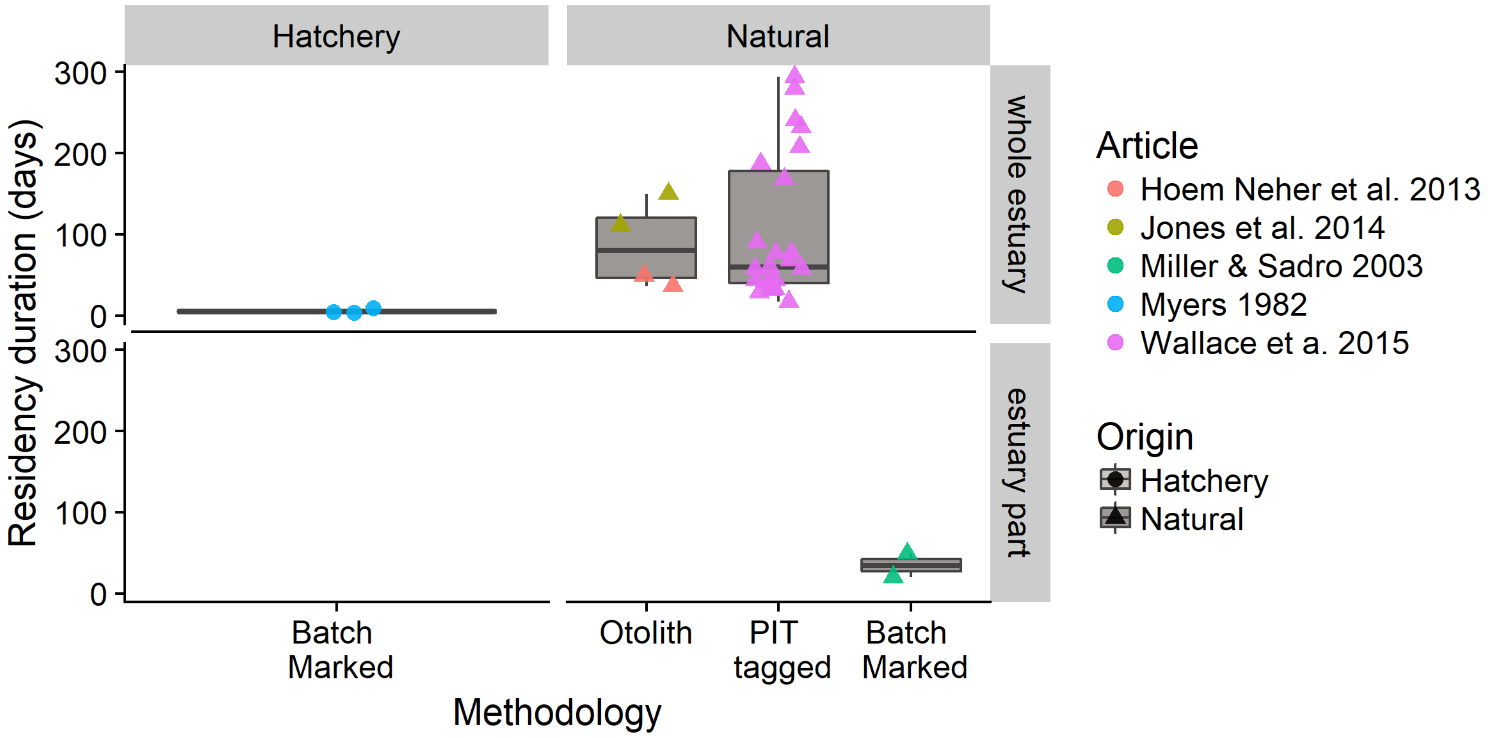


Figure B2. Average (mean or median) 0+ coho residency estimates compared across methodology and separated by spatial extent (whole estuary or estuary part) and origin (hatchery or natural).

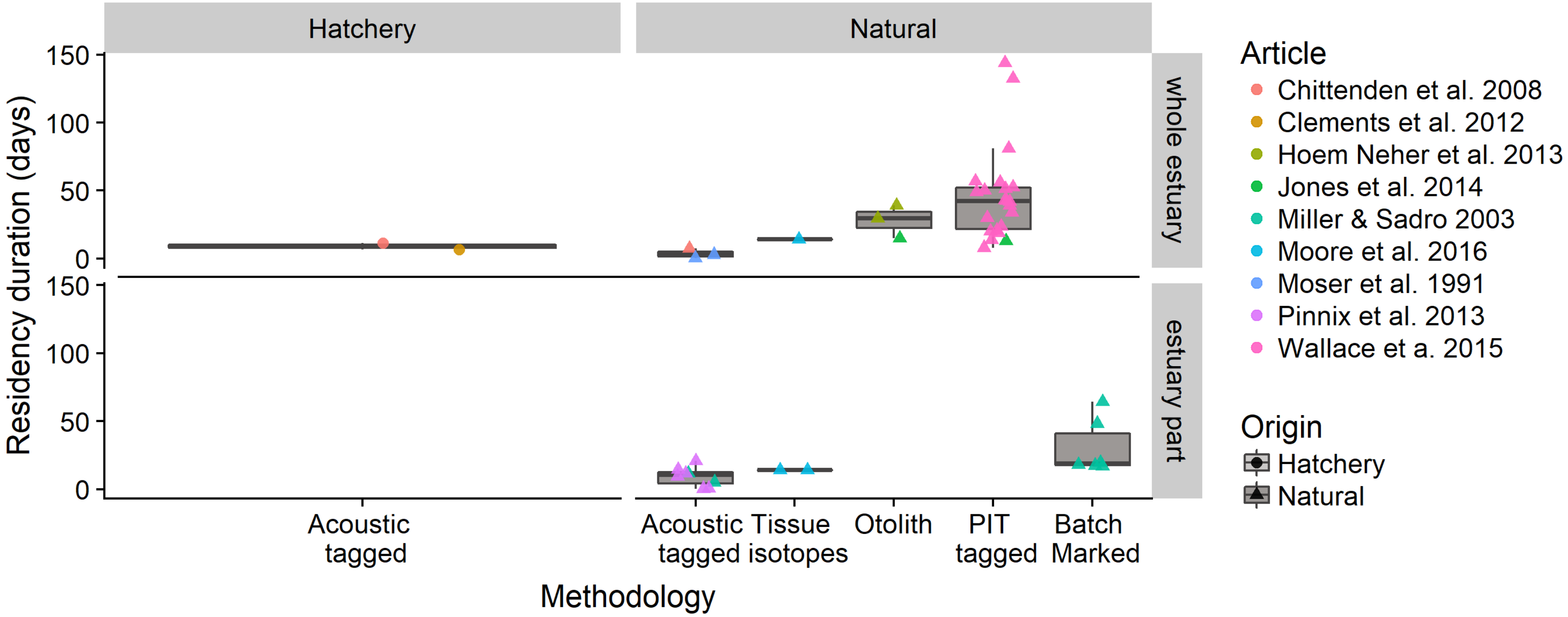


Figure B3. **Average (mean or median) 1+ coho residency estimates compared across methodology and separated by spatial extent (whole estuary or estuary part) and origin (hatchery or natural).**

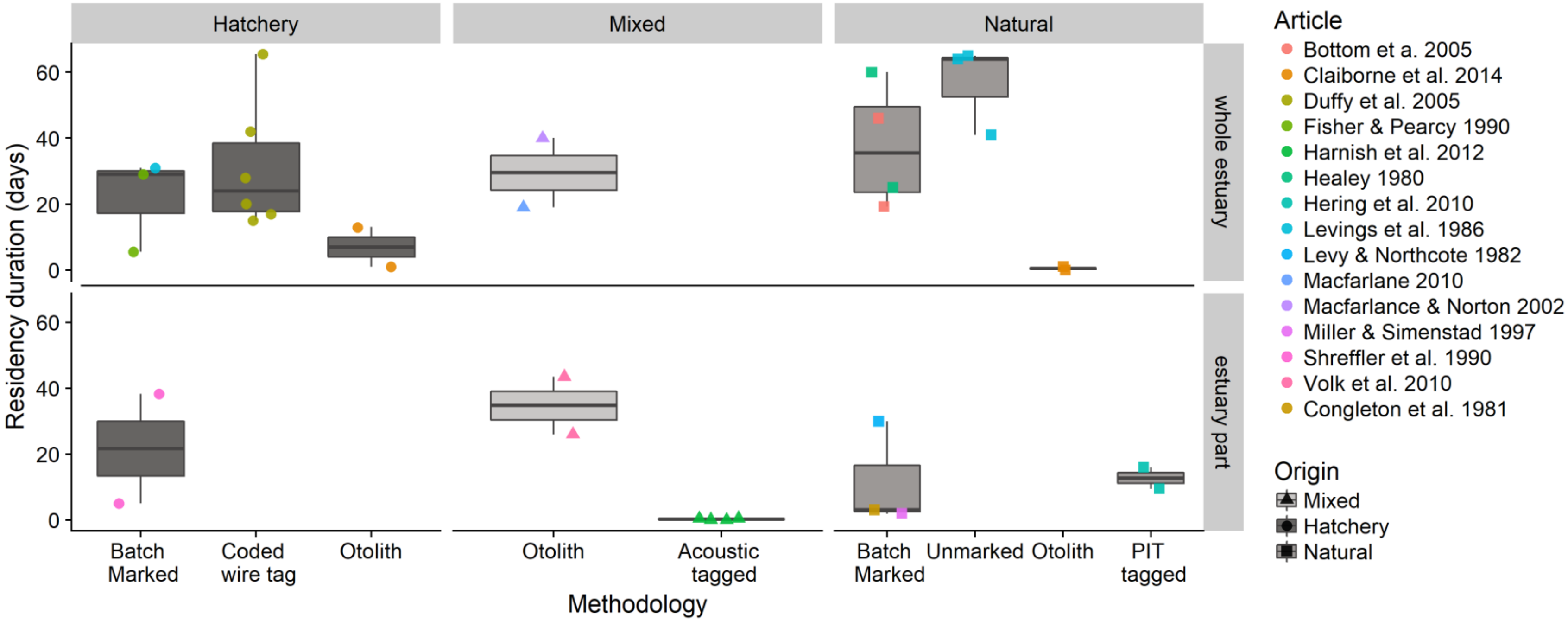


Figure B4. **Average (mean or median) 0+ Chinook residency estimates compared across methodology and separated by spatial extent (whole estuary or estuary part) and origin (hatchery, mixed, or natural).**

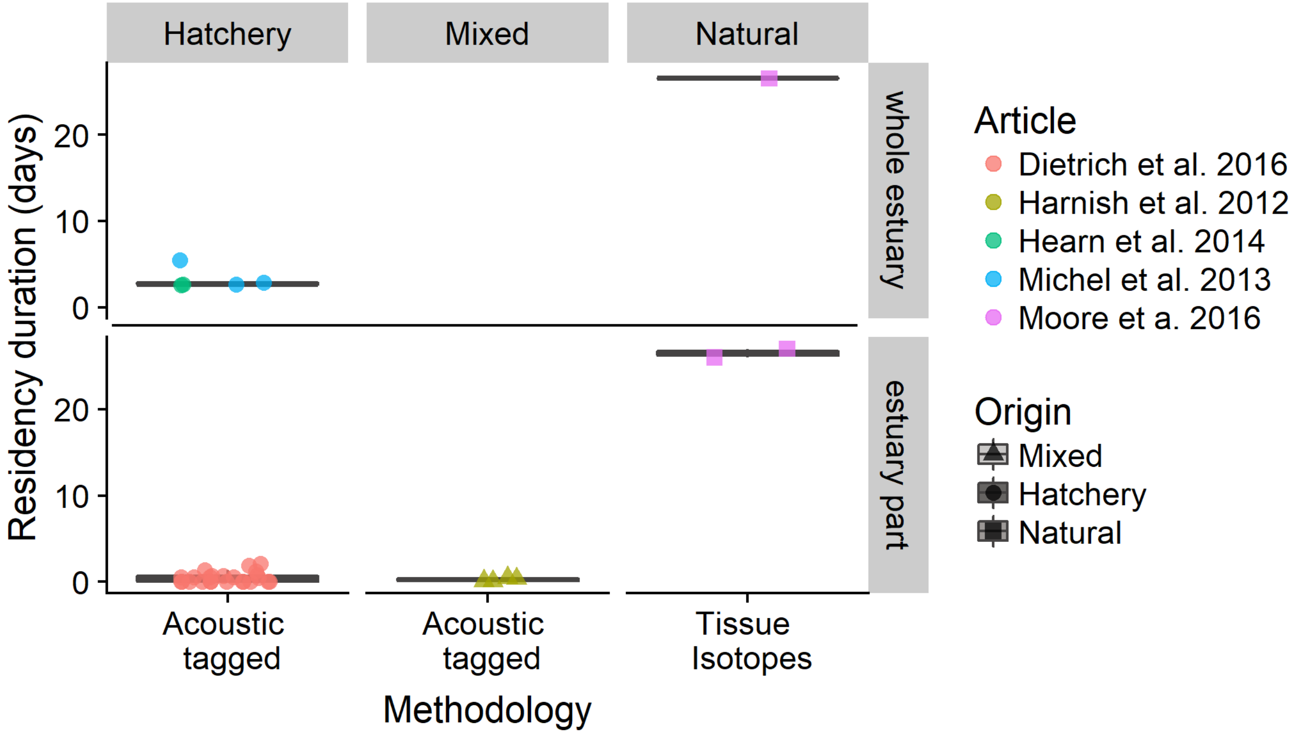


Figure B5. **Average (mean or median) 1+ Chinook residency estimates compared across methodology and separated by spatial extent (whole estuary or estuary part) and origin (hatchery, mixed, or natural).**

Table B1. **Database of juvenile salmon estuary growth and residency literature and empirical estimates.**

https://www.dropbox.com/s/fedblb8wuc7ic8h/Table%20B1.xlsx?dl=0

Table B2. **Estuaries associated with the numbers in Figure 3.1.**

Number	Estuary	Latitude	Longitude
1	Fox River	59.789176	-151.00226
2	Anchor River	59.775471	-151.86114
3	Auke Bay	58.372803	-134.68287
4	Chignik Lagoon	56.298673	-158.59101
5	Skeena River	54.193097	-130.30723
6	Campbell River	50.055495	-125.26133
7	Nanaimo River	49.15276	-123.90913
8	Fraser River	49.114158	-123.17796
9	Carnation Creek	48.913117	-125.00465
10	Nooksack River	48.774722	-122.59917
11	Cowichan River	48.746723	-123.60269
12	Skagit River	48.31268	-122.36884
13	Snohomish River	48.021111	-122.20833
14	Commencement Bay	47.286916	-122.44925
15	Nisqually River	47.108611	-122.70306
16	Grays Harbor	46.951167	-124.05267
17	Columbia River	46.241629	-123.77404
18	Nehalem	45.697408	-123.91409
19	Netarts Bay	45.402914	-123.94601
20	Salmon River	45.0389	-123.99323
21	Yaquina Bay	44.617397	-124.01899
22	Alsea Bay	44.436694	-124.04231
23	Coos Bay	43.39299	-124.20184
24	Sixes River	42.852482	-124.54175
25	Humbolt Bay	40.752439	-124.21967
26	San Francisco Bay	37.866024	-122.39088

Table B3. Average growth rates of juvenile Chinook, coho, chum, pink, or sockeye salmon across ages 0+ and 1+, reported in different units. n = the number of estimates reported with the specified units, where ranges were broken into two occasions. Articles = the number of articles that reported in the specified units per species-age. Papers with multiple estimates were done across different spatial or temporal scales or across different years.

Age	0+							1+
Units	% g/day	g/g/day	% mm/day	g/day	ln(g)/day	log10(g)/day	mm/day	mm/day
Species	Chinook							
Minimum			2	0.02	0.007	0.004	0.18	
Mean	5.800		3.500	0.062	0.019	0.006	0.469	0.480
Median				0.057	0.02	0.006	0.479	
Maximum			5	0.115	0.027	0.009	1.32	
Estimates	1		2	7	10	12	64	1
Articles	1		1	4	1	1	11	1
Species	Coho							
Minimum		0.01					0.1	0.115
Mean		0.711					0.219	0.450
Median		0.835					0.17	0.335
Maximum		1.29					0.63	1.22
Estimates		8					31	24
Articles		1					4	3
Species	Pink							
Minimum	2.93							
Mean	4.621						0.220	
Median	4.55							
Maximum	6.66							
Estimates	28						1	
Articles	1						1	
Species	Chum						Sockeye	
Minimum	1.61							
Mean	2.990						0.330	0.390
Median	2.11							
Maximum	6.2							
Estimates	8						1	1
Articles	2						1	1

Table B4. **Average residency in days of juvenile Chinook, coho, chum, pink, or sockeye salmon across ages 0+, 1+, and 2+. n = the number of estimates reported, where ranges were broken into two occasions. Articles = the number of articles. Papers with multiple estimates were done across different spatial or temporal scales or across different years.**

	Age		
	0+	**1+**	**2+**
Species	**Chinook**		
Minimum	0.0	0.03	
Mean	23.5	3.0	
Median	19.25	0.5	
Maximum	65.5	27.0	
n	35	36	
papers	15	5	
Species	**Coho**		
Minimum	3.7	0.3	6.0
Mean	88.9	30.6	10.4
Median	53.7	19.6	
Maximum	294	144	14.8
n	32	47	2
papers	5	9	1
Species	**Chum**		
Minimum	1.7		
Mean	7.3		
Median	5.2		
Maximum	18.5		
N	14		
papers	5		
Species	**Pink**	**Sockeye**	
Minimum	2.0	1.0	
Mean	14.8	3.7	
Median	14.0	2.0	
Maximum	30.5	18.0	
n	25	9	
papers	3	1	

Text B1. Extended summary of possible biases introduced through differing methodology from five studies.

Five studies explicitly used multiple methodologies to estimate residency and thus enabled more insight into the possibility that different approaches may generate different estimates. The first study (Shreffler et al. 1990) employed cohort-based methods but used a semi-experimental design that directly released cohorts of hatchery-origin 0+ Chinook into a marsh in addition to natural sampling of cohorts of the same size that entered volitionally. Cohorts that entered the estuary of their own volition averaged 5 days of residence (1-40 days, full range), whereas those that were directly released there resided more than 7 times as long with an average of 38 days (29-43 days, full range). The second study (Jones et al. 2014) used two individual-based methodologies on wild-origin 1+ coho. Jones et al.'s (2014) mean estimation of residency using PIT tags was only two days shorter than their median estimate using otolith microchemistry and structure, however, the maximum PIT tag estimate was only 34 days whereas the maximum otolith estimate was more than double at 84 days. Two possibilities that could explain this difference is that there may be effects on behavior from tagging fish or fish were unevenly sampled across the population to be used in each method (Jones et al. 2014). The third study (Miller & Sadro 2003) used one individual- and one cohort-based methodology on wild-origin 1+ coho. Miller & Sadro's (2003) single mean estimation of residency using acoustic tags was 11.6 days (± 3.63 SE), which is lower than their lowest of multiple mean estimates using recaptured batch-marked cohorts, 17.5 days (± 2.24 SE) and five times lower than maximum batch-mark mean, 64.4 days (± 6.82 SE). The fourth study (Healey 1980a) employed two analytical methods on the same batch-marked wild-origin 0+ Chinook data; one method used an emigration rate decay-curve to estimate the half-life of marked-fish residence, whereas the other method used an estimated growth rate to infer how long fish must have stayed to obtain the observed change in average size. Healey (1980) surmised that the decay-curve average estimate was high (60 days) and his growth rate-derived residency estimate (25 days) agreed with population size estimates more and it was within the decay-curve estimates 95% confidence interval, thus he favored the lower average residency duration estimate. The last paper (Levings et al. 1986) duplicated Healey's (1980) analytical approaches and found a similar discrepancy in its decay-curve average residency estimate (65 days) and growth rate-derived residency estimate (41 days). Collectively, these direct examples highlight possible sources of systematic error that may be introduced through treating or handling fish differently (Shreffler et al. 1990, Miller & Sadro 2003, Jones et al. 2014), sampling different parts of the population (Miller & Sadro 2003, Jones et al. 2014), using individual- versus cohort-based approaches (Miller & Sadro 2003), and the analytical approach used on data (Healey 1980a, Levings et al. 1986).