FORAGING ECOLOGY OF JUVENILE FRASER RIVER SOCKEYE SALMON ACROSS MIXED AND STRATIFIED REGIONS OF THE EARLY MARINE MIGRATION

by

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B.Sc., The University of British Columbia, 2012

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE in
THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES
(Oceanography)

THE UNIVERSITY OF BRITISH COLUMBIA (Vancouver)

September 2019

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FORAGING ECOLOGY OF JUVENILE FRASER RIVER SOCKEYE SALMON
ACROSS MIXED AND STRATIFIED REGIONS OF THE EARLY MARINE MIGRATION

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the degree of Master of Science
in Oceanography

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Abstract

Pacific salmon hold tremendous ecological, cultural, and economic value to communities and ecosystems throughout British Columbia. The productivity of several populations, however, has declined since the early 1990s. The cause of the decline is still not fully understood, though bottom-up drivers and trophic interactions during the early marine migration are believed to be contributing factors. For juveniles leaving the Fraser River, their migration crosses a range of stratified and well-mixed waters with varying levels of productivity. The purpose of this study is therefore to a) characterize the foraging ecology of juvenile sockeye salmon across the range of environmental conditions they encounter during the early marine migration, and b) test whether foraging success is lower in tidally mixed waters. In 2015 and 2016, environmental conditions, prey dynamics, and sockeye diets were sampled at high spatial and temporal resolution in the Discovery Islands and Johnstone Strait during the outmigration period. Analyses revealed two unique diet types, one dominated by meroplankton, cladocerans, and larvaceans in the warmer, fresher waters of the Discovery Islands and the other dominated by large calanoid copepods in the cooler, saltier waters of Johnstone Strait. In all diets, sockeye exhibited strong selection for prey items larger than 2 mm. Furthermore, foraging success was low throughout the tidally-mixed regions of the Discovery Islands and Johnstone Strait, providing strong support for the hypothesis that this region is a ‘trophic gauntlet’ for outmigrating salmon. Foraging hotspots were also discovered along the interface between mixed and stratified waters. These frontal areas may in fact be important foraging grounds for juveniles to facilitate their migration through otherwise challenging conditions. This research addresses a critical knowledge gap in the foraging ecology of juvenile salmon across different environmental conditions during their early
marine migration and can be used to improve our ability to monitor fish condition, growth, survival, and ultimately recruitment.
Lay Summary

The iconic Fraser River sockeye salmon have been decreasing in number in the last few decades, and we still don’t know why. Scientists now believe that something is happening during the first few months at sea that is causing the decrease in numbers. One theory is that it is food-related. This research looked at what young sockeye are eating, where they are eating it, and why. It was found that what sockeye eat can rapidly change from one area to the next depending on the water conditions and amounts of food available. It also depends on when they migrate through different areas, since the types and amounts of food change over time. Finally, certain regions along the coast of British Columbia are harder for young salmon to find food than others. It is important to know where and when food is limiting so we can account for bottle-necks in survival.
Preface

This thesis is the original, unpublished work of Samantha James. The research was designed by my supervisors and myself to contribute to a larger research initiative, the Hakai Institute’s Juvenile Salmon Program, which is a partnership between the Hakai Institute, University of British Columbia, University of Toronto, Simon Fraser University, Salmon Coast Field Station, the Pacific Salmon Foundation, and Fisheries and Oceans Canada (DFO). The objective of the Juvenile Salmon Program is to investigate the factors influencing the early marine survival of juvenile Pacific salmon, particularly sockeye salmon. The field data were collected by the program’s field crews, including myself in 2016, operating out of Hakai’s Quadra Island research station and Salmon Coast Field Station. Samples were collected under DFO license number ‘XR 63 2019’ with approval from UBC’s Animal Care Committee (Protocol A19-0025). Subsequent lab analyses of the zooplankton data were done by Samantha James and undergraduate lab assistants Andrea Lee and Jessica Shaub. Analyses of the stomach samples, as well as all data analyses, were performed by Samantha James. As per Hakai’s ‘Policy for Open Science’ these data will be publicly available (http://dx.doi.org/10.21966/1.566666).
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Acknowledgements

There are so many people to acknowledge for their support throughout this process. First of all, I am forever grateful to my supervisors, Dr. Evgeny Pakhomov and Dr. Brian Hunt, for taking me on as a master’s student upon such short notice. I am very fortunate to have found my way (very circuitously) to you when I did so that I could pursue this amazing research. Thank you for teaching me the ins and outs of fish stomach processing (literally), for introducing me to oceanography, and for patiently mentoring me through the scientific process. Your questions and advice helped me to constantly improve and produce higher quality results. I would also like to thank Dr. Francis Juanes for his perspectives and recommendations during this work.

I am very appreciative of the financial support received from the Natural Sciences and Engineering Research Council, the Tula Foundation, Mitacs, and the donors behind the R. Grant Ingram Memorial Scholarship in Oceanography and the Robert Rutherford Rae Scholarship. Your investment in this research and my education meant a great deal to me. This work is also part of a broader collaboration through the Hakai Institute’s Juvenile Salmon Program. Without the support of Hakai and the Tula Foundation, this work would not have been possible. Thank you for your continued support of the many researchers involved in this program.

Working with the Hakai Institute has been an incredible experience. I would like to thank Sean Godwin for introducing me to the Juvenile Salmon Program in the first place, and all the amazing people I’ve had the privilege to work with through my time at Hakai. In particular, Brett Johnson, Luke Rogers, Brianna Knowles (my salmon sister), Julian Gan, Carly Janusson, and all the Salmon Coasters.. thank you for your ridiculously hard work, brilliant ideas, spontaneous
dance parties, for sharing the salmon adventure with me, and for keeping me laughing every step of the way. Working with you has absolutely been the highlight of my master’s experience.

To my lab mates, I truly could not have done this without you. Thank you for brainstorming ideas with me, providing helpful feedback, going through the statistics (again and again), and answering my endless slew of questions. A huge thank you to Natalie Mahara especially for helping me with absolutely everything; your research lay the groundwork for much of my own for which I am eternally grateful. Your prowess with zooplankton identification, your thoughtful edits, and your brilliant humour were invaluable to me.

I am immensely grateful to have had such incredible friends and family providing endless love, support, and encouragement through the good times and the bad. Friends, thank you for the Tuesday girls’ nights, early morning swims, Whistler days, week-long climbing trips, beach nights, annual cabin retreats, afternoon walks across campus, and just generally brightening my days. To my parents, I cannot express my gratitude enough. Your love, support, and coaching through this, and every adventure I’ve taken in life, has gotten me to where I am today, so thank you. And to my partner in life, I am beyond grateful; you truly supported me in every possible way. Your patience and constant motivation kept me grounded and helped me to see the bigger picture.

And one final thank you to my mentors along the way who inspired me to pursue my life scientific: Dr. Suzie Lavallee, Dr. Scott Hinch, Kat Anderson, Ross Whippo, Matt Siegle, Stacey Hrushowy, and Dr. Rick Routledge. Whether you know it or not, your mentorship is what led me to pursue my passions.
To my family
Chapter 1: Introduction

Survival rates during an animal’s early life stages can have significant consequences for population dynamics. This is exemplified by marine fishes, many of which experience high fecundity, but have high mortality early in life (Miller and Kendall 2009). Pacific salmon are a group of fish species that exhibit these characteristics. They exhibit anadromous life histories spread between both fresh and salt water life stages, however, the greater part of their lives is spent in the marine environment where they grow and mature (Burgner 1991). The first few months at sea are a critical time and can determine the abundance of returning adults (Friedland et al. 2000; Mueter et al. 2005). Juvenile salmon experience high mortality in the early marine phase (Parker 1968; Bax 1983), with survival strongly related to size (Friedland et al. 2000; Moss et al. 2005). The impact of local environmental conditions on juvenile fish condition and growth can propagate through the life-cycle to affect overall survival and productivity (Healey 2011).

Pacific salmon hold tremendous economic, ecologic, and social value to people and ecosystems. In Canada, commercial and recreational salmon industries contribute millions of dollars to British Columbia’s gross domestic product and generate thousands of jobs (BC Stats 2018). Their anadromous life cycle allows for the transfer of marine-derived nutrients to coastal aquatic and terrestrial ecosystems when adults return to their natal streams and rivers to spawn (Naiman et al. 2002; Janetski et al. 2009). Furthermore, the cultural, spiritual, and physical well-being of many First Nations communities is dependent on the salmon fishery (Cohen 2012). Of the Pacific salmon species, sockeye salmon (Oncorhynchus nerka) are the most economically important and the largest run in Canada is that from the Fraser River (Burgner 1991; Cohen
Several of the Fraser River populations have experienced severe declines in recent years (Peterman and Dorner 2011). Changes in salmon productivity may be explained by changes to oceanographic conditions experienced by juveniles, including alterations to prey quantity and quality (Beamish et al. 2004; Saito et al. 2009; Duffy and Beauchamp 2011; McKinnell et al. 2014). Biological productivity in the north Pacific is projected to decrease as a result of climate change, which would alter foraging opportunities and behaviour, depress fish stocks, and threaten marine ecosystems (Rijnsdorp et al. 2009; Healey 2011). Because salmon provide such immense benefits to ecosystems and societies, it is important that we investigate the factors affecting their early marine survival, both to understand general relationships between marine survival and fish population dynamics and to improve our ability to model and predict returns based on these relationships.

Marine growth and survival of salmon is tightly coupled to ocean productivity (Beamish et al. 2004; Saito et al. 2009; Hertz et al. 2016). Phytoplankton are the primary producers at the base of coastal marine food webs, however, zooplankton are the main vector for energy transport between primary producers and higher trophic levels including sockeye salmon. The timing of the salmon migrations is linked to the phenology of bottom-up oceanographic processes, including spring bloom timing and zooplankton abundance (Chittenden et al. 2010; Malick et al. 2015). Changes in prey quality and quantity along their migratory route could explain the variability of sockeye salmon survival and returns to the Fraser River in British Columbia.

In the Fraser River watershed, adults spawn in freshwater in the fall, leaving their eggs to develop over winter before hatching the following spring (Groot and Margolis 1991). Young sockeye then spend one to two years rearing in fresh water before making the downstream
migration to the ocean where they spend one to four (although typically two to three) years growing and maturing (Groot and Margolis 1991). Smolts emerge from the Fraser River into the Strait of Georgia where the majority reside for 43 to 54 days (Preikshot et al. 2012) before exiting the Strait via the northern passages of the Discovery Islands and Johnstone Strait (Groot and Cooke 1987; Welch et al. 2009). From there, juveniles continue their migration north along the coast of British Columbia until they reach the north Pacific where they spend the remainder of their marine lives before making the return migration as adults to their natal streams to spawn (Groot and Cooke 1987).

The zooplankton communities in coastal temperate environments have been changing in recent years. In the Strait of Georgia, there has been a large decrease in total zooplankton biomass, particularly that of a dominant species, *Neocalanus plumchrus* (Johannessen and Macdonald 2009; Li et al. 2013). The decrease in *N. plumchrus* specifically may be attributed to a phenological mismatch with their phytoplankton prey; peak biomass of *N. plumchrus* has shifted two months earlier in recent years, reducing their overlap with the spring phytoplankton bloom (Johannessen and Macdonald 2009). Variability in zooplankton abundance, phenology, and composition is often correlated with anomalous environmental conditions, especially temperature, with warmer water temperatures leading to an advancement of key life-history events, and a poleward shift in species distributions (Mackas et al. 2001, 2007; Edwards and Richardson 2004). The Strait of Georgia is warming, which may be driving a shift in coastal phenology and an increase in trophic mismatches between phytoplankton, zooplankton, and salmon (Mackas et al. 2013).
To maximize growth, and thus marine survival, juvenile salmon need to consume enough food to balance the energetic requirements of foraging, predator evasion, and migration through different ocean conditions (Higgs et al. 1995). The amount and type of prey consumed depends on a number of factors, including prey type, size, and contrast (O’Brien 1979; Hargreaves and LeBrasseur 1985; Schabetsberger et al. 2003), diel migrations of prey (Armstrong et al. 2005), and the degree of predation risk associated with pursuing that prey (Scheuerell and Schindler 2003). The main prey of juvenile sockeye travelling through the Strait of Georgia in the 1960s were calanoid copepods, although insects, fishes, amphipods, decapods, and larvaceans were also consumed (Preikshot et al. 2010; Osgood et al. 2016). Similar to trends in the zooplankton community, diets have experienced a dramatic decrease in the abundance of calanoid copepods, fishes, and insects, with higher abundances of amphipods and decapods measured since the 1960s (Preikshot et al. 2010; Neville et al. 2016). Copepods and fishes are high energy food items (Davis et al. 1998), therefore their loss from salmon diets may be limiting salmon’s ability to meet their energetic requirements for growth during the early marine phase.

Existing research salmon diets has been focused in the Strait of Georgia (Phillips and Barraclough 1978; Beamish et al. 2004; Osgood et al. 2016; Chittenden et al. 2018), however, little is known about the feeding conditions experienced by juveniles as they continue north through the Discovery Islands and Johnstone Strait, a region hypothesized to be a ‘trophic gauntlet’ for migrating salmon (McKinnell et al. 2014). Waters from the Strait of Georgia flush through the narrow channels and steep-sided inlets of the Discovery Islands becoming highly mixed in some areas. The southern and eastern portions of the Discovery Islands stratify in the spring and summer months, whereas the northern and western passages experience some of the strongest tidal rapids in the world (Lin and Fissel 2014). Johnstone Strait lies to the northwest
and consists of one main channel that is fully vertically mixed, creating light-limited, high nutrient, low chlorophyll conditions (Thomson 1981). These two regions make up the narrow inside passage between Vancouver Island and mainland British Columbia, connecting the Strait of Georgia to the oceanic waters of Queen Charlotte Strait and Queen Charlotte Sound. Despite their proximity, the water exchange between the two regions is limited (Khangaonkar et al. 2017) and environmental conditions and zooplankton communities are significantly different from one another (Dosser in prep; Mahara in prep). Low production in mixed waters could limit the foraging success and growth of migratory salmon, inducing an energy-deficit (McKinnell et al. 2014). Impacts on marine survival are likely cumulative (Healey 2011; Miller et al. 2014), and thus an energy-deficit is of concern in years when juveniles enter the region in poor condition, or when foraging opportunities are poor later in the migration. However, little is known of the diets of juvenile salmon in mixed coastal waters, and until now, no research has investigated salmon diets in Johnstone Strait.
Figure 1.1: Map of the Inside Passage between Vancouver Island and mainland British Columbia that connects the Strait of Georgia to Queen Charlotte Sound, highlighting the dynamic regions of the Discovery Islands and Johnstone Strait.

The purpose of this study is to examine the diets of migratory juvenile Fraser River sockeye salmon across fine spatial and temporal scales in mixed coastal waters. The conditions experienced by juvenile sockeye salmon migrating through these narrow waterways are highly dynamic, therefore the analyses conducted herein rely on high-resolution spatial and temporal data on environmental conditions, prey fields, diets, and foraging success. By looking at the relationships between juvenile diets and bottom-up drivers, we can determine whether this region is acting as a trophic gauntlet, and how the timing of the juvenile migration may influence
foraging success. Therefore, in Chapter 2, the main objectives are to investigate: a) how the prey and diet composition are distributed across fine spatial scales, b) what environmental parameters are correlated to prey and diet distributions, and c) how foraging success varies across a spatial gradient of stratified and mixed waters to determine the existence and extent of the trophic gauntlet. Chapter 3 expands upon the findings of Chapter 2 by exploring these relationships over fine temporal scales. Thus, the main objectives of Chapter 3 are to measure a) how surface zooplankton communities, juvenile sockeye diets and foraging success change over the migratory period, b) how migration timing and environmental conditions are correlated to diets and foraging success, and c) whether the ‘trophic gauntlet’ exists and persists throughout the migratory period. These objectives are further expanded by comparing the results between two years and two oceanographic regions. This research provides novel information on salmon diets in tidally mixed oceanographic conditions and improves our understanding of the factors affecting early marine growth and survival of sockeye salmon in an understudied section of their coastal migration.
Chapter 2: Spatial analysis of juvenile sockeye salmon diets across a range of oceanographic conditions

2.1 Introduction

Upon entering the ocean, juvenile salmon (*Oncorhynchus* spp.) must navigate the complex waterways of the British Columbia (BC) coast as they migrate north to the Gulf of Alaska. The coastal waters of BC are located within the transition zone between the California Current system to the south and the Gulf of Alaska system to the north. The influence of each of these systems varies seasonally, however, the oceanography of the BC coast is also influenced by smaller scale environmental forces, such as coastal topography and freshwater inputs (Crawford and Thomson 1991; Jackson et al. 2015). Therefore, the oceanographic conditions encountered by migratory juvenile salmon have a high degree of spatial and temporal variability which translates into changes in their prey field, and ultimately their growth and survival (Ware & Thomson 2005).

There are many factors regulating growth and survival throughout the life cycle of Pacific salmon, however, it is well known that the first summer at sea is a crucial time for determining marine survival (Pearcy 1992; Beamish and Mahnken 2001; Duffy and Beauchamp 2011). Mortality during this phase can be size-selective (Sogard 1997; Moss et al. 2005). Slower-growing individuals are more susceptible to predation (Beamish and Mahnken 2001) while larger smolts have a higher smolt to adult survival ratio (Chittenden et al. 2010). Early marine growth can be linked to the abundance of prey (Farley et al. 2007) and feeding intensity of juvenile salmon (Metcalfe et al. 1999) and so high feeding intensity may be essential for meeting the energetic requirements of migration and growth during this critical period. Therefore, it is
important to understand the capacity of different ocean environments to provide adequate prey to sustain juvenile salmon growth in the early marine phase.

Upon leaving the Fraser River, juvenile sockeye salmon spend their first summer at sea transitioning between the different ocean regimes of the BC coastline. Juveniles first encounter the highly stratified and productive waters of the Strait of Georgia (Jackson et al. 2015) where they reside for 43-54 days (Preikshot et al. 2012). The majority of juveniles then travel through the tidally-mixed channels of the Discovery Islands and Johnstone Strait, before continuing north through Queen Charlotte Sound and Hecate Strait en route to the Gulf of Alaska (Tucker et al. 2009). As they migrate along the coast, the in situ growth rates of juvenile salmon vary at the same spatial and temporal scales as their ocean environments (Ferriss et al. 2014). It is believed that the most likely cause for regional differences in growth is variation in the quantity and quality of salmon prey (Ferriss et al. 2014).

The well-mixed section of the juvenile salmon coastal migration through Johnstone Strait has been hypothesized to be a ‘trophic gauntlet’, where low productivity may be causing an energy-deficit for migrating salmon. McKinnell et al. (2014) described the conditions in Johnstone Strait as being in an ‘eternal state of winter’, where temperatures remain relatively low throughout the water column, with no seasonal phytoplankton bloom in the surface waters. This is due to intense mixing, which causes primary producers to be light-limited, creating high-nutrient, low chlorophyll conditions (McKinnell et al. 2014). The low productivity of these waters could limit the growth of juvenile salmon, having significant implications for overall marine survival in years when conditions experienced prior to and after the gauntlet are unable to support adequate growth (McKinnell et al. 2014). Recent research has shown evidence of
reduced growth in this region (Ferriss et al. 2014; Journey et al. 2018), however, the factors regulating growth in this section of their outmigration remain unknown.

Prior to entering Johnstone Strait, juvenile salmon leaving the northern Strait of Georgia first have to navigate the Discovery Islands. While it was previously believed that waters from the Strait of Georgia were exchanged with the Pacific Ocean through these narrow passages, recent research suggests that this is not the case. A series of shallow sills at the intersection between Johnstone Strait and the Discovery Islands force the inflowing water from the north to be upwelled, mixed, and returned back in the direction it came as surface outflow (Khangaonkar et al. 2017). As a result, the oceanography of these two separate water masses is significantly different (Dosser, in prep). The Discovery Islands host a network of constricted, steep-sided channels with some of the strongest tidal currents in the world (Lin and Fissel 2014). Unlike Johnstone Strait, these waters experience both spatial and seasonal fluctuations in temperature and salinity and are strongly influenced by freshwater inputs from the Fraser River to the south and local rivers, including the Homathko, Salmon, and Oyster Rivers (Chandler et al. 2017a). Therefore, upon leaving the Strait of Georgia via the Discovery Islands-Johnstone Strait corridor, juvenile salmon are crossing a wide gradient in environmental conditions in less than 200 km. However, it is unclear how this rapid transition influences the foraging ecology of juvenile salmon.

This study explores the relationships between environmental conditions, prey dynamics, and juvenile sockeye salmon diets in the complex waters between the northern Strait of Georgia and Queen Charlotte Strait. The purpose is to determine: a) how the prey and diet composition are distributed across fine spatial scales, b) what environmental parameters are correlated to prey and diet distributions, and c) how foraging success varies across a gradient of stratified and
mixed waters to determine the extent of the trophic gauntlet. It is predicted that the transition between different water masses will be reflected by changes to the prey and diet composition at the same spatial scale. It is also expected that highly mixed areas of low productivity will be food limiting for migrating juvenile sockeye, resulting in low foraging success. This work will shed light on the complexities of juvenile salmon diets in an intriguing and previously unexplored region of the BC coast and contribute to the latest research on the bottom-up drivers affecting early marine growth and survival of juvenile sockeye.

2.2 Methods

2.2.1 Fish sampling and processing

Juvenile sockeye salmon were collected from the Discovery Islands and Johnstone Strait from a single sampling event occurring between June 1 and June 9, 2015 as part of the Hakai Institute’s Juvenile Salmon Program. This period was selected to capture the peak sockeye outmigration through the study area (see Johnson et al. 2018). Twelve sampling sites were strategically positioned to capture the full range of environmental conditions experienced by juvenile salmon in each of the migratory routes through these regions (Figure 2.1). In the Discovery Islands, these are the western (D06, D11), central (D07, D09), and eastern (D08, D10) routes running through Discovery Passage, Okisollo Channel, and Desolation Sound, respectively. In Johnstone Strait, salmon can take either a southern (J07, J08, J09) or northern (J06, J04, J02) route along the shore. Sites were sampled using a hand-operated purse seine deployed from a small open boat. Up to thirty sockeye were retained per sampling event and euthanized using a lethal dose of MS-222 before being frozen in cryogenic dry shippers for transport and transferred to -80°C freezers on land.
In the lab, a subsample of ten sockeye from each seine had stomachs removed and stored in 95% ethyl alcohol. Ethanol preservation can make samples brittle and difficult to manipulate. Therefore prior to analysis, stomachs were removed from the preservative and soaked in water for 30 minutes for rehydration. Samples were then blotted dry and weighed to the nearest 0.1 mg. Ethanol preservation can also cause samples to lose weight (Wetzel et al. 2005), and so an ethanol conversion factor was applied to stomach content weights to make them comparable with the fish weights and other diet fresh weights in the literature (see Appendix A).

Stomachs were cut open from the start of the esophagus to the pyloric sphincter with contents removed, weighed, and identified to the lowest taxonomic resolution possible using a
Zeiss Stemi 508 microscope. ‘Empty’ stomachs were those visually assessed as containing no traces of food. Contents were also sorted within each taxonomic unit by digestive state from 1 (fresh) to 4 (highly digested), with a fifth digestive state for highly digested and unrecognizable material. Average lengths were taken for each taxonomic group, allowing prey items to be grouped into one of five size categories: <1, 1-2, 2-5, 5-10, and >10 mm. Each taxonomic group was counted and weighed to determine relative abundance and relative biomass.

2.2.2 **Zooplankton and environmental data collection**

The prey field was measured by collecting a horizontal surface tow at each sampling location after fish samples were taken. Sampling targeted surface waters as salmon are visual feeders and it is believed that they feed near the surface (Brodeur 1989; Landingham et al. 1998). A 250 µm mesh zooplankton net equipped with a flowmeter was towed behind the boat through the top meter of the water column as the boat travelled in a wide circle for three minutes, or until there was visible coloration in the cod-end. Samples were transferred to Polyethylene terephthalate (PET) jars and preserved in buffered formalin. The volume of water filtered was calculated as:

\[ Volume = \pi r^2 \times Distance \]

In the lab, zooplankton were size fractioned using a 250, 1000, 2000 µm sieve stack. Each size fraction was blotted dry and weighed to the nearest 0.1 mg (wet weight). When necessary, the 250 µm size fraction was split until a subsample of approximately 300 specimens was achieved to facilitate analysis. Samples were then poured into a Bogorov tray to be measured and identified to the lowest taxonomic level.

A Yellow Springs Instruments (YSI) Pro30 was used to measure water temperature and salinity at the surface and at 1 m, along with a Secchi disc to measure water clarity.
Environmental measurements were taken at each site after the fish had been collected and processed.

2.2.3 Data analysis

Welch’s two sample t-test was used to compare juvenile sockeye fork lengths. Due to the non-normal distribution of fish weight and zooplankton abundance and biomass data, a Mann-Whitney U test was used to compare differences between regions. When significant differences were detected, visual observation was used to determine which region had the higher values.

For visualization of diet and zooplankton composition, the taxonomic categories were simplified into the following major groupings: Amphipods, Barnacles, Calanoid Copepods, Cladocerans, Decapods, Euphausiids, Larvaceans, and ‘Other’. The latter category consisted mainly of gastropods, bivalves, polychaetes, insects, and fish and zooplankton eggs. Unidentifiable digested matter was excluded from taxonomic analyses. Detailed taxonomic information was retained for multivariate analyses. Taxa that were only found in a single sample were grouped with other samples at a higher taxonomic level.

Non-parametric, multivariate techniques were used to analyse the diet composition. Relative abundance and biomass were arcsine square root transformed to spread out the distribution of values and reduce the influence of abundant or rare species (Zar 1999). A cluster analysis was then performed using the average-linkage method between Bray-Curtis rank dissimilarities to determine what diet types are found across the two regions (Ferreira and Hitchcock 2009). An analysis of similarity (ANOSIM), the non-parametric multivariate analogue to ANOVA, was also conducted to test for significant differences in taxonomic composition within and between sites and regions (Clarke 1993). This method compares within and between group ranked differences, producing a global R-value which approaches ‘0’ when within group
differences are greater than between group differences, and approaches ‘1’ when the opposite is true. When significant differences were detected between groups, a similarity percentages test (SIMPER) was conducted to determine which taxa best explained the differences between groups.

Non-metric multidimensional scaling (NMDS) ordination was used to project the rank dissimilarities between samples into a two-dimensional ordinate space. The ordination plots individual diets that are more similar closer together, and those that are dissimilar further apart. The compression of multidimensional relationships into two-dimensional space creates ‘stress’ and ordinations with stress values $\geq 0.2$ should not be used to assess differences in community structure (Clarke 1993). A version of Clarke and Ainsworth’s (1993) BIO-ENV model (Oksanen 2018) was run to determine which environmental parameters had the maximum correlation with the diet rank dissimilarities. The best-fitting model outputs were overlain on the ordination as vectors with the direction of the arrow indicating an increase in the value of that parameter.

The prey selectivity of juvenile sockeye salmon in each region was calculated using the Ivlev electivity index (Ivlev 1961):

$$E_i = \frac{(r_i - p_i)}{(r_i + p_i)},$$

where $r_i$ is the numerical proportion of the $i^{th}$ taxon in the diet and $p_i$ is the proportion of the $i^{th}$ taxon in the environment. Values of the index range from -1 to +1, where -1 indicates complete avoidance and +1 indicates the strongest selectivity. Electivity values were calculated for each fish and then averaged by site and region.

A gut fullness index (GFI) was used as a measure of foraging success, expressed as the proportion of the fish body weight made up by the stomach contents:
\[ GFI = M_{sc}(M)^{-1} \times 100, \]

where \( M_{sc} \) is the mass of the stomach contents (g) and \( M \) is the mass of the fish (g). This formula standardizes for differences in fish size (Chipps and Garvey 2007). GFIs from this study were compared to a coast-wide interquartile range of juvenile sockeye salmon GFIs adapted from Brodeur et al. (2007), who compiled diet information for juvenile Pacific Salmon from northern California to the Gulf of Alaska from 2000 to 2002.

All statistical analyses were conducted in R statistical software v3.5.2 (R Development Core Team 2018) with multivariate analyses performed using the “Vegan” package in R (Oksanen 2018).

2.3 Results

2.3.1 Environmental conditions

Surface waters in the Discovery Islands were warmer and fresher on average than in Johnstone Strait (Table 2.1). In the Discovery Islands, average surface temperatures were 3.2°C higher than in Johnstone Strait, with the warmest temperatures measured at D07 and D08, which were 4.5–7.5°C warmer than the other Discovery Island sites. The coldest temperatures were measured in Johnstone Strait at sites J06 and J02. Surface waters were the least saline at D08. Secchi depth was shallowest at the southern and northern-most sites (D06 and J02) and highest at the next most proximate sites (D07 and J09) (see Appendix B Figure B.1 for visualization).
Table 2.1: Environmental parameters measured after a single fish collection at each site in the Discovery Islands (DI) and Johnstone Strait (JS) in June 2015. Temperature and salinity values are an average of the surface and 1 m measurements collected with a YSI. Zooplankton abundance (individuals/m$^3$) and biomass (mg/m$^3$) were collected from a single surface tow at each site.

<table>
<thead>
<tr>
<th>Region</th>
<th>Site</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Date</th>
<th>Temp (°C)</th>
<th>Sal (psu)</th>
<th>Secchi (m)</th>
<th>Zoop Abund (individuals/m$^3$)</th>
<th>Zoop Biom (mg/m$^3$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DI</td>
<td>D06</td>
<td>50.09809</td>
<td>-125.271</td>
<td>June 4</td>
<td>12.3</td>
<td>28.2</td>
<td>10.8</td>
<td>2,146</td>
<td>414.3</td>
</tr>
<tr>
<td></td>
<td>D07</td>
<td>50.19112</td>
<td>-125.142</td>
<td>June 5</td>
<td>18.2</td>
<td>25.4</td>
<td>14.9</td>
<td>3,847</td>
<td>1,245.0</td>
</tr>
<tr>
<td></td>
<td>D08</td>
<td>50.31962</td>
<td>-125.04</td>
<td>June 4</td>
<td>16.8</td>
<td>19.3</td>
<td>11.5</td>
<td>1,689</td>
<td>205.0</td>
</tr>
<tr>
<td></td>
<td>D09</td>
<td>50.30787</td>
<td>-125.329</td>
<td>June 5</td>
<td>11.8</td>
<td>28.4</td>
<td>13.3</td>
<td>567</td>
<td>46.8</td>
</tr>
<tr>
<td></td>
<td>D10</td>
<td>50.44365</td>
<td>-125.279</td>
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<td>10.7</td>
<td>28.4</td>
<td>13.2</td>
<td>2,159</td>
<td>319.3</td>
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<td></td>
<td>D11</td>
<td>50.34851</td>
<td>-125.448</td>
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<td>11.0</td>
<td>29.0</td>
<td>12.6</td>
<td>2,028</td>
<td>257.6</td>
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<td>JS</td>
<td>J06</td>
<td>50.47796</td>
<td>-126.028</td>
<td>June 7</td>
<td>9.9</td>
<td>28.6</td>
<td>12.2</td>
<td>721</td>
<td>106.4</td>
</tr>
<tr>
<td></td>
<td>J07</td>
<td>50.45747</td>
<td>-126.169</td>
<td>June 6</td>
<td>10.0</td>
<td>28.7</td>
<td>13.6</td>
<td>910</td>
<td>83.9</td>
</tr>
<tr>
<td></td>
<td>J04</td>
<td>50.5268</td>
<td>-126.387</td>
<td>June 8</td>
<td>10.0</td>
<td>28.8</td>
<td>13.2</td>
<td>736</td>
<td>143.5</td>
</tr>
<tr>
<td></td>
<td>J08</td>
<td>50.48048</td>
<td>-126.413</td>
<td>June 7</td>
<td>10.8</td>
<td>28.5</td>
<td>11.8</td>
<td>2,684</td>
<td>244.4</td>
</tr>
<tr>
<td></td>
<td>J09</td>
<td>50.53978</td>
<td>-126.782</td>
<td>June 7</td>
<td>11.7</td>
<td>28.7</td>
<td>13.9</td>
<td>2,680</td>
<td>903.5</td>
</tr>
<tr>
<td></td>
<td>J02</td>
<td>50.6026</td>
<td>-126.702</td>
<td>June 9</td>
<td>9.5</td>
<td>29.1</td>
<td>9.1</td>
<td>1,252</td>
<td>166.9</td>
</tr>
</tbody>
</table>
2.3.2  Prey field

The relative abundance of zooplankton taxa across sites was similar, with a few notable differences. Cladocerans were relatively abundant throughout most of the sites in the Discovery Islands, as well as at the three sites along the south shore of Johnstone Strait (Figure 2.2). Barnacles were present in low numbers in all samples in both regions. Calanoid copepods were relatively more abundant throughout Johnstone Strait and at the south end of Discovery Passage (D06). Furthermore, larvaceans were relatively more abundant at the northern sites in the Discovery Islands (D10 and D11), while euphausiids and decapods were relatively more abundant midway along the north side of Johnstone Strait (J04) and at the western-most site on the south shore of Johnstone Strait (J09), respectively. Overall, cladocerans were more dominant in the Discovery Islands while calanoid copepods were more dominant in Johnstone Strait (Figure 2.2).

The highest zooplankton abundance and biomass were measured at the south end of the central migratory route (D07) with the lowest values observed in Okisollo Channel (D09), as well as at the eastern half of the Johnstone Strait sites (J06, J07, and J04) (Table 2.1). By region, abundance and biomass of zooplankton were not significantly different (Mann-Whitney U test, \( p = 0.59 \)), however, values were slightly higher in the Discovery Islands. In Johnstone Strait, zooplankton abundance was highest at sites along the south shore (J09 and J08), with J09 having more than three times the biomass of any other site in the region. Zooplankton abundance and biomass were relatively low at all other sites in Johnstone Strait (Table 2.1).

The abundance and biomass of zooplankton in the surface waters of both regions were dominated by organisms <1 mm in size, although higher proportions of larger zooplankton were observed in Johnstone Strait (Figure 2.3A; biomass shows in Appendix B Figure B.2). In the
Discovery Islands, calanoid copepods, cladocerans, and larvaceans dominated the smaller size classes (<2 mm), while amphipods and decapods dominated the larger size classes. In Johnstone Strait, barnacles, calanoid copepods, and ‘other’ zooplankton dominated the smaller size classes while calanoid copepods and decapods dominated the larger size classes (data shown in Appendix B Figure B.3).

![Figure 2.2: Relative abundance of zooplankton taxa at each site (positioned from south to north along the x-axis) in the Discovery Islands (DI) and Johnstone Strait (JS) from a single sampling event in early June 2015. Sites Only taxa contributing more than 5% of the abundance in each sample are displayed.](image-url)
Figure 2.3: Relative abundance of A) zooplankton from surface waters and B) prey items in salmon stomachs, in each size category (<1, 1-2, 2-5, 5-10, >10 mm) at each site (positioned from south to north along the x-axis) in the Discovery Islands (DI) and Johnstone Strait (JS) from one sampling event in early June 2015.

2.3.3 Fish

A total of 120 juvenile sockeye stomachs were analyzed. Juvenile sockeye ranged from 89 to 132 mm in fork length, averaging 108 mm (SD +/- 7.8 mm) (Table 2.2). Fish weights ranged from 6.0 to 22.3 g, with a median weight of 13.9 g. There was no significant difference in
fork lengths ($t$-test; $p = 0.25$) or weights (Mann-Whitney U test; $p = 0.26$) between the Discovery Islands and Johnstone Strait.

Table 2.2: Numbers of fish collected with median values for fish fork length (FL; mm) and weight (FW; g) with ranges in parentheses for each site in the Discovery Islands (DI) and Johnstone Strait (JS).

<table>
<thead>
<tr>
<th>Region</th>
<th>Site</th>
<th>n</th>
<th>FL</th>
<th>FW</th>
</tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>(mm)</td>
<td>(g)</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>(95-119)</td>
<td>(9.3-17.3)</td>
</tr>
<tr>
<td>DI</td>
<td>D06</td>
<td>10</td>
<td>105</td>
<td>13.5</td>
</tr>
<tr>
<td></td>
<td>D07</td>
<td>9</td>
<td>109</td>
<td>15.6</td>
</tr>
<tr>
<td></td>
<td>D08</td>
<td>10</td>
<td>107</td>
<td>11.8</td>
</tr>
<tr>
<td></td>
<td>D09</td>
<td>10</td>
<td>115</td>
<td>15.0</td>
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<tr>
<td></td>
<td>D10</td>
<td>10</td>
<td>105</td>
<td>13.3</td>
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<tr>
<td></td>
<td>D11</td>
<td>10</td>
<td>102</td>
<td>10.3</td>
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<td>JS</td>
<td>J06</td>
<td>10</td>
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<td></td>
<td>J04</td>
<td>10</td>
<td>111</td>
<td>15.8</td>
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<td></td>
<td>J08</td>
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<td>J09</td>
<td>11</td>
<td>106</td>
<td>12.1</td>
</tr>
<tr>
<td></td>
<td>J02</td>
<td>10</td>
<td>111</td>
<td>14.8</td>
</tr>
</tbody>
</table>

2.3.4 Diet composition

Spatial patterns were observed in the diet contents of juvenile sockeye salmon. Larvaceans dominated the diets throughout the central zone of the Discovery Islands (D07, D09) as well as in Calm Channel (D08) and at the north end of Discovery Passage (D11), while calanoid copepods dominated all samples from Johnstone Strait and those from the southern and northern-most sites in the Discovery Islands (D06, D10) (Figure 2.4). Euphausiids also dominated the southern end of Discovery Passage (D06) by weight. Decapods contributed relatively more biomass to stomach weights at two stations in Johnstone Strait (J04 and J09), although they were also present in diets throughout the Discovery Islands (D08, D09, D10, and D11). Barnacles and cladocerans were almost entirely absent from the diets. The diets of
individual fish were usually dominated by a single taxon, however, the total number of taxa per stomach ranged from 1-15, with a median of seven taxa per stomach in both regions. Furthermore, the level of similarity within each site was higher than between sites (ANOSIM, $R = 0.75$, $p = 0.001$). Specifically, within-site similarity was highest at D11, J02, J07, and J08 and lowest at J04 and J09 (Table 2.2).

Cluster analysis identified two groups of diets based on the relative abundance of their contents, separated at 92% dissimilarity (Figure 2.5). Cluster A consisted of all sockeye from Johnstone Strait, as well as all sockeye from the southern-most site in the Discovery Islands (D06), and one from the northern-most sites (D10). Cluster B consisted of the remaining sockeye, all from sites in the Discovery Islands. The relative abundances of three taxa contributed to 75% of the differences in diet composition between clusters. Larvaceans made up a greater proportion of the diets in Cluster B, while the calanoid copepods of the *Metridia* and *Calanus* genera made up a greater proportion of the diets in Cluster A (SIMPER; Appendix B Table 2.3). Within Cluster A, there were two sub-clusters which separated at 72% dissimilarity. Cluster A1 contained most of the samples from Johnstone Strait, as well D06, and was dominated by *Calanus* spp., while Cluster A2 contained all the sockeye from J08, with some from J04 and D06 and was dominated by *Metridia* spp. (Figure 2.5). Cluster B was further divided into three sub-clusters at 61% dissimilarity. Cluster B1 contained a few outlying samples from D08 and D07 with higher proportions of amphipods and barnacles; Cluster B2, the majority of samples from the Discovery Islands dominated by larvaceans; Cluster B3, exclusively samples from D10 containing higher proportions of calanoid copepods.

When plotted using an NMDS ordination and correlated with environmental parameters, Clusters A and B were separated in non-dimensional space along a gradient of temperature and
salinity (Figure 2.6). Cluster A represented diets observed in cooler waters with higher salinity, and Cluster B represented diets found in warmer water with lower salinity. Variability in Cluster A was correlated with changes in zooplankton abundance, while variability in Cluster B was correlated with differences in temperature and salinity (BIOENV; Figure 2.6).

Diets in the Discovery Islands consisted of larger food items on average than in Johnstone Strait (Figure 2.3A). Although most prey items consumed in both regions fell within the 2-5 mm size range, 96.7% of the prey consumed in the Discovery Islands were >2 mm, while 86.9% of the diet was >2 mm in Johnstone Strait. While all sites in the Discovery Islands were dominated by prey items >2 mm, in Johnstone Strait sites J04, and J09 were dominated by prey items <2 mm (Figure 2.3B) (see Appendix B Table B.2 for prey lengths).
Figure 2.4: Relative a) abundance and b) biomass of prey items averaged from 10 stomachs per site (positioned from south to north along the x-axis) in the Discovery Islands (DI) and Johnstone Strait (JS) in June 2015. Only items contributing >5% to relative abundance/biomass are included.
Figure 2.5: Dendrogram of a cluster analysis comparing diet composition between each fish using Bray-Curtis rank dissimilarities of transformed relative abundances. Clusters A and B are coloured black and grey, respectively. Fish are coloured by migratory route for the western (red), central (orange), and eastern (pink) Discovery Islands and northern (green) and southern (blue) Johnstone Strait.
Table 2.3: Results of SIMPER analysis of juvenile sockeye salmon diets in Clusters A and B. Average relative abundances are listed for each taxon in each cluster, as well as the cumulative (Sum) contribution of each taxa to the overall dissimilarity between regions.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Average Relative Abundance</th>
<th>A</th>
<th>B</th>
<th>Sum</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Oikopleura</em></td>
<td></td>
<td>1.1</td>
<td>75.0</td>
<td>39.8</td>
</tr>
<tr>
<td><em>Metridia</em></td>
<td></td>
<td>49.8</td>
<td>1.1</td>
<td>66.1</td>
</tr>
<tr>
<td><em>Calanus</em></td>
<td></td>
<td>15.7</td>
<td>3.7</td>
<td>75.4</td>
</tr>
</tbody>
</table>

Figure 2.6: Ordination of Bray-Curtis rank dissimilarities derived from transformed relative abundance of diet items using non-metric multidimensional scaling. Ellipses represent 95% confidence intervals and identify Clusters A and B. Best environmental parameters (meantemp = mean sea surface temperature, meansal = mean sea surface salinity, z.abundance = zooplankton abundance) as identified by the BIOENV model are overlain as vectors. Samples from the Discovery Islands are in red, Johnstone Strait in blue.
2.3.5 Prey selectivity

Despite the diversity of prey taxa present in the diets and available in the surface waters, juvenile sockeye salmon selected strongly for those taxa that were greater than 2 mm in length (Figure 2.7). These larger prey items included amphipods, larvaceans, and euphausiids (see details in Appendix B Table B.2). There was also strong selection for decapods in the Discovery Islands, although they were less preferred in Johnstone Strait. Although calanoid copepods were one of the most frequently occurring prey items in the diets, they were selected against in the Discovery Islands, with moderate selection for them in Johnstone Strait (Figure 2.7). However, when selectivity was assessed using only zooplankton and diet items larger than 2 mm, there was no discernable pattern in selectivity other than a selection against larvaceans and amphipods in Johnstone Strait (data not shown).
2.3.6 Foraging success

Gut fullness indices (GFIs) were lower than the coast-wide range throughout the Discovery Islands and Johnstone Strait, with the exception of the northern and southernmost sites, D06 and J02, where they were higher (Figure 2.8; Appendix B Table B.3). Excluding these sites (due to their proximity to stratified waters beyond the study area), the median GFIs were 0.20% in the Discovery Islands and 0.48% in Johnstone Strait. The lowest GFIs measured were from the eastern-most site in Johnstone Strait (J06) with a median of 0.06% body weight. Overall, the proportion of empty stomachs was low in both regions, with 1.7% empty in the Discovery Islands and no empty stomachs in Johnstone Strait.
Figure 2.8: Median and interquartile values of gut fullness indices across samples for each site in the Discovery Islands (DI) and Johnstone Strait (JS) from June 2015. Boxplot whiskers represent the farthest non-outlier values from the median. Outliers are plotted as dots. The grey band represents the first to third quartile of gut fullness values for juvenile sockeye collected along the northeast Pacific coast from California to Alaska in 2000-2002 (Brodeur et al. 2007).

2.4 Discussion

2.4.1 Diet characterization

This study was the first to characterize the foraging ecology of juvenile salmon in well-mixed waters and described how the prey and diet composition were distributed across fine spatial scales. Diet composition was separated into two clusters along a gradient of environmental conditions. Cluster A captured the diets of juvenile sockeye in Johnstone Strait, representing a cooler environment with higher salinities where diets were dominated by calanoid copepods. Cluster B captured most of the diets in the Discovery Islands, representing warmer, fresher water, where diets were dominated by larvaceans. Within Johnstone Strait, there were
two main diet types: one dominated by *Metridia* spp. and the other by *Calanus* spp. Unlike the larvacean-dominated diets found elsewhere in the Discovery Islands, juveniles in the southern Discovery Passage consumed mostly *Metridia* spp. and *Calanus* spp., while those in the northern Discovery Islands also consumed *Calanus* spp. Furthermore, the environmental conditions of these two regions in the Discovery Islands were more closely related to those of Johnstone Strait. Therefore, the types of prey encountered and consumed by juvenile salmon are correlated to the local environmental conditions, particularly temperature and salinity. As juvenile salmon migrate through the study area, they are crossing a wide range of environmental conditions and their diets vary at the same fine spatial scale as their environment. Overall, environmental conditions and sockeye diets exhibited greater spatial heterogeneity across the Discovery Islands than in Johnstone Strait.

Although juvenile sockeye exhibited strong selective feeding behaviours, this selection appeared to be based on size, rather than on prey type; juvenile sockeye salmon consistently selected for prey items > 2 mm. This agrees with previous studies that have found salmon to be visually oriented, size-selective predators (Brodeur 1989; Ladingham et al. 1998; Schabetsberger et al. 2003; Bollens et al. 2010) that selectively prey upon food items > 1.4 mm (Craddock et al. 1976; English 1983). Selectivity is believed to be a function of prey profitability and behaviour (Healey 1991), however, abiotic factors such as light intensity and turbidity may also contribute to foraging success. Other studies have suggested that juvenile sockeye prefer copepods and insects (Healey 1980), or amphipods and larvaceans (Price et al. 2013), however, when the data were filtered to only include food items > 2 mm, juvenile sockeye appeared to be generalists, eating all taxa, with the exception of amphipods and larvaceans in Johnstone Strait, which were avoided. Sampling the prey field, however, is challenging and defining selectivity
based on net tows should be done with caution (Bollens et al. 2010). Larger zooplankton may be able to evade the net opening, causing them to be underrepresented in the prey field measurements, while smaller prey are likely to be over-represented. Therefore, there is a chance that the estimates of selectivity reported here could be biased. Furthermore, the large disparity between the surface zooplankton community and diet composition suggests that juvenile sockeye are likely feeding at various depths and not just in the top meter of the water column where the prey field was measured.

2.4.2 Bottom-up drivers of diet

Sea surface temperature, sea surface salinity, and zooplankton abundance were the environmental parameters most strongly correlated to prey and diet distributions. The Discovery Islands were warmer, fresher, and dominated by different prey than in Johnstone Strait. This study supports recent findings that recognize the Discovery Islands and Johnstone Strait as two distinct oceanographic regions along the juvenile salmon migratory corridor (Dosser, in prep; Khangaonkar et al. 2017; Mahara 2018). Since zooplankton distribution is largely determined by water movement, the zooplankton community in the Discovery Islands is similar to that seen in the Strait of Georgia (i.e. seasonal variation with small copepods and meroplankton), while the community in Johnstone Strait resembles that of the boreal shelf zooplankton communities seen in Queen Charlotte Sound (i.e. *Pseudocalanus, Calanus*, and *Acartia* spp.) (Mackas and Galbraith 2002). Therefore, as juvenile salmon travel north from the Fraser River, they encounter a range of environmental conditions. As they leave the thermally stratified and productive waters of the Strait of Georgia (Harrison et al. 1983), they may encounter foraging hotspots along a front as they cross into the dynamic narrow passages of the Discovery Islands. They then transition abruptly to the cooler, well-mixed, high nutrient-low chlorophyll waters of Johnstone
Strait (Thomson 1976; McKinnell et al. 2014) before reaching another potential foraging hotspot upon crossing into the productive waters of Queen Charlotte Strait.

Moving through these waters, juvenile salmon also experienced a shift in their prey field. The prey community changed from one in which cladocerans were the most abundant to one in which small copepods were the most. The differences in the surface zooplankton community composition in this study, however, were not statistically significant. Despite differences in the oceanographic properties of the two study regions, they are both tidally-mixed. Zooplankton are drifters and therefore the strong mixing common to both regions may have caused the two prey fields to be more similar. Furthermore, significant differences in the zooplankton communities (from full water column tows) between these two regions has been previously documented (Mahara 2018). Therefore, the surface tows in this study may not have captured larger scale differences in the prey community. Other factors, such as net avoidance by larger zooplankton and the time of day samples were collected, may have also limited the ability to measure the prey field during this study.

Furthermore, it is important to note that 2015 was an anomalously warm year due to the influence of the ‘Blob’ across the Northeast Pacific. This mass of warm water developed over the northeast Pacific in the winter of 2013/2014 due to anomalous weather patterns which reduced ocean heat loss to the atmosphere and cold water advection into the upper ocean (Bond et al. 2015). Increases in sea surface temperatures in the Strait of Georgia, however, were not as great as seen elsewhere along the BC coast (Chandler et al. 2016) and were within historical ranges (data from Chandler et al. 2017 in Mahara 2018). Furthermore, temperatures observed throughout the Discovery Islands and Johnstone Strait were similar to previous measurements in these areas (Price et al. 2013; Journey et al. 2018). Therefore, while warmer than average, the
conditions reported here are within the natural ranges observed for this area. Observations made during warmer years, however, may be useful in understanding how ecosystems could respond to a warming climate in the future.

2.4.3 **Low foraging success and the trophic gauntlet**

The fullness indices measured in this study were indicative of poor foraging success throughout the Discovery Islands and Johnstone Strait and were lower than previous values measured along the coast of southern BC. In a study spanning the Strait of Georgia and the Discovery Islands in the summers of 2009 and 2010, the average GFI reported for sockeye salmon was 1.93\% (Price et al. 2013), although values from the Discovery Islands were the lowest with a median of 0.98\%. Earlier accounts from the Strait of Georgia reported values of 0.73-1.15\% for chum, coho, and chinook salmon in the summers of 1975 and 1976 (Healey 1980). In addition, a summary of seven different sampling programs from Washington to Alaska from April to November of 2000-2002 reported median values from 0.48\% in the western Gulf of Alaska to 1.84\% off the coast of southern British Columbia (Brodeur et al. 2007). In Hecate Strait to the north, values were recorded between 0.27 and 0.86\% in the summer of 1986, which were believed to be low enough to limit growth for juvenile sockeye salmon (Healey 1991). Thus, while previous studies have recorded some of the highest GFIs along the coast of southern BC, these studies were mostly in more stable, stratifying waters. This present study measured values that were often far below previously reported ranges and more closely resembled the limiting values recorded from the north coast. This suggests that in well-mixed waters, juvenile sockeye salmon may not be consuming enough prey to meet their basic metabolic needs and supports the hypothesis that juvenile sockeye experience an energy deficit during their passage through Johnstone Strait (McKinnell et al. 2014). Although this study provides evidence that the
extent of the trophic gauntlet in fact extends to the southern end of the Discovery Islands, suggesting that juvenile salmon are likely experiencing an energy deficit over greater distances than previously expected. Furthermore, the average GFI measured in the Discovery Islands was lower than in Johnstone Strait, which is likely related to the higher proportions of smaller prey in the surface waters and of larvaceans in the diets.

However, this study also recorded exceptionally high foraging success at the southern and northern-most sites. They are situated where the stratified waters of the Strait of Georgia and Queen Charlotte Strait meet the mixed waters of the Discovery Islands and Johnstone Strait, respectively. Throughout the world’s coastal oceans, convergence of thermally stratified and mixed waters creates ‘fronts’, where productivity is notably higher than in the surrounding waters (Boyd 1973; Simpson and Hunter 1974; Perry et al. 1983; Franks 1992). The increase in productivity in such areas can be explained by the constant resupply of nutrients from depth in mixed waters to the stable, nutrient-limited surface waters nearby (Simpson and Hunter 1974). Plankton accumulate along these fronts (Franks 1992; Genin et al. 2005), attracting all manner of organisms, from cetaceans (Davis et al. 2002) to albacore tuna (Polovina et al. 2001). The ability to locate and use these dense prey aggregations can be essential for higher trophic levels to meet their energetic needs (Anraku 1975; Mohammadian et al. 1997). I suggest that the northern and southern-most sites in this study can be characterized as fronts, where juvenile salmon are able to take advantage of dense aggregations of prey along the interface between the two water masses. Higher densities of zooplankton were not detected at these sites, however, this is likely due to the limitations of horizontal surface tows in capturing prey that may be aggregating vertically in the water column. Fueling up on dense patches of prey could facilitate growth and reduce the amount of time and energy spent foraging as well as their exposure to predators. Given the low
foraging success observed in well-mixed waters, frontal areas may in fact be important hotspots for outmigrating juvenile salmon.

Throughout the well-mixed waters of the Discovery Islands and Johnstone Strait, the concentrations of zooplankton measured at the surface suggest that juvenile sockeye were not limited by the quantity of prey; similar concentrations have been observed in the northern and central Strait of Georgia (Mahara 2018, Galbraith et al. 2018) and on BC’s central coast (Tommasi 2013). Furthermore, the diets analysed in Johnstone Strait contained a higher proportion of ‘fresh’ food items than in the Discovery Islands, suggesting that they are actively feeding, despite low foraging success. Thus, the mechanisms behind the low foraging success are likely more complex and may include prey distribution and prey size. Indeed, the amount of energy required to locate and successfully capture prey can determine the relationship between food and growth (LeBrasseur 1969). While dense patches of prey may provide ample feeding opportunities for outmigrating salmon along fronts, mixed waters may have a more dispersed prey field requiring greater time and energy spent foraging.

Juvenile sockeye at sites J04, J06, and J09 had the lowest foraging success of all the Johnstone Strait sites and also contained the highest proportion of small prey items. In fact, some of the smaller taxa were found exclusively in the diets at these sites. *Pseudocalanus* spp., a small calanoid copepod typically ranging from 0.7 to 2 mm, and unidentified small calanoids (< 2 mm) were only present in the diets at sites J06 and J09. Furthermore, many of the *Aetideus* spp. measured in the diets at J04 were also < 2 mm. Therefore, the size of the prey may have limited the juveniles’ ability to fill their stomachs. This finding is consistent with those of English (1983), who found that the growth of juvenile Chinook salmon was significantly related to the abundance of medium and large zooplankton (1.4 – 4.5 mm), but not to small zooplankton (< 1.4
mm). Furthermore, English found that the ability to successfully locate prey was directly related to prey size and contrast, with larger sized prey requiring less search time. Therefore, the presence of zooplankton < 2 mm in the stomachs of juvenile sockeye in Johnstone Strait suggests that encounter rates with large zooplankton was low for these fish.

2.5 Conclusion

This study provides the first detailed description of the foraging ecology of juvenile sockeye salmon across a tidally-mixed section of their outmigration. The prey communities and diet types were described across fine spatial scales and correlated to changes in their environment. With descriptions of the quantities and types of prey being consumed in different marine environments, we are better equipped to understand the bottom-up drivers of marine survival. When paired with more detailed information on the energetic quality of their prey and salmon growth rates, we can begin to piece together the puzzle of marine survival. However, further research is required to develop these relationships.

Furthermore, strong evidence was found to support the trophic gauntlet hypothesis and map the full extent of the gauntlet. Foraging success was low compared to previous values observed along the south coast of BC, although foraging hotspots at the southern and northern-most sites were also discovered that may be providing essential energy to juveniles during this section of their outmigration. Knowing the extent and duration of poor foraging success, future research can relate this information to migration timing to quantify the duration of possible starvation. In addition, future research could investigate whether foraging hotspots like the one discovered between Johnstone Strait and Queen Charlotte Strait provide adequate resources for juvenile salmon to recover post-starvation.
While this study provides new insight into the connections between environmental conditions and juvenile salmon diets during a critical life stage, it is a snapshot in time. Further research should be done to verify whether the diet characteristics and distributions of high and low foraging success observed in this study persist throughout the migratory period and across years. In particular, continued monitoring of environmental conditions, prey dynamics, and juvenile salmon diets is required to determine if these ecological relationships are also present in years without anomalous climate events like the warm Blob of 2015. Furthermore, observing salmon diets and their prey throughout the migratory period could provide useful information on the importance of migration timing in relation to foraging success and the quality of their diets.
Chapter 3: Characteristics of juvenile sockeye salmon diets over the course of their outmigration through dynamic coastal waters

3.1 Introduction

Pacific salmon life histories are closely linked to seasonal cycles in environmental conditions (Groot and Margolis 1991; Pearcy 1992; Martins et al. 2012). For example, the timing of the juvenile outmigration can be an important determinant of their marine survival (Quinn 2005; Scheuerell et al. 2009) and may be coupled with the abundance of their prey in estuarine and marine environments (Pearcy 1992). The match-mismatch theory suggests that there is an optimal time for key life cycle events that corresponds to favourable environmental conditions (Cushing 1990). A mismatch between the timing of fish reproduction and peak biomass of zooplankton, for instance, can lead to poor recruitment (Cushing 1990; Durant et al. 2007). Previous research suggests that salmon survival is higher when the marine outmigration overlaps with periods of favourable ocean conditions, including high prey abundance (Chittenden et al. 2010; Satterthwaite et al. 2014). This synchrony allows juvenile salmon to reach a critical size and improve their chances of survival through the first winter at sea (Beamish and Mahnken 2001). However, with a changing climate, trophic interactions are becoming desynchronized, having significant ramifications for coastal food webs (Edwards and Richardson 2004; Asch et al. 2019). It is therefore important to observe and understand temporal changes in environmental conditions and prey dynamics and how they relate to foraging success during the juvenile salmon outmigration.

Every spring along temperate coastal margins, the longer photoperiod, warmer temperatures, and increased stratification initiate a spring phytoplankton bloom, which supports
seasonal cycles of productivity throughout the food web (Harrison et al., 1983; Boyce et al., 2017). Phytoplankton and zooplankton abundance are positively correlated; an increase in phytoplankton concentration often leads to zooplankton growth and reproduction, resulting in peak zooplankton biomass shortly after the peak of the spring bloom (Harrison et al. 1983; Ware and Thomson 2005). Similarly, life history events of higher trophic levels, including fish, often coincide with periods of peak prey biomass (Groot and Margolis 1991). However, productivity along the coastal margin of the northeast Pacific is highly variable, and not all regions experience the same seasonal cycles (Ware and Thomson 2005).

The availability of nutrients and light required for phytoplankton growth are determined by the mixing and stratification of the water column (Pingree 1978). Increased stability and nutrient concentrations in surface waters can generate high rates of primary production, however, such systems become nutrient-limited as growing phytoplankton rapidly deplete available nutrients (Barry and Dayton 1991). In contrast, well-mixed regions often have sufficient nutrients to support primary producers, however, phytoplankton are constantly being mixed to depth, becoming light-limited. The most productive waters have been found in the frontal regions between stratified and mixed regions, where nutrient entrainment from depth meets with nutrient-limited surface waters (Pingree 1978). These frontal regions can also support aggregations of zooplankton and higher trophic levels (Pingree et al. 1974). Along the coast of British Columbia, the transition between these ocean environments occurs across both fine and coarse spatial scales (Perry et al. 1983), influencing the physical water properties experienced by migrating salmon and the distributions of their prey.

The Fraser River is the largest sockeye salmon system in British Columbia. Every spring, sockeye fry migrate down the Fraser towards the ocean where they emerge into the highly
stratified and productive waters of the Strait of Georgia. During this initial marine period, juvenile sockeye forage on a wide range of zooplankton, insects, and fish (Osgood et al. 2016), with an increase in decapods and amphipods observed in the diets in recent years (Preikshot et al. 2010; Neville et al. 2016). The vast majority of sockeye continue north, transiting the well-mixed and relatively unproductive waters of the Discovery Islands and Johnstone Strait, a region postulated to be a trophic gauntlet for migratory salmon (McKinnell et al., 2014), before reaching the productive waters of Queen Charlotte Strait (Welch et al. 2009). It has been hypothesized that during migration through this highly dynamic region juvenile salmon incur an energy deficit (McKinnell et al. 2014). Reduced growth in these well-mixed regions supports this hypothesis (Ferriss et al. 2014; Journey et al. 2018). The primary factor influencing growth is the quantity and quality of prey consumed (Beauchamp 2009), yet prior to this study, no research has explored the diets of juvenile sockeye through the presumed trophic gauntlet.

This study aims to measure the intra- and interannual dynamics of environmental conditions, the salmon prey field, and salmon diets, across two different regions of the coastal migration: a seasonally stratified area of the southern Discovery Islands and the well-mixed Johnstone Strait. Specifically, the main objectives are to measure a) how surface zooplankton communities, juvenile sockeye diets and foraging success change over the migratory period, b) how migration timing and environmental conditions are correlated to diets and foraging success, and c) whether the ‘trophic gauntlet’ exists and persists throughout the migratory period. Furthermore, sampling across fine temporal scales over two years will shed light on the importance of migration timing and prey phenology in determining juvenile sockeye diets. It was expected that the prey and diet composition would differ between the Discovery Islands and Johnstone Strait, and that the Discovery Islands would exhibit greater temporal variation due to
its broader spatiotemporal heterogeneity in environmental conditions. Furthermore, it was expected that foraging success would be higher and more variable in the Discovery Islands, but low in Johnstone Strait throughout the migratory period. This study provides new insight into the foraging dynamics of juvenile salmon in mixed coastal waters, and explores the relationships between the environment, prey, and salmon under changing ocean conditions. Understanding these relationships can improve our ability to forecast marine survival and model trophic interactions in a changing climate.

3.2 Methods

3.2.1 Study area

This study compares two distinct oceanographic regions: the Discovery Islands and Johnstone Strait (Figure 3.1). Water in the Discovery Islands is mostly sourced from the Strait of Georgia to the south, whereas water is advected into Johnstone Strait via Queen Charlotte Sound and Queen Charlotte Strait (Khangaonkar et al. 2017). While both are characterized by strong tidal mixing, a series of shallow sills at the eastern end of Johnstone Strait creates a density front that limits water exchange between the two regions (Dosser in prep). Thus, even though these two bodies of water are adjacent to one another, the Discovery Islands are warmer and less saline than Johnstone Strait, which is subject to a stronger oceanic influence due to its proximity to Queen Charlotte Sound and the coastal upwelling that occurs along the continental shelf (Dosser in prep).
In 2015 and 2016, juvenile salmon were sampled at high spatial and temporal resolution in the Discovery Islands and Johnstone Strait during the period of outmigration as part of the ongoing Hakai Institute Juvenile Salmon Program. For the purpose of this study, the site with the best temporal coverage throughout the migratory period was selected for each region. The Discovery Islands sampling site, D07, was located in Hoskyn Channel south of Surge Narrows, located between Quadra Island and Read Island. While this site experiences tidal mixing, it is located south of the tidal rapids through the Discovery Islands, and still exhibits thermal stratification and relatively high productivity in the spring and summer months (Mahara 2018). Furthermore, of six different locations surveyed in the Discovery Islands, this site had the highest
zooplankton abundance and biomass (Chapter 1; this study). This site represents intermediate conditions between the fully stratified waters to the south and fully mixed waters to the north, however, due to the presence of seasonal stratification, it is classified as a ‘stratified’ site for the purposes of this study. The Johnstone Strait site, J07, was located midway along the Strait at Saint Vincent Bight, where productivity remains low year-round and is classified as a ‘well-mixed’ site (Figure 3.1).

3.2.2 Zooplankton and environmental data collection

The zooplankton prey field was measured by collecting a horizontal surface tow at each sampling location after fish samples were taken (n = 19). Sampling targeted surface waters as salmon are visual feeders and it is believed that they feed near the surface (Brodeur 1989; Landingham et al. 1998). A 250 µm mesh zooplankton net equipped with a flowmeter was towed behind the boat through the top meter of the water column as the boat travelled in a wide circle for three minutes, or until there was visible coloration in the cod-end. Samples were preserved in 10% buffered formalin-seawater solution in the field. The volume of water filtered was calculated as:

\[ \text{Volume} = \pi r^2 \times \text{Distance} \]

In the lab, zooplankton were size fractioned using a 250, 1000, 2000 µm sieve stack. Each size fraction was blotted dry and weighed to the nearest 0.1 mg (wet weight). When small zooplankton were abundant, the 250 µm size fraction was split until a subsample of approximately 300 specimens was achieved to facilitate analysis. Samples were then poured into a Bogorov tray to be measured and identified to the lowest taxonomic level possible.

A Yellow Springs Instruments (YSI) Pro30 was used to measure water temperature and salinity at the surface and at 1 m, along with a Secchi disc to measure water clarity.
Environmental measurements were taken at each site after the fish had been collected and processed.

3.2.3 Fish sample collection and processing

Juvenile sockeye salmon were collected at both sites between May and June in 2015 and 2016 to capture the peak outmigration. Samples were collected using a modified purse seine deployed from an eight-meter twin-outboard motored vessel. From each seine, up to thirty sockeye were retained and euthanized using a lethal dose of MS-222 before being frozen in cryogenic dry shippers for transport and transferred to -80 °C freezers in the laboratory. Of these, ten sockeye were randomly selected for detailed dissections and analyses with 200 juvenile sockeye analyzed in total for this study.

Stomachs were removed and stored in 95% ethyl alcohol. Ethanol preservation can make samples brittle and difficult to manipulate. Therefore prior to analysis, stomachs were removed from the preservative and soaked in tap water for 30 minutes for rehydration. Samples were then blotted dry and weighed to the nearest 0.1 mg. Ethanol preservation can also cause samples to lose weight (Wetzel et al. 2005), therefore an ethanol conversion factor was applied to stomach content weights to revert them to ‘fresh’ weights and make them comparable with fish weights and other diet weights in the literature (see Appendix A).

Stomachs were cut open from the start of the esophagus to the pyloric sphincter and a visual estimate of stomach fullness was recorded as one of five categories: empty, 1-25, 26-50, 51-75, or 76-100% full. ‘Empty’ stomachs were those visually assessed as containing no food. Contents were then removed, weighed, and identified to the lowest taxonomic resolution possible using a Zeiss Stemi 508 microscope. Average lengths were taken for each taxonomic group,
allowing prey items to be grouped into one of five size categories: <1, 1-2, 2-5, 5-10, and >10 mm. Each taxonomic group was counted and weighed to determine abundance and biomass.

3.2.4 Data analysis

Two-way analysis of variance (ANOVA) was used to assess differences in zooplankton abundance and biomass, juvenile sockeye gut fullness indices, and diet variability between regions and years. To meet assumptions of normality, zooplankton data were first natural log-transformed and gut fullness indices (GFIs) were square-root-transformed. When significant differences were observed, Tukey honestly significant difference (HSD) tests or visual observations were conducted to determine which year or region had higher values.

For visualization of zooplankton and diet composition data, the taxonomic categories were simplified into the following major groups: Amphipod, Barnacle, Calanoid Copepod, Cladoceran, Decapod, Euphausiid, Larvacean, and ‘Other’. Detailed taxonomic information was retained for multivariate analyses.

Analyses of zooplankton and diet community composition were performed using non-parametric, multivariate techniques. Relative abundance and biomass data were arcsin-square-root-transformed to spread out the distribution of values and reduce the influence of abundant or rare species (Zar 1999). These data were compared using average linkages to generate a Bray-Curtis dissimilarity matrix, which determines ranked differences between community assemblages. An analysis of similarity (ANOSIM), the non-parametric multivariate analogue to ANOVA, was conducted to determine statistical differences in prey and diet composition between regions and years (Clarke 1993). This method compares within and between group differences, producing a global $R$-value which approaches ‘0’ when within group differences are greater than between group differences, and approaches ‘1’ when the opposite is true. When
significant differences were detected between groups, a similarity percentages test (SIMPER) was conducted to determine which taxa best explained the differences between groups. To visualize the fine-scale differences between groups, ranked differences were projected into a two-dimensional ordinate space using non-metric multidimensional scaling ordination. The compression of multidimensional relationships into two-dimensional space creates ‘stress’ and ordinations with stress values ≥ 0.2 should not be used to assess differences in community structure (Clarke 1993). The ordination plots samples (stomachs or tows) that are more similar closer together, and those that are dissimilar further apart. In addition, a version of Clarke and Ainsworth’s (1993) BIO-ENV model was run to determine which environmental parameters had the maximum correlation with the community rank dissimilarities (Oksanen 2018). The best model outputs were overlain on the ordinations as vectors with the direction of the arrow indicating an increase in the value of that parameter.

A gut fullness index (GFI) was used as a measure of foraging success, expressed as the proportion of the fish body weight made up by the stomach contents:

\[ GFI = \frac{M_{sc}}{M} \times 100 \]

where \( M_{sc} \) is the mass of the stomach contents (g) and \( M \) is the mass of the fish (g). This formula standardizes for differences in fish size (Chipps and Garvey 2007). GFIs from this study were compared to a regional interquartile range of juvenile sockeye salmon GFIs adapted from Brodeur et al. (2007), who compiled diet information for juvenile Pacific Salmon from northern California to the Gulf of Alaska from 2000 – 2002.

The GFIs were evaluated against ten environmental and temporal parameters using Spearman’s rank correlations. Temporal parameters included the day of the year and time of day; environmental parameters included mean sea surface temperature and salinity, Secchi depth,
zooplankton abundance and biomass, the relative abundance of zooplankton larger than 2 mm, and the relative biomass of zooplankton in the larger size fractions (1000 µm sieve or higher). Finally, fish fork lengths were also compared to GFI to test for ontogenetic diet shifts. The statistic rho ($r_s$) from the correlation can be used to measure effect size, with 0.10 to < 0.30 representing a small effect size, 0.30 to < 0.50 a medium effect size, and ≥ 0.50 a large effect size (Cohen 1988). Only those parameters with medium to large effect sizes are discussed.

All statistical analyses were conducted in R statistical software v3.5.2 (R Development Core Team 2018) with multivariate analyses performed using the “Vegan” package (Oksanen 2018).

3.3 Results

3.3.1 Environmental conditions

Environmental conditions in the Discovery Islands were more variable over the course of the sockeye migratory period than in Johnstone Strait (Table 3.1). Sea surface temperatures varied by as much as 6.4 (1.2) °C and surface salinity by 3.5 (2.3) psu in the Discovery Islands (Johnstone Strait). Furthermore, Secchi depths in the Discovery Islands showed evidence of seasonal productivity, with shallow readings early in the migratory period suggesting higher productivity, whereas Secchi readings were consistently deep in Johnstone Strait, suggesting low productivity throughout the migratory period. Interannual comparisons showed little difference in temperatures for each region, however, salinity in Johnstone Strait was higher in 2016 than 2015. Conditions in the Discovery Islands in mid-June 2015, were much cooler with higher salinities and deeper Secchi readings than in any other time during the two years of sampling.
Table 3.1: Environmental parameters measured at both sites after each set on a school of salmon in the Discovery Islands (DI) and Johnstone Strait (JS). Temperature and salinity values are an average of the surface and 1m measurements collected with a YSI. Zooplankton abundance (individuals/m$^3$) and biomass (mg/m$^3$) were collected from a single surface tow at each site.

<table>
<thead>
<tr>
<th>Region</th>
<th>Year</th>
<th>Date</th>
<th>Temperature (°C)</th>
<th>Salinity (psu)</th>
<th>Secchi (m)</th>
<th>Zoop Abund (ind/m$^3$)</th>
<th>Zoop Biom (g/m$^3$)</th>
</tr>
</thead>
<tbody>
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<td>DI</td>
<td>2015</td>
<td>16-May</td>
<td>14.1</td>
<td>27.4</td>
<td>5</td>
<td>2,619</td>
<td>0.112</td>
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<td></td>
<td></td>
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<td>27.8</td>
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<td>2,640</td>
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<td></td>
<td></td>
<td>05-Jun</td>
<td>18.2</td>
<td>25.4</td>
<td>15</td>
<td>3,847</td>
<td>1.245</td>
</tr>
<tr>
<td></td>
<td></td>
<td>09-Jun</td>
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<td>28.6</td>
<td>12</td>
<td>673</td>
<td>0.037</td>
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<tr>
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<td>13-Jun</td>
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<td>11</td>
<td>115</td>
<td>0.020</td>
</tr>
<tr>
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<td>15.2</td>
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<td>2</td>
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<td>27.7</td>
<td>4</td>
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<tr>
<td>JS</td>
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<td>03-Jun</td>
<td>15.7</td>
<td>25.8</td>
<td>9</td>
<td>9,616</td>
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</tr>
<tr>
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<td>3,192</td>
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<td>9</td>
<td>2,149</td>
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<td>28.9</td>
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<td>28.9</td>
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<tr>
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<td>29.2</td>
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<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td></td>
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<td>10.0</td>
<td>31.4</td>
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<td>31.5</td>
<td>12</td>
<td>409</td>
<td>0.894</td>
</tr>
<tr>
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<td></td>
<td>11-Jun</td>
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<td>30.8</td>
<td>13</td>
<td>445</td>
<td>0.093</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20-Jun</td>
<td>10.3</td>
<td>30.6</td>
<td>13</td>
<td>1,034</td>
<td>1.022</td>
</tr>
</tbody>
</table>

3.3.2 Prey Field

Zooplankton abundance and biomass were highly variable across the one-month sampling period in both regions (Table 3.1). In 2015, the highest abundance of zooplankton in the Discovery Islands was observed mid-season on June 5$^{th}$, with the lowest abundance observed at the end of the sampling period in mid-June. In Johnstone Strait, the opposite pattern was observed, with the highest abundance observed during the last sampling event on June 29$^{th}$, with the lowest abundance in the first week of June. In 2016, both regions experienced high
zooplankton abundances early in the season with peak zooplankton abundance occurring three weeks earlier in the Discovery Islands and four weeks earlier in Johnstone Strait than in 2015. Abundances early in 2016, however, were more than six times higher in the Discovery Islands than in 2015. Zooplankton biomass exhibited similar trends (Table 3.1).

Zooplankton biomass was significantly different between years (ANOVA; $p = 0.03$), with higher biomass in 2016 than in 2015 in both regions (Figure 3.2). Zooplankton abundance was higher in 2016 in the Discovery Islands, with abundances more than double those of 2015 throughout the entire sampling period (Table 3.1). No significant difference was detected in zooplankton abundance or biomass between the two regions. Zooplankton size distributions, however, varied by year and region, with a higher relative biomass of large (>2 mm) zooplankton in 2015 in the Discovery Islands and in 2016 in Johnstone Strait (Appendix B, Figure B.6). Overall, zooplankton samples were dominated numerically by organisms less than 1 mm in size in both years in both regions.
Figure 3.2: Abundance (individuals/m$^3$) and biomass (g/m$^3$) of zooplankton in the surface waters of two sites in the Discovery Islands (DI) and Johnstone Strait (JS) in 2015 and 2016.

The variability in surface zooplankton community composition was higher within years than between years (ANOSIM, $R = -0.1$, $p = 0.973$). In the Discovery Islands, May was dominated by barnacle nauplii and cladocerans while calanoid copepods and ‘other’ zooplankton increased in abundance in June (Figure 3.3). In Johnstone Strait, calanoid copepods were relatively abundant throughout the migratory period, however, cladocerans and barnacle nauplii were also more abundant early in the migratory period. ‘Other’ zooplankton taxa increased in abundance later in June. ‘Other’ zooplankton are described in greater detail for samples in which they contributed more than 50% to total abundance. In the Discovery Islands, this occurred in June 2015, wherein ‘other’ was composed predominantly of gastropod eggs. In Johnstone Strait, the samples from June 29, 2015 and June 20, 2016 contained large numbers of euphausiid eggs (data not shown).
Figure 3.3: Relative abundance of zooplankton taxa in each sample at two sites in the Discovery Islands (DI) and Johnstone Strait (JS) in 2015 and 2016.

There was also a greater difference in zooplankton community composition between the two regions than within each region (ANOSIM; $R = 0.731$, $p = 0.001$). The taxa contributing most to the difference between regions include *Evadne* spp., barnacles, *Acartia* spp., and *Pseudocalanus* spp. (SIMPER; Appendix B Table B.4). Proportions of *Evadne* spp. and barnacles were higher in the Discovery Islands, while proportions of *Acartia* and *Pseudocalanus* spp. were higher in Johnstone Strait.

The NMDS ordination of the zooplankton community data demonstrated the changes in composition in relation to temporal and local environmental parameters (Figure 3.4). The
difference within and between samples was best correlated to a model containing four parameters: day of the year, time of day, surface temperature, and surface salinity (BIOENV; \( r = 0.67 \)). Zooplankton communities were separated along a temperature-salinity gradient, with warmer temperatures and less saline water correlated with communities in the Discovery Islands and cooler temperatures and more saline water correlated with communities in Johnstone Strait (Figure 3.4). The types of zooplankton within each cluster varied with the day of year and the time of day.
3.3.3 Fish

In the Discovery Islands, the largest fish of each migratory period were caught during the first sampling event, followed by some of the smallest fish the following week (Table 3.2). In Johnstone Strait, the largest fish were also observed during the first sampling event of 2015, however, in 2016, the largest fish were observed at the end of the migratory period. On average, the juvenile sockeye sampled in 2015 were larger than those captured in 2016 in both regions.
Table 3.2: Locations, dates, sample sizes (n), median fork lengths (FL) (mm), and fish weight (FW) (g) with ranges in parentheses for the juvenile sockeye salmon collected from the two sites in Discovery Islands (DI) and Johnstone Strait (JS) for this study.

<table>
<thead>
<tr>
<th>Location</th>
<th>Year</th>
<th>Date</th>
<th>n</th>
<th>FL (range)</th>
<th>FW (range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DI</td>
<td>2015</td>
<td>16-May</td>
<td>10</td>
<td>102 (94-128)</td>
<td>10.9 (9-22.5)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>21-May</td>
<td>10</td>
<td>100 (96-104)</td>
<td>9.8 (7.8-11.2)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>05-Jun</td>
<td>9</td>
<td>109 (104-119)</td>
<td>15.6 (11.9-19.3)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>09-Jun</td>
<td>10</td>
<td>106 (104-114)</td>
<td>14.2 (12.2-17.1)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>13-Jun</td>
<td>10</td>
<td>103 (90-119)</td>
<td>13.5 (9.1-18.3)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total</td>
<td>Median 49</td>
<td>104</td>
<td>12.9</td>
</tr>
<tr>
<td></td>
<td>2016</td>
<td>14-May</td>
<td>10</td>
<td>114 (88-128)</td>
<td>12.9 (5.6-17)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>26-May</td>
<td>10</td>
<td>92 (79-98)</td>
<td>6.4 (5.8-8.1)</td>
</tr>
<tr>
<td></td>
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<td>10</td>
<td>94 (89-104)</td>
<td>7.8 (6.6-9.4)</td>
</tr>
<tr>
<td></td>
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<td>10</td>
<td>92 (84-110)</td>
<td>8.4 (7-10.4)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>16-Jun</td>
<td>10</td>
<td>97 (88-103)</td>
<td>8.6 (6.7-11.3)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total</td>
<td>Median 50</td>
<td>95</td>
<td>8.2</td>
</tr>
<tr>
<td>JS</td>
<td>2015</td>
<td>26-May</td>
<td>9</td>
<td>109 (99-130)</td>
<td>16.8 (10.5-25.2)</td>
</tr>
<tr>
<td></td>
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<td>11</td>
<td>115 (101-132)</td>
<td>14.6 (11.4-19.8)</td>
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<td>18.3 (11.6-22.5)</td>
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<tr>
<td></td>
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<td>Total</td>
<td>Median 51</td>
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<td>18.0</td>
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<tr>
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<td>2016</td>
<td>21-May</td>
<td>10</td>
<td>97 (92-118)</td>
<td>8.8 (7.1-14.3)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>27-May</td>
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<td>90 (85-99)</td>
<td>7.3 (5.9-7.9)</td>
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<tr>
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<td>9.2 (7.2-13.8)</td>
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<td>11-Jun</td>
<td>10</td>
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<td>10.9 (8.4-14.4)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20-Jun</td>
<td>10</td>
<td>114 (103-128)</td>
<td>13.9 (10.6-16.9)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total</td>
<td>Median 50</td>
<td>102</td>
<td>9.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total</td>
<td>Mean 200</td>
<td>104</td>
<td>11.6</td>
</tr>
</tbody>
</table>

3.3.4 Diet composition

Over the migratory period, diet variability was significantly greater in the Discovery Islands than in Johnstone Strait (ANOVA; p < 0.001). In 2015, cladocerans dominated diets numerically early in the migration through the Discovery Islands, transitioning to larvaceans in early June and to calanoid copepods by mid to late June (Figure 3.5). In 2016, ‘other’ zooplankton, in this case zooplankton eggs, and barnacles dominated early in the migratory
period and in early June, while larvaceans dominated in the other time periods. In Johnstone Strait, calanoid copepods dominated numerically throughout the migration in both years, although larvaceans were also present early in the migration (Figure 3.5). Diet composition was similar by weight (Appendix B Figure B.7). Microplastics (plastic pieces \( \leq 5\)mm) were found in 3.1% of all stomachs and were equally distributed between the two regions, however, they never constituted more than 5% of the diet. In both regions, the diets of individual fish were often dominated by one or two taxa.

Figure 3.5: Relative abundance of taxa in the diets of juvenile sockeye salmon averaged from 10 stomachs per sampling event in the Discovery Islands (DI) and Johnstone Strait (JS) in 2015 and 2016. Only items contributing > 5% to relative abundance are included.
Overall, diet composition varied significantly by region (ANOSIM; $R = 0.42$, $p = 0.001$), with no significant difference between years (ANOSIM; $R = 0.06$, $p = 0.002$). The average dissimilarity in diets between the Discovery Islands and Johnstone Strait showed that differences in relative abundances of *Calanus* spp., larvaceans, *Metridia* spp., and barnacles contributed to 50.8% of the difference between regions (SIMPER; Appendix B Table B.6). Diets in the Discovery Islands exhibited higher variability than in Johnstone Strait, and while the majority of the diets were separated between the two regions in the NMDS ordination, diets from mid-June, 2015, closely resembled those in Johnstone Strait (Figure 3.6). Furthermore, of the temporal and environmental parameters used in the BIOENV analysis, the combination of mean sea surface temperature and zooplankton abundance was best correlated to the differences in diet composition overall (Figure 3.6; Appendix B Table B.7). Inter-regional differences appeared to be more strongly related to differences in mean sea surface temperature, with warmer temperatures corresponding to the Discovery Islands diets and cooler temperatures to Johnstone Strait diets. Intra-regional variation in diets appeared to be driven largely by changes in zooplankton abundance.
Figure 3.6: Non-metric multidimensional scaling ordination of Bray-Curtis rank dissimilarities derived from transformed diet compositions of juvenile sockeye salmon in the Discovery Islands (DI) and Johnstone Strait (JS). Ellipses represent 95% confidence intervals around the mean of each location (red = DI, blue = JS). Best environmental parameters as identified by the BIOENV model are overlain as vectors (meantemp = mean sea surface temperature, z.abundance = zooplankton abundance). Circles represent samples from 2015; triangles, from 2016.

The abundance and biomass of large prey (>2 mm) was higher in 2015 than in 2016 in both regions, although the Discovery Islands diets had a higher proportion of diet items <1 mm than in Johnstone Strait in both years (Appendix B Figure B.8).

3.3.5 Foraging success

In the Discovery Islands, GFI s (gut fullness indices) in 2015 ranged from 0.26% at the beginning of the season to 1.58% by the end (Figure 3.7). However, in 2016, GFI s remained
fairly constant at the lower end of expected values for the coast (0.48-1.59\%, adapted from Brodeur et al. 2007). In Johnstone Strait, GFIs were variable in both years, with values ranging from 0.01 to 1.01\% in 2015 and from 0.28 to 1.32\% in 2016 (Figure 3.7). The only empty stomachs observed in this study were from Johnstone Strait in 2015, where 16\% of the stomachs sampled were empty. All but one of the empty stomachs were measured in the first arrivals on May 26th, when 78\% of the stomachs were empty.

Figure 3.7: Average gut fullness indices for juvenile sockeye salmon sampled in the Discovery Islands (DI) and Johnstone Strait (JS) in 2015 and 2016. Boxes represent the first to third quartile around the median (center line), with whiskers reaching to farthest non-outlier values. Outliers are displayed as dots. The grey bands represent the interquartile range of gut fullness values for juvenile sockeye collected along the Pacific coast from California to Alaska in 2000-2002 (Brodeur et al. 2007).

No difference in GFIs was detected between years, however, values in the Discovery Islands were significantly higher than in Johnstone Strait in 2015 (Tukey HSD, \( p = 0.001 \)).
was no significant difference between locations in 2016. Although the difference between years was not significant, GFIs in the Discovery Islands were higher in 2015 than in 2016 (Appendix B Table B.8).

In the Discovery Islands, the GFI was significantly correlated to all ten explanatory variables with the strongest positive correlation to Secchi depth ($r_s = 0.61$, $p < 0.001$). GFI was also positively correlated to day of year, time of day, surface salinity, and the relative biomass of large zooplankton with medium effect sizes (Table 3.3). The GFI was negatively correlated to surface temperature, zooplankton biomass, and the relative abundance of large zooplankton with medium effect sizes, and to zooplankton abundance with a large effect size. In Johnstone Strait, the GFI was significantly negatively correlated to zooplankton abundance and positively correlated with the relative abundance and biomass of large zooplankton. The strongest correlation was to the relative abundance of large zooplankton ($r_s = 0.50$, $p < 0.001$) (Table 3.3).

Table 3.3: Spearman’s rank correlations ($r_s$) between the explanatory variables and gut fullness indices in the Discovery Islands and Johnstone Strait, including significance of the correlation (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns = not significant).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Discovery Islands</th>
<th>Johnstone Strait</th>
</tr>
</thead>
<tbody>
<tr>
<td>Day of year</td>
<td>0.48***</td>
<td>-0.11 ns</td>
</tr>
<tr>
<td>Time of day</td>
<td>0.48***</td>
<td>0.16 ns</td>
</tr>
<tr>
<td>SST</td>
<td>-0.34***</td>
<td>0.00 ns</td>
</tr>
<tr>
<td>SSS</td>
<td>0.33 **</td>
<td>-0.04 ns</td>
</tr>
<tr>
<td>Secchi</td>
<td>0.61***</td>
<td>0.05 ns</td>
</tr>
<tr>
<td>Z abundance</td>
<td>-0.52***</td>
<td>-0.30 **</td>
</tr>
<tr>
<td>Z biomass</td>
<td>-0.45***</td>
<td>0.06 ns</td>
</tr>
<tr>
<td>% abundance large Z</td>
<td>-0.30 **</td>
<td>0.50***</td>
</tr>
<tr>
<td>% biomass large Z</td>
<td>0.30 **</td>
<td>0.19 *</td>
</tr>
<tr>
<td>Fork length</td>
<td>0.17 *</td>
<td>-0.12 ns</td>
</tr>
</tbody>
</table>
3.4 Discussion

This study found significant differences between the environmental conditions, prey fields, and diets encountered by juvenile sockeye salmon over the course of their outmigration through two markedly different oceanographic regions. As expected, the more stratified site in the Discovery Islands exhibited warmer temperatures and lower salinity than the mixed waters of Johnstone Strait, but also greater variability in environmental conditions over the migratory period. Zooplankton community composition was significantly different between regions, and the timing of peak zooplankton abundance varied between years. Despite the differences in environmental conditions and taxonomic composition, zooplankton biomass was not lower in Johnstone Strait than in the Discovery Islands. Juvenile sockeye diets were also significantly different between regions, with lower variation in well-mixed waters. Foraging success (as measured by gut fullness indices) was surprisingly low in the Discovery Islands, however, small-scale weather-induced turbulence may have provided brief periods of improved foraging conditions. Also unexpected was the high degree of variability in foraging success in Johnstone Strait. While foraging success in mixed waters was often lower than the coast-wide range, there were times when foraging success was within or higher than the coast-wide range. Overall, the GFIs observed in this study suggested that the trophic gauntlet extends beyond the mixed waters of Johnstone Strait to the southern extent of the Discovery Islands. While most migrating salmon may experience low foraging success navigating the gauntlet, the fine scales at which environmental and prey conditions vary can also create periods of favourable foraging conditions.
3.4.1 Prey phenology and migration timing

This study captured fine scale variability in zooplankton phenology in the surface waters of two distinct oceanographic regions along the coastal migratory pathway of juvenile sockeye salmon. Although the highest zooplankton abundances were observed later in 2015 than in 2016, the difference in magnitude suggests that the 2015 survey may not have captured the true seasonal peak in zooplankton. Indeed, research conducted by Mahara (2018) concurrent with this program observed peak zooplankton abundance in the central Discovery Islands at the end of April, 2015, and near May 20, 2016. Therefore, peak zooplankton abundance in the Discovery Islands did not occur during the juvenile sockeye migration in 2015 but did in 2016. The difference in zooplankton phenology is likely related to the marked difference in spring bloom timing between the two years. The 2015 phytoplankton bloom occurred six weeks earlier in 2015 (late February) than in 2016 (early April), likely due to earlier surface stratification (Mahara 2018). In mixed waters, seasonal peak abundances were substantially lower than those measured in stratified waters, although there was no significant difference in zooplankton abundance or biomass overall between the two regions.

Despite the difference in zooplankton timing, juvenile sockeye salmon arrived in the Discovery Islands and Johnstone Strait at the same time in both years. Juvenile sockeye were first captured in the Discovery Islands on May 12, 2015 and May 13, 2016. The peak outmigration, or the date at which 50% of the juveniles had passed through the area, was on May 31, 2015 and May 30, 2016 (Johnson et al. 2018). Sockeye were first captured in Johnstone Strait on May 20 in both years with peak migrations on June 3 and June 6 in 2015 and 2016, respectively. Therefore, the peak outmigration through the Discovery Islands occurred four weeks after the peak in zooplankton abundance in 2015, and only 1.5 weeks after the peak in
2016. While the Discovery Islands waters are sourced primarily from the Strait of Georgia, waters in Johnstone Strait, and the zooplankton communities carried with them, are sourced from Queen Charlotte Strait. Therefore, trends in zooplankton abundance observed in Johnstone Strait are likely related to trends in productivity in Queen Charlotte Strait, rather than the Strait of Georgia. Thus, in 2015 there was in fact a two-month interval between peak prey abundance in each region. Therefore, juvenile sockeye arrived in Johnstone Strait five weeks after the peak in zooplankton abundance in the southern Discovery Islands and almost four weeks prior to the peak observed in Johnstone Strait. In 2016, they arrived during the peak zooplankton abundance in both regions. This interannual shift in prey phenology relative to migration timing likely influenced the foraging opportunities and therefore condition of juvenile sockeye during their migration through these waters.

The foraging success of the earliest migrants was exceptionally low in 2015 in both regions. In the Discovery Islands, temperatures were warm, prey were relatively abundant, and Secchi depths were shallow at that time. The only sockeye with high foraging success in the Discovery Islands were those captured in mid-June 2015, when conditions were somewhat anomalous relative to the other data collected at this site in both years. Temperatures dropped significantly, Secchi depths increased, zooplankton abundance was the lowest, and diets shifted to contain calanoid copepods predominantly. Historical weather data from the Campbell River airport weather station (Weather Underground) show that the strongest winds of the entire migration occurred in the second week of June, which likely generated enough turbulence to mix the stratified surface layer, bringing cooler temperatures and nutrients from depth (Figure B.9). While small-scale mixing may have dispersed otherwise dense aggregations of small prey at the surface resulting in low measurements of zooplankton abundance, larger zooplankton typically
occurring in deeper waters may also have been brought to the surface. Indeed, higher concentrations of zooplankton were not observed in the horizontal tows, however, stomachs were the fullest, suggesting either that larger zooplankton are better at avoiding the zooplankton net, or that prey were distributed in a way that was better captured by fish than by horizontal zooplankton tows.

In Johnstone Strait, the extended interval between periods of prey abundance in 2015 may have resulted in a trophic mismatch, causing the high proportion of empty stomachs (78%) observed at the start of the migration. Surface temperatures at that time were also the coldest and zooplankton biomass the lowest. Interestingly, despite the mismatch between salmon and their prey, the highest foraging success of 2015 was observed during the peak outmigration in the first week of June. This coincided with the period of highest foraging success in the Discovery Islands, and stomachs from both regions were dominated by large numbers of *Metridia* spp. Similar to the Discovery Islands, historical weather data from the Port Hardy airport weather station (Weather Underground) also show four days of strong winds at the end of May, which may have increased the abundance of larger copepods (i.e. *Metridia* spp.) in the upper water column of Queen Charlotte Strait prior to being transported into Johnstone Strait (Appendix B Figure B.9). The current study did not analyze wind speeds, therefore no correlations can be made between diets and weather events, however, their impact on prey distributions could be an area for future research.

In contrast to 2015, the first sockeye to enter Johnstone Strait in 2016 had the highest foraging success of that year’s outmigration. No zooplankton sample was collected at this time, however, data from Mahara (2018) for this region suggest that abundance was relatively high (4,000 – 7,000 individuals/m³ from full water column samples). Furthermore, in this study, the
same type of prey was available during the early migration in both years (*Acartia* spp.), and environmental conditions were similar, therefore the increase in the quantity of prey is likely responsible for the higher foraging success.

Although this study period only spanned four weeks, clear ‘seasonal’ patterns were still observed in surface zooplankton communities in both regions and were stronger than interannual differences. Barnacles and cladocerans had the highest relative abundances in the Discovery Islands in mid- to late May, shifting to calanoid copepods and gastropod eggs in early June. Calanoid copepods were relatively abundant in Johnstone Strait throughout the migratory period, however, barnacles and cladocerans were also present at the end of May and early June, while euphausiid eggs dominated in mid- to late June. Within the calanoid copepods, *Acartia* spp. were more abundant at the end of May and *Pseudocalanus* spp. in June. These temporal patterns are typical of this region (Harrison et al. 1983) wherein the spring phytoplankton bloom incurs reproduction in surface zooplankton and other marine invertebrates and a migration of deep water copepods (e.g. *Calanus* and *Metridia* spp.) to the surface.

Thus, the phenology of juvenile salmon prey varies by region over fine temporal scales, affecting the quantity and quality of food available during the outmigration. The first juvenile sockeye reached the Discovery Islands when the early developmental stages (i.e., eggs, larvae, nauplii) of zooplankton were in high abundance. The energy density of these zooplankton is relatively low (2,280 J/g wet weight; Boldt 2001), therefore despite their abundance, early migrants may have encountered an energy-limited prey field. During the peak juvenile sockeye migration in both years, larvaceans, which have a higher energetic content (3,290 J/g wet weight; Boldt 2001) became an important part of the diet. The late migrants in 2016 continued to consume larvaceans, while later migrants consumed larger, more energy-rich calanoid copepods.
In Johnstone Strait, by contrast, the quality of the prey remained consistently high, with calanoid copepods dominating in both the surface zooplankton and diets. The types of copepods in the diet varied over time, shifting between a dominance of *Metridia* and *Calanus* spp., however, overall, the quality of prey available to migratory salmon in Johnstone Strait was in fact higher than in the Discovery Islands. Therefore, while the quality of prey seemed to drive foraging success in the Discovery Islands, the quantity and size of prey were more important in Johnstone Strait. Overall, the timing of the migration through each region was an important determinant of the environmental conditions, and quantity and quality of prey encountered by juvenile sockeye salmon.

### 3.4.2 Comparisons across fine spatial scales and the extent of the trophic gauntlet

Within a 200 km stretch of the coastal outmigration, juvenile salmon must transition from the highly stratified and productive waters of the Strait of Georgia, through the tidally-mixed waters of the Discovery Islands and Johnstone Strait, to the productive but cooler and denser waters of Queen Charlotte Strait and Queen Charlotte Sound. Thus, the two regions of study represent a transitional zone in which juvenile sockeye migrate from estuarine-like to oceanic conditions across a relatively short distance. The decreasing returns of Fraser River sockeye salmon since the 1990s have drawn attention to this region as a potential bottleneck in marine survival (Price et al. 2013; McKinnell et al. 2014). The constant mixing of the water column in Johnstone Strait keeps productivity low year-round, which has led researchers to propose that this region may act as a trophic gauntlet for migratory salmon (McKinnell et al. 2014). Unless juveniles enter the gauntlet in relatively good condition, they may not have the reserves, nor the prey available, to meet their energetic needs and survive this challenging section of their migration. Previous studies have found evidence of lower growth rates through Johnstone Strait.
(Ferriss et al. 2014; Journey et al. 2018), however, until now, no study has measured prey availability or juvenile sockeye diets directly.

This is the first study to investigate the complex interactions between juvenile sockeye salmon, their prey, and the environmental conditions in the tidally-mixed waters of Johnstone Strait. As expected, environmental conditions remained colder and saltier with higher water clarity throughout the salmon outmigration in both years. The taxonomic composition of both the prey field and salmon diets were significantly different than in the Discovery Islands. Calanoid copepods were the most abundant zooplankton both in the surface waters and in juvenile sockeye diets. Waters in Johnstone Strait are sourced predominantly from Queen Charlotte Strait, with a series of shallow sills at the eastern end of Johnstone Strait limiting water exchange with Discovery Islands and Strait of Georgia to the south (Khangaonkar et al. 2017). Therefore, the copepod-dominant prey community is likely reflective of the community structure in Queen Charlotte Strait. Indeed, higher proportions of Acartia and Pseudocalanus spp. were found in Johnstone Strait, taxa that are associated with boreal shelf conditions north of the Strait (Mackas and Galbraith 2002). Furthermore, inflow and outflow speeds in Johnstone Strait are more than ten times faster than those observed in the southern Discovery Islands (Khangaonkar et al. 2017), which may also explain why calanoid copepods were more abundant. Many of the larger calanoid copepods (e.g., Metridia and Calanus spp.) migrate vertically through the water column and have lower rates of advection compared to zooplankton that are restricted to surface waters (e.g., larvaceans and cladocerans) (Tommasi et al. 2014). In the Discovery Islands, meroplankton (organisms that are typically only planktonic during the larval life stage, e.g., barnacles) were more prevalent, which is likely due to the bathymetry of the region. The intricate network of
narrow channels and inlets of varying depths provides more substrate for the later stages of these benthic invertebrates to settle and grow.

Prey availability was previously thought to be low in well-mixed waters, however, zooplankton biomass in Johnstone Strait was similar to that measured in the stratified waters of the Discovery Islands and the northern Strait of Georgia (Mahara 2018). Furthermore, calanoid copepods are larger, higher energy prey than the meroplankton found in the Discovery Islands (Healey 1991; Davis 1993; Boldt 2001), and thus prey quality may actually be better in Johnstone Strait. The low foraging success experienced throughout this region may therefore be related to a shift in prey distribution and foraging behavior. Predator-prey contact rates are determined in part by turbulence (Rothschild and Osborn 1988), therefore the high degree of mixing may create a more dispersed prey field with lower contact rates. The metabolic cost and duration of foraging under such conditions may be higher, which in turn could increase vulnerability to predation. Therefore, despite the increase in prey quality, energy gains are likely lower in turbulent waters, which may cause sockeye to forage less (Lewis and Bala 2008). However, understanding the physics of predator-prey distributions in turbulent waters and their relation to foraging success is an area for future research.

The coast-wide range of gut fullness indices used for comparison with the data generated in this study comes from juvenile sockeye salmon collected along the coast from northern California to the Gulf of Alaska from 2000 to 2002 (Brodeur et al. 2007). It is worth noting that within that dataset, juveniles from southern British Columbia had some of the highest gut fullness indices of the entire region, and yet many of the values observed in this study were at the lowest end of the coast-wide range.
Foraging success in Johnstone Strait was low relative to the coast-wide range, however, it was more variable than anticipated and similar to levels in the Discovery Islands. The variability in foraging success was most strongly correlated to the proportion of larger zooplankton in the water column, which is driven by zooplankton phenology and possibly by turbulence. Larger prey are more visible and generally provide more energy per specimen than small prey. If salmon reduce their feeding activity due to prey dispersal in mixed waters, consumption of a few larger prey could significantly alter gut fullness indices. These findings are similar to those of English (1983) who found no relationship between growth rates of juvenile Chinook and the abundance of small zooplankton (<1.4 mm), but measured a positive correlation between growth rates and the abundance of medium to large zooplankton (1.4 – 4.5 mm).

The low foraging success observed in the Discovery Islands, however, was unprecedented. Seasonal stratification, shallow Secchi readings and higher zooplankton abundances were predicted to improve foraging conditions for juvenile salmon, however, foraging success was the lowest under these conditions. This is not to say juveniles were unable to capture prey (stomachs at this time had some of the highest prey counts), however, the sizes of prey available to them were small, and the energy density low, resulting in low gut fullness indices. Furthermore, poor visibility may have inhibited their ability to locate and successfully capture larger prey. Therefore, despite high levels of primary and secondary productivity in this area (Mahara 2018; Chapter 2, this thesis), the southern Discovery Islands region did not provide sufficient quantities and quality of prey for migratory salmon in 2015 and 2016. Given similar prey abundance and relatively low foraging success in both regions relative to the range of observed values from along the coast, it is believed that the trophic gauntlet in fact extends beyond Johnstone Strait through to the Discovery Islands.
Interestingly, microplastics were found in 3.1% of all stomachs. Half of these were found in stomachs with some of the lowest gut fullness indices, while the other half were in stomachs with average to above average fullness. This study was not designed to test the effects of microplastics on juvenile salmon diets, however, their presence in nearly empty stomachs warrants further research into their prevalence in juvenile salmon and impacts on foraging success and growth.

3.4.3 Limitations

Juvenile salmon are visual predators selecting for larger prey and are typically found in the top 15m of the water column (English 1983; Emmett et al. 2004). In this study, salmon prey were measured by sampling the top meter of the water. However, except for during peaks in cladocerans and meroplankton, very little overlap was found between the sizes and taxa of prey found in the surface tows and in juvenile sockeye diets. Surface tows were dominated numerically by organisms < 1 mm, while diets were often dominated by organisms > 2 mm. For instance, *Acartia* and *Pseudocalanus* spp. (0.75 – 1.9 mm) were the most abundant calanoid copepods in surface zooplankton tows, while *Metridia* and *Calanus* spp. (2.3 – 3.4 mm) were the most abundant in the diet. Although this may be due to strong selectivity for larger prey, surface zooplankton tows may also be inadequate at capturing juvenile salmon prey fields. Alternative methods such as oblique or vertical tows within the top 15 m may be better suited to capture the juvenile salmon prey field.

This study also examined the diets of juvenile sockeye salmon over two anomalously warm years: 2015 and 2016. In 2015, upper ocean temperatures in the Northeast Pacific were higher due to the influence of the warm ‘Blob’ that developed in the winter of 2013 – 2014. Due to anomalous atmospheric patterns, sea level pressure increased, and heat loss and cold water
advection to the upper ocean decreased, creating a warm water mass at the surface (Bond et al. 2015). This warm year was followed by a second, caused by El Niño conditions that developed in the Pacific Ocean late in 2015, wherein weakened trade winds resulted in decreased cold water upwelling and a warmer eastern Pacific (Chandler et al. 2017b). It is uncertain how these anomalous conditions affected prey fields and diets of juvenile salmon during the early marine migration. However, the intense tidal mixing in the central and northern Discovery Islands and Johnstone Strait kept temperatures in the top 30 m of the water column within historical averages during the both years (Chandler et al. 2017a). Zooplankton, however, are advected into these regions from the Strait of Georgia and Queen Charlotte Sound, respectively. Therefore, changes in those environments in response to The Blob and El Niño may have influenced the zooplankton and diet composition observed in this study. Indeed, the relative abundance and frequency of occurrence of small prey items (i.e., cladocerans, barnacles, euphausiid eggs) was much higher in this study than in previous research in the Strait of Georgia and Discovery Islands (e.g., Price et al. 2013; Neville et al. 2016; Osgood et al. 2016). While this provides preliminary insight into climate-driven shifts in trophic interactions, further research during non-anomalous years is required to explain the relationship between large-scale climate patterns and fine scale variability in juvenile salmon foraging success and ultimately growth and survival. Furthermore, continued monitoring of the dynamic waters of the Discovery Islands and Johnstone Strait is required to determine how the conditions experienced by migrating salmon will respond to a changing climate.

3.5 Conclusion

The relationships between the environment, prey, and juvenile salmon are dynamic over fine spatial and temporal scales. Local and large-scale climate patterns can drive seasonal cycles
in stratification and primary production, which regulate zooplankton phenology and the degree of synchrony with higher trophic levels. When the juvenile salmon outmigration is out of sync with the phenology of their prey, foraging success, and ultimately growth and survival, can be low. Migration timing not only influences the quantity of prey juvenile salmon encounter, but also the quality, which can determine their ability to meet their energetic needs along this critical section of their coastal migration. Warming ocean conditions are changing salmonid migration times as well as zooplankton phenology, increasing the likelihood of trophic mismatches, as may have been observed in this study in 2015. Anomalous climate conditions like the Blob are predicted to become more common in the future, thus the findings of this study may also be predictive of future foraging conditions for juvenile salmon in the coastal waters of British Columbia.

Previously, the narrow inlets and channels connecting the Strait of Georgia and Queen Charlotte Strait were thought to be low in productivity and poor foraging areas for juvenile salmon. However, prey abundance and biomass observed in this study are similar to those previously measured in the northern Strait of Georgia. Thus, while salmon may not be limited by the number of prey, the type, size, and distribution of their prey may be limiting foraging success. This study provides the first detailed record of juvenile sockeye diets in Johnstone Strait, the hypothesized ‘trophic gauntlet’, and the Discovery Islands over the entire migratory period. Relatively high quantities and qualities of prey can be found in this region, however, the level of mixing may increase the energetic cost of foraging in a more dispersed prey field, reducing time spent foraging. Furthermore, the low foraging success experienced upon entering the Discovery Islands suggests that the trophic gauntlet extends south to include this region. Overall, the findings of this study provide strong support for the trophic gauntlet hypothesis.
High-resolution data on salmon diets and their prey such as this can be used to further our understanding of growth and survival during the early marine phase. Furthermore, they could be used to inform food web models and return forecasts to improve the adaptability of management strategies to changing environmental conditions. In-season measurements of zooplankton abundance and biomass could be used to rapidly assess the quantity and quality of salmon prey in the early marine environment in any given year. Paired with data on migration timing and stomach fullness, in-season estimates of foraging success could be made and used to inform models of marine survival. Future research should explore ways in which to incorporate these types of data into Pacific salmon management strategies.
Chapter 4: Conclusions

The cause of declines in salmon productivity over the past few decades is still not fully understood, however, research has shown that conditions in the marine environment, especially in the first few months at sea, have a significant influence on salmon survival (Beamish and Mahnken 2001; Duffy and Beauchamp 2011). In particular, the quantity and quality of salmon prey is believed to be one of the leading drivers of growth, and ultimately marine survival (Beamish et al. 2012; Thomson et al. 2012; McKinnell et al. 2014). For the iconic Fraser River sockeye, passage through regions of low productivity has been shown to decrease growth, and it is hypothesized that poor foraging conditions are the cause. However, trophic interactions in areas of low productivity were unknown. This study therefore arose from the need to improve our understanding of the foraging ecology of juvenile salmon across the range of environmental conditions they experience during the early marine period.

The second chapter described juvenile sockeye salmon diet composition and foraging success relative to the environmental conditions and prey fields encountered in the Discovery Islands and Johnstone Strait. This region consists of tidally-mixed waters of low productivity, separating the more productive waters of the Strait of Georgia and Queen Charlotte Strait to the south and north. The water properties of each region were markedly different from one another, supporting recent findings that these are in fact two separate water masses with little exchange occurring between them (Dosser in prep, Mahara in prep). Despite the proximity of the regions, salmon diets exhibited significantly different characteristics, with a larvacean-dominated diet in the warmer waters of the Discovery Islands and a calanoid copepod-dominated diet in the cooler waters of Johnstone Strait. However, in both regions, juvenile sockeye consistently selected for larger prey and avoided prey < 2 mm. Foraging success was low throughout the study area,
except at the northern and southern-most sites, where foraging success was relatively high. The degree of mixing in Johnstone Strait likely influences prey distributions and encounter rates, as well as prey-selectivity in ways that we do not fully understand, but that may reduce the foraging success of juvenile salmon (e.g. Rothschild and Osborn 1988; Härkönen et al. 2014). These results therefore provide strong evidence for the trophic gauntlet hypothesis, but also highlight the presence of foraging hotspots along frontal areas between mixed and stratified waters. Hotspots such as these may allow migrating salmon to build up/replenish their energetic reserves prior to/after migrating through tidally-mixed and low productivity waters.

Building on the results from Chapter 2, the analyses in Chapter 3 measured changes in prey dynamics and juvenile sockeye diets over the course of their migration through these two distinct regions. A relatively productive and seasonally stratifying site within the southern Discovery Islands was selected for the analysis to highlight differences in foraging ecology across oceanographic conditions. Just as the environmental conditions in Johnstone Strait remain relatively constant over the summer months, the composition of both zooplankton and stomach contents exhibited less temporal variability than in the Discovery Islands. In contrast, greater temporal variation in environmental conditions in the Discovery Islands was reflected by changes in the zooplankton and diet composition at similar temporal scales. Smaller, lower quality zooplankton dominated earlier in the migration, shifting towards a dominance of large, higher quality prey later in the migration. Furthermore, peaks in zooplankton abundance were variable in their magnitude and timing in both regions, exhibiting greater overlap with the salmon migration in 2016. Despite such fine scale temporal changes in prey quantity and quality, the juvenile sockeye migration through these waters occurred at the same time in both years, suggesting that some migrants experienced better foraging conditions than others. Therefore,
migration timing is important in determining the degree of trophic match, or mismatch, between juvenile salmon and their prey.

Foraging success exhibited greater temporal variability than was anticipated, particularly in tidally-mixed waters, and was strongly correlated with zooplankton abundance, the proportion of large prey in the surface waters, and Secchi depths. Although environmental conditions and prey composition varied little over the migratory period through Johnstone Strait, foraging success was strongly positively correlated to the proportion of large zooplankton in surface waters and negatively correlated to zooplankton abundance overall. Similar positive relationships have been observed between the growth of juvenile Chinook salmon and the abundance of medium to large prey (English 1983). Furthermore, since juvenile salmon are visual predators, higher water clarity can also allow for higher foraging success. The negative correlation between total zooplankton abundance and foraging success in both regions could be attributed to prey size, since periods of higher abundance were often those with higher proportions of small prey. This analysis suggests that the ‘winners’ through the Discovery Islands and Johnstone Strait are often those that arrive after the peak abundance of smaller zooplankton (< 1 mm) associated with the spring bloom, when the water clarity has increased and larger prey increase in relative abundance.

This research addresses a critical knowledge gap in the foraging ecology of juvenile salmon across different environmental conditions during their early marine migration. Understanding the quantities and qualities of prey in the water and in the diets over spatial and temporal scales relevant to the juvenile salmon outmigration can improve our ability to measure fish condition, growth, survival, and ultimately recruitment. It is also the first study to ever document salmon diets in the well-mixed waters of Johnstone Strait and provide empirical
evidence affirming the trophic gauntlet hypothesis. Foraging success is indeed lower here and through most of the Discovery Islands than has been measured elsewhere along the coast of the northeast Pacific (Brodeur et al. 2007), and is likely responsible for the lower growth rates observed through these areas (Ferriss et al. 2014; Journey et al. 2018). With this information, we are better able to measure the cumulative effects on juvenile marine survival during the early marine period. For example, in years when fish condition measured in the Strait of Georgia is low, we might expect to see lower survival through the tidally-mixed region. Similarly, if climate anomalies create unfavourable foraging conditions in Queen Charlotte Strait, salmon may experience extended periods of low foraging success and reduced growth, which may reduce overall survival. Furthermore, when paired with more detailed information on the energetic quality of the prey, juvenile salmon growth rates, and the trophic ecology of co-migrating pink and chum salmon, we can better explain the bottom-up mechanisms driving early marine survival.

This research has also generated many more questions on the trophic dynamics of juvenile salmon, providing several opportunities for future research. More data are needed on the environmental and foraging conditions in Queen Charlotte Strait in order to predict the cumulative impacts of low foraging success across the entire migration through the dynamic Inside Passage. In addition, further research could be done on the nature of the foraging hotspots discovered in the frontal regions in this study to determine whether they persist throughout the migratory period and whether they provide adequate resources for juvenile salmon to ‘refuel’ after passing through the trophic gauntlet. It is also important that programs continue to monitor environmental conditions, prey dynamics, and salmon diets throughout this region in years with more typical climate conditions. Without a baseline for this region, it will be difficult to measure
the effects of climate change moving forward. Furthermore, migration timing and prey phenology could be paired with genetic stock information to predict stock-specific trophic mismatches. Research should also aim to develop a model through which a few key parameters (e.g. zooplankton biomass, migration timing, stomach fullness, growth rates) can be used to estimate growth and survival through this region and be paired with forecasts of adult returns.
References


Beamish, R.J., Neville, C., Sweeting, R., and Lange, K. 2012. The synchronous failure of


Chittenden, C.M., Sweeting, R., Neville, C.M., Young, K., Galbraith, M., Carmack, E., Vagle, S., Dempsey, M., Eert, J., and Beamish, R.J. 2018. Estuarine and marine diets of out-


Ferriss, B.E., Trudel, M., and Beckman, B.R. 2014. Regional and inter-annual trends in marine
growth of juvenile salmon in coastal pelagic ecosystems of British Columbia, Canada. Mar.

1–12.

between ocean climate, post-smolt growth, and survival of Atlantic salmon (Salmo salar L.)

doi:10.1126/science.1107834.

Salmon (Oncorhynchus nerka) in the Near-Shore Waters Related? p. 53-60. In Sockeye
Salmon (Oncorhynchus nerka) Population Biology and Future Management. Edited by H.D.

Press, Vancouver.

Hargreaves, B.N., and LeBrasseur, R.J. 1985. Species selective predation on juvenile pink
(Oncorhynchus gorbuscha) and chum salmon (O. keta) by coho salmon (O. kisutch). Can. J.

of turbulence and different predation regimes on zooplankton in highly colored water-
doi:10.1371/journal.pone.0111942.


Lewis, D.M., and Bala, S.I. 2008. An examination of saltatory predation strategies employed by


Appendices

Appendix A  Ethanol conversion factor

Methods

Given that samples lose mass when preserved in ethanol (Wetzel et al. 2005), I conducted a lab experiment to determine the extent of weight loss due to preservation and to derive a correction factor. The purpose of the correction factor was to allow for the comparison of grams of fresh weight of stomach contents to grams of fresh weight of fish in calculating the gut fullness index, a measure of foraging success. A sample of thirty juvenile sockeye was collected using the same methods presented in the main study. Stomach contents were weighed fresh (FW) prior to storage in 95% ethanol for a period of eight weeks. Stomachs were then removed from ethanol, blotted and re-weighed (ETOHW) prior to submerging in water for 30 minutes. Contents were then poured through a 64um sieve to remove water, blotted and weighed a final time (WW). The conversion factor (k) was calculated as:

\[ k = \frac{FW}{WW} \]

Results

After preservation in 95% ethanol, stomach contents weighed 72% of the original fresh weight and after rehydration in water, weighed only 65% of the fresh weight (Figure A.1). Therefore, the k-value was 1.54. All content weights in the main study were multiplied by the conversion factor to calculate the gut fullness index.
Figure A.1: Weights of stomach content samples after ethanol preservation (ETOHW) and rehydration post ethanol storage (WW) relative to the fresh weight (FW).
Appendix B  Additional data

B.1  Chapter 2

Figure B.1: Clockwise from top left: surface temperatures, salinities, secchi depths and sampling locations across the Discovery Islands and Johnstone Strait in June 2015.
Figure B.2: Relative biomass of A) zooplankton from surface waters and B) prey items in salmon stomachs in each size category (<1, 1-2, 2-5, 5-10, >10 mm) at each site in the Discovery Islands (DI) and Johnstone Strait (JS) from one week in June 2015.
Figure B.3: Taxonomic composition of each size class of zooplankton found in the surface waters of the study area.
Figure B.4: Dendrogram of a cluster analysis comparing diet composition between each fish using Bray-Curtis rank dissimilarities of transformed relative biomass. Clusters A and B are indicated in black and grey, respectively. Fish are coloured by migratory route for the western (red), central (orange), and eastern (pink) Discovery Islands and northern (green) and southern (blue) Johnstone Strait.
Figure B.5: Ordination of Bray-Curtis rank dissimilarities derived from transformed relative biomass of diet items using non-metric multidimensional scaling. Ellipses represent 95% confidence intervals and identify Clusters A and B. Best environmental parameters (meantemp = mean sea surface temperature) as identified by the BIOENV model is overlain as a vector. Samples from the Discovery Islands are in red; Johnstone Strait in blue.

Table B.1: Correlations of various combinations of temporal and environmental parameters to ranked dissimilarities in the relative biomass of juvenile sockeye stomach contents using the BIOENV analysis.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>( r_s )</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>meantemp</strong></td>
<td><strong>0.46</strong></td>
</tr>
<tr>
<td>meantemp meansal</td>
<td>0.4492</td>
</tr>
<tr>
<td>meantemp meansal z.abundance</td>
<td>0.4479</td>
</tr>
<tr>
<td>time.adj meantemp meansal z.abundance</td>
<td>0.425</td>
</tr>
<tr>
<td>time.adj meantemp meansal z.abundance z.biomass</td>
<td>0.4063</td>
</tr>
<tr>
<td>time.adj meantemp meansal fork_length z.abundance z.biomass</td>
<td>0.3762</td>
</tr>
<tr>
<td>time.adj meantemp meansal meansecchi fork_length z.abundance z.biomass</td>
<td>0.3407</td>
</tr>
</tbody>
</table>
Table B.2: Median lengths and ranges of eight key taxa in juvenile salmon stomachs. Lengths are only reported for fresh stomach contents (digestive index = 1), for which the sample size is given (n).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Length (mm)</th>
<th>Range</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amphipod</td>
<td>3.8</td>
<td>1.9-6.5</td>
<td>87</td>
</tr>
<tr>
<td>Barnacle</td>
<td>0.8</td>
<td>0.4-1.8</td>
<td>76</td>
</tr>
<tr>
<td>Calanoid copepod</td>
<td>2.8</td>
<td>1.0-5.0</td>
<td>4,858</td>
</tr>
<tr>
<td>Cladoceran</td>
<td>0.8</td>
<td>0.7-0.9</td>
<td>3</td>
</tr>
<tr>
<td>Decapod</td>
<td>2.4</td>
<td>1.7-4.2</td>
<td>11</td>
</tr>
<tr>
<td>Euphausiid</td>
<td>3.1</td>
<td>0.3-22.7</td>
<td>88</td>
</tr>
<tr>
<td>Larvacean</td>
<td>3.7</td>
<td>2.3-10.3</td>
<td>1,063</td>
</tr>
<tr>
<td>Other</td>
<td>1.0</td>
<td>0.0-18.8</td>
<td>70</td>
</tr>
</tbody>
</table>

Table B.3: The median and range of gut fullness indices (GFI) measured in juvenile sockeye salmon, as well as the percent similarity of the diet composition for each site in the Discovery Islands (DI) and Johnstone Strait (JS).

<table>
<thead>
<tr>
<th>Region</th>
<th>Site</th>
<th>GFI</th>
<th>Range</th>
<th>% Sim</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DI</td>
<td>D06</td>
<td>2.53</td>
<td>1.50-5.46</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td>D07</td>
<td>0.95</td>
<td>0.32-1.95</td>
<td>72</td>
</tr>
<tr>
<td></td>
<td>D08</td>
<td>0.10</td>
<td>0.06-0.21</td>
<td>62</td>
</tr>
<tr>
<td></td>
<td>D09</td>
<td>0.21</td>
<td>0.04-0.51</td>
<td>80</td>
</tr>
<tr>
<td></td>
<td>D10</td>
<td>0.18</td>
<td>0.00-0.64</td>
<td>58</td>
</tr>
<tr>
<td></td>
<td>D11</td>
<td>0.29</td>
<td>0.01-0.79</td>
<td>91</td>
</tr>
<tr>
<td>JS</td>
<td>J06</td>
<td>0.05</td>
<td>0.02-0.14</td>
<td>65</td>
</tr>
<tr>
<td></td>
<td>J07</td>
<td>0.94</td>
<td>0.56-1.53</td>
<td>88</td>
</tr>
<tr>
<td></td>
<td>J04</td>
<td>0.13</td>
<td>0.03-0.86</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>J08</td>
<td>0.97</td>
<td>0.52-2.15</td>
<td>89</td>
</tr>
<tr>
<td></td>
<td>J09</td>
<td>0.24</td>
<td>0.14-0.58</td>
<td>51</td>
</tr>
<tr>
<td></td>
<td>J02</td>
<td>3.50</td>
<td>2.31-4.75</td>
<td>87</td>
</tr>
</tbody>
</table>
Figure B.6: A) Relative abundance of zooplankton each size class (mm) and B) relative biomass in each sieve (µm) from surface tows in the Discovery Islands (DI) and Johnstone Strait (JS) in 2015 and 2016.
Table B.4: Results of SIMPER analysis of zooplankton community composition between Clusters 1 and 2. Average abundances are listed for each taxa in each region, as well as the average (Avg) and cumulative (Sum) contribution of each taxa to the overall dissimilarity between regions.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Average Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Acartia</td>
<td>6.8</td>
</tr>
<tr>
<td>Pseudocalanus</td>
<td>0.0</td>
</tr>
<tr>
<td>Evadne</td>
<td>35.5</td>
</tr>
<tr>
<td>Barnacle</td>
<td>33.7</td>
</tr>
<tr>
<td>Paracalanus</td>
<td>20.7</td>
</tr>
<tr>
<td>Larvacean</td>
<td>18.1</td>
</tr>
<tr>
<td>Podon</td>
<td>15.5</td>
</tr>
<tr>
<td>Gastropoda</td>
<td>6.0</td>
</tr>
<tr>
<td>Corycaeus</td>
<td>10.4</td>
</tr>
<tr>
<td>Bryozoa</td>
<td>1.3</td>
</tr>
</tbody>
</table>

Table B.5: Correlations of various combinations of temporal and environmental parameters to ranked dissimilarities in surface zooplankton community composition using the BIOENV analysis.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>(r_s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>meantemp</td>
<td>0.593</td>
</tr>
<tr>
<td>yday, meantemp</td>
<td>0.6406</td>
</tr>
<tr>
<td>yday, meantemp, meansal</td>
<td>0.6557</td>
</tr>
<tr>
<td><strong>yday, set.time, meantemp, meansal</strong></td>
<td><strong>0.6665</strong></td>
</tr>
<tr>
<td>yday, set.time, meantemp, meansal, secchi</td>
<td>0.6663</td>
</tr>
<tr>
<td>month, yday, set.time, meantemp, meansal, secchi</td>
<td>0.651</td>
</tr>
<tr>
<td>year, month, yday, set.time, meantemp, meansal, secchi</td>
<td>0.6086</td>
</tr>
</tbody>
</table>
Figure B.7: Relative biomass of each taxonomic category in the stomach contents of juvenile sockeye collected from the Discovery Islands (DI) and Johnstone Strait (JS) in 2015 and 2016.
Figure B.8: A) Relative abundance and B) relative biomass of diet items in each size class (mm) sampled from the Discovery Islands (DI) and Johnstone Strait (JS) in 2015 and 2016.

Table B.6: Results of SIMPER analysis of juvenile sockeye salmon diets by region (DI = Discovery Islands, JS = Johnstone Strait). Average abundances are listed for each taxon in each region, as well as the average (Avg) and cumulative (Sum) contribution of each taxa to the overall dissimilarity between regions.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>DI</th>
<th>JS</th>
<th>Avg</th>
<th>Sum</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Calanus</em></td>
<td>5.4</td>
<td>38.0</td>
<td>12.5</td>
<td>15.5</td>
</tr>
<tr>
<td>Larvacean</td>
<td>32.3</td>
<td>5.5</td>
<td>11.8</td>
<td>30.0</td>
</tr>
<tr>
<td><em>Metridia</em></td>
<td>20.1</td>
<td>30.2</td>
<td>11.3</td>
<td>44.0</td>
</tr>
<tr>
<td>Barnacle</td>
<td>15.9</td>
<td>3.5</td>
<td>5.4</td>
<td>50.8</td>
</tr>
<tr>
<td><em>Pseudocalanus</em></td>
<td>0.5</td>
<td>15.5</td>
<td>5.4</td>
<td>57.4</td>
</tr>
<tr>
<td>Calanoid</td>
<td>5.5</td>
<td>15.0</td>
<td>4.6</td>
<td>63.0</td>
</tr>
<tr>
<td><em>Podonidae</em></td>
<td>9.1</td>
<td>1.2</td>
<td>3.5</td>
<td>67.3</td>
</tr>
<tr>
<td>Zooplankton eggs</td>
<td>7.2</td>
<td>0.2</td>
<td>2.8</td>
<td>70.8</td>
</tr>
</tbody>
</table>
Table B.7: Correlations of various combinations of temporal and environmental parameters to ranked dissimilarities in juvenile sockeye salmon diet composition using the BIOENV analysis.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>$r_s$</th>
</tr>
</thead>
<tbody>
<tr>
<td>mean temp</td>
<td>0.5959</td>
</tr>
<tr>
<td><strong>mean temp, z.abundance</strong></td>
<td><strong>0.6487</strong></td>
</tr>
<tr>
<td>mean temp, secchi, z.abundance</td>
<td>0.6333</td>
</tr>
<tr>
<td>yday, mean temp, meansal, z.abundance</td>
<td>0.6183</td>
</tr>
<tr>
<td>yday, mean temp, meansal, secchi, z.abundance</td>
<td>0.6146</td>
</tr>
<tr>
<td>yday, mean temp, meansal, secchi, z.abundance, z.biomass</td>
<td>0.6019</td>
</tr>
<tr>
<td>year, yday, mean temp, meansal, secchi, z.abundance, z.biomass</td>
<td>0.5721</td>
</tr>
<tr>
<td>year, month, yday, mean temp, meansal, secchi, z.abundance, z.biomass</td>
<td>0.5308</td>
</tr>
<tr>
<td>year, month, yday, set.time, mean temp, meansal, secchi, z.abundance, z.biomass</td>
<td>0.4853</td>
</tr>
</tbody>
</table>

Table B.8: Median values of the gut fullness indices from each sampling event in the Discovery Islands (DI) and Johnstone Strait (JS) in 2015 and 2016.

<table>
<thead>
<tr>
<th>Region</th>
<th>Year</th>
<th>Date</th>
<th>Median</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2015</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 16</td>
<td>0.13</td>
<td>0.02-1.64</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 21</td>
<td>0.26</td>
<td>0.08-0.81</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 5</td>
<td>0.95</td>
<td>0.32-1.95</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 9</td>
<td>1.46</td>
<td>0.93-1.67</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 13</td>
<td>1.66</td>
<td>1.00-1.86</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 14</td>
<td>0.55</td>
<td>0.09-0.83</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 26</td>
<td>0.51</td>
<td>0.27-1.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 3</td>
<td>0.72</td>
<td>0.31-2.12</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 9</td>
<td>0.54</td>
<td>0.34-0.83</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 16</td>
<td>0.47</td>
<td>0.22-0.91</td>
</tr>
<tr>
<td></td>
<td>2016</td>
<td>May 26</td>
<td>0.00</td>
<td>0.00-0.10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 6</td>
<td>0.94</td>
<td>0.56-1.53</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 14</td>
<td>0.13</td>
<td>0.00-0.44</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 20</td>
<td>0.82</td>
<td>0.21-2.43</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 29</td>
<td>0.40</td>
<td>0.11-1.32</td>
</tr>
<tr>
<td>JS</td>
<td>2015</td>
<td>May 21</td>
<td>1.21</td>
<td>0.77-2.08</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 27</td>
<td>0.26</td>
<td>0.12-0.54</td>
</tr>
<tr>
<td></td>
<td>2016</td>
<td>June 3</td>
<td>0.55</td>
<td>0.24-1.69</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 11</td>
<td>0.55</td>
<td>0.39-1.50</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 20</td>
<td>0.29</td>
<td>0.06-1.39</td>
</tr>
</tbody>
</table>
Figure B.9: Maximum wind speeds (km/h) recorded at the Campbell River (red) and Port Hardy (blue) airport weather stations during the 2015 juvenile salmon migration. Data taken from www.wunderground.com.