STRATEGIES FOR COEXISTING: JUVENILE PINK AND CHUM SALMON DIETS AND INTERACTIONS IN A CHALLENGING SECTION OF COASTAL MIGRATION

by

Vanessa Rose Zahner (Skil Jaadaa)
B.Sc., The University of British Columbia, 2015

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The following individuals certify that they have read, and recommend to the Faculty of Graduate and Postdoctoral Studies for acceptance, a thesis entitled:

**STRATEGIES FOR COEXISTING: JUVENILE PINK AND CHUM SALMON DIETS AND INTERACTIONS IN A CHALLENGING SECTION OF COASTAL MIGRATION**

submitted by Vanessa Rose Zahner in partial fulfillment of the requirements for the degree of Master of Science in Oceanography

**Examiner Committee:**

Evgeny A. Pakhomov, Professor, Earth and Ocean Sciences, UBC

Co-Supervisor

Brian P.V. Hunt, Assistant Professor, Institute for the Oceans and Fisheries, UBC

Co-Supervisor

Colin D. Levings, Adjunct Professor, Institute for Resources, Environment and Sustainability, UBC

Supervisory Committee Member

Michelle Tseng, Assistant Professor, Zoology, UBC

Additional Examiner
Abstract

The cultural and ecological contributions of salmon cannot be understated, as these keystone species have underpinned coastal ecosystems and societies from time immemorial. Despite this millennia-long intimate relationship with Pacific salmon, returns of stocks have become unpredictable and difficult to manage from overfishing and multiple complex stressors. Research has shown that juvenile salmon feeding is a crucial factor for growth and recruitment, and the ocean conditions driving prey availability are tightly coupled with survival of salmon. Pink and chum are abundant co-migratory species of salmon that may exert competitive pressure for food resources during their vulnerable early marine phase. However, competition research on juvenile pink and chum salmon is limited, especially within the complex British Columbia coast. This research aimed to fill gaps in understanding of juvenile pink and chum foraging strategies and interactions in areas of good and poor foraging conditions during their coastal outmigration. In the Discovery Islands and Johnstone Strait regions, there were foraging deserts and oases, where juvenile salmon mean stomach fullness values ranged from < 0.5% to > 6% body weight. In good foraging conditions, juvenile pink and chum both consumed the same high-quality crustacean prey with limited competition, but under poor foraging scenarios, salmon diets differed. Chum salmon consistently consumed gelatinous prey and pink salmon relied more heavily on copepods and nearshore zooplankton, differing in niche in response to competitive interactions. There was a match between predators and prey in 2015, when salmon fed on larger prey, and were in healthier condition (K = 1.0). There was a potential mismatch in 2016, when small prey taxa may have caused poorer condition for juvenile salmon (K = 0.94). Chum salmon had a stronger relationship to prey size than pink, when larger chum successfully consumed the
largest prey. These foraging strategies of opportunistic specialization may indeed provide salmon with resilience to face the challenges of shifting climates. Pink and chum salmon can be monitored as indicators for ecosystem health and zooplankton availability. Salmon reflect the health of socio-ecological systems and require our understanding and care to view them holistically as they migrate through diverse, challenging habitats.
Lay Summary

Salmon are important to people and ecosystems, they bring nutrients to habitats and those who eat them, and they have been interconnected with human societies for thousands of years. However, salmon populations have been declining lately, and scientists don’t exactly know why. A big mystery is the ocean phase of their life cycle, especially the first few vulnerable months. One incredibly important factor for salmon’s survival is getting enough to eat to grow quickly. This research looked at young pink and chum salmon to see if the species ate differently and how that changed over time as salmon swam throughout the Inside Passage region of southern B.C. Frequently, there wasn’t enough food, when chum salmon ate jellyfish and pink salmon ate smaller zooplankton. But other areas had a lot of food where both species ate nutritious prey. Salmon diets reflect ecosystem health and holistic perspectives are recommended to help salmon.
Preface

This thesis research was the independent, original and unpublished work of Vanessa Rose Zahner. Co-supervisors Dr. Evgeny Pakhomov and Dr. Brian Hunt helped shape the initial project ideas and layout of fish sample sites. The research was done in collaboration with the Hakai Institute’s Juvenile Salmon Program to gain a better understanding of the early marine migration of salmon. Hakai field crews at Quadra Island Station and Salmon Coast Field Station collected juvenile outmigrating salmon and lab crews performed necessary dissections. The fish sampling was approved by UBC’s Animal Care Committee, Protocol A19-0025, and under the DFO license numbers: XR 42 2015 and XR 92 2016. Sample processing for the zooplankton taxonomy was performed by Andrea Le, Samantha James, Jihyun Kim and Jessica Schaub. All of the salmon stomach content processing and data analysis was done solely by Vanessa Rose Zahner. The raw dataset of salmon diets and zooplankton can be found with citable DOI here: https://doi.org/10.21966/ean1-n995. All of the code for the analyses are also freely accessible at: https://github.com/vanzahner/pink-chum-diets.

In this thesis the language of animacy is utilized, for example, salmon are referred to as: salmon who experience certain conditions, rather than salmon that experience certain conditions. This distinction is made to not to anthropomorphize salmon but to recognize salmon as beings rather than objects, to acknowledge their connection to humans as our relatives, not as resources. The use of this language in no way, shape or form detracts from the objectivity of this scientific study but learns from Indigenous ecologists and scholars who advocate for this worldview to be represented within the sciences (Cajete, 2018; Kimmerer, 2017; Reid, 2020; Whyte et al., 2016).
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± 

Plus-minus

μm 

Micrometre ($10^{-6}$ m)

‰ 

Parts per thousand

°C 

Degrees Celsius
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<th>Abbreviation</th>
<th>Definition</th>
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<tr>
<td>AHC</td>
<td>Agglomerative hierarchical clustering</td>
</tr>
<tr>
<td>B.C.</td>
<td>British Columbia</td>
</tr>
<tr>
<td>BW</td>
<td>Body weight</td>
</tr>
<tr>
<td>DI</td>
<td>Discovery Islands</td>
</tr>
<tr>
<td>FL</td>
<td>Fork length</td>
</tr>
<tr>
<td>GFI</td>
<td>Gut fullness index</td>
</tr>
<tr>
<td>JS</td>
<td>Johnstone Strait</td>
</tr>
<tr>
<td>mg</td>
<td>Milligrams ($10^{-3}$ g)</td>
</tr>
<tr>
<td>mm</td>
<td>Millimetres ($10^{-3}$ m)</td>
</tr>
<tr>
<td>NMDS</td>
<td>Non-metric multidimensional scaling</td>
</tr>
<tr>
<td>PSI</td>
<td>Percent similarity index</td>
</tr>
<tr>
<td>SE</td>
<td>Standard error</td>
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<tr>
<td>WW</td>
<td>Wet weight</td>
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<tr>
<td>YSI</td>
<td>Yellow Springs Instrument</td>
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Náanii Sandy

iiíl’ kuuníísii

Saa ‘láana

Damaan uu díí tl’ tl’aa dagwii Géelgang

Háw’aa dálang ‘wáadluwaan aa uu Hl kil ‘láagang
Chapter 1: Introduction

1.1 Historical salmon coexistence

Since time immemorial, humans have coexisted with Pacific salmon (*Oncorhynchus* spp.), with archaeological evidence dating back to 11,500 years for anadromous salmon use (Halffman et al., 2015). Both salmon and humans existed in areas of glacial refugia during the last major ice age, co-evolving and adapting into the expanse of complex river and lake systems of the modern age (Haggan et al., 2006). Therefore, salmon stocks have evolved to their unique environments over thousands of years and humans played a role in shaping that evolution and understood the cyclical patterns of salmon (Lepofsky & Caldwell, 2013). However, in the past 200 hundred years, humans have altered salmon habitats, the climate, and the size and health of salmon stocks due to over-exploitation (Gustafson et al., 2007; Newell, 1993; NRC, 1996). Therefore, understanding salmon survival is more complex than ever in the face of threatened stocks and climate change. Much deeper knowledge of salmon life history is needed to improve fisheries management, specifically the early marine stage and its impact on population dynamics.

Furthermore, more research is needed on species-specific life history, feeding strategies and behaviour, as each species has unique characteristics and diverse specializations to survive. All modern species of Pacific salmonids, pink (*O. gorbuscha*), chum (*O. keta*), sockeye (*O. nerka*), chinook (*O. tshawytsha*), coho (*O. kisutch*) salmon and steelhead (*O. mykiss*) evolved at least 6 million years ago (Stearley & Smith, 1993). Unlike the single salmon species in the Atlantic Ocean (*Salmo salar*), Pacific salmon radiated into different species in a highly dynamic
environment, filling multiple ecological niches in newly created habitats (Montgomery, 2000). The evolutionary history of Pacific salmon species still remains largely unknown and species-specific strategies and adaptations may provide insight into conditions mediating their survival. Salmon have demonstrated phenomenal resilience in the face of climate shifts and many external pressures, but as the threats increase and climate warms at an unprecedented rate, salmon remain vulnerable and may not adapt at these same rates. If humans are to continue to rely on salmon for ecosystem services, sustenance, and economy, we must understand and conserve their diversity.

1.2 Current state of salmon stocks

Salmon populations are naturally variable and fluctuate significantly from year to year. Historically, Indigenous peoples dealt with these challenges in salmon production by complex social systems based on sharing resources and diversifying food harvests of other marine animals (Campbell & Butler, 2010). For over 5,000 years, salmon stocks persisted in high abundance during periods of intense fishing pressure by First Nations, due to place-based, selective fisheries and cultural practices of sustainability and cultivation (Atlas et al., 2021; Thornton et al., 2015). However, in the late 1800’s, colonization of the coast forced a shift away from these traditional management practices to the current paradigm of centralized control, when commercial fisheries and the canning industry began to intensely harvest salmon (Newell, 1993). Modern fishing pressures have also decreased overall size and age at maturity for salmon, eliminating large, fecund individuals from populations, reducing resiliency and biodiversity (Jeffrey et al., 2017).
Certain salmon stocks have experienced local declines as a result of fishing pressure, landslides, freshwater habitat alteration from harmful logging practices, and hydroelectric dams (Grant et al., 2019). Currently, 41 salmon stocks are listed as endangered (24), threatened (10) or of special concern (4) in British Columbia (SARA, 2021). Most of the endangered and threatened stocks are sockeye (16) and chinook (22), as well as coho (1) and steelhead (2), who spend more of their life cycles in freshwater than pink and chum salmon. However, salmon populations of all species have begun to decline throughout their entire range, indicating higher mortality and variability in the ocean phase, in addition to the freshwater stage (Malick & Cox, 2016). While the exact cause of salmon declines cannot yet be pinned down, one important factor is human-induced climate change, as rising temperatures affects salmon physiology and prey choices by altering food web structures (Groot et al., 1995; Mackas et al., 2007). Salmon also shift northward in distribution from warming related to climate cycles and long-term trends, which likely leads to detrimental effects on stocks near the southern ranges of species and may perturb northern ecosystems (Carothers et al., 2019; Herbold et al., 2018; Nielsen et al., 2013).

Salmon declines have catastrophic impacts on riparian and aquatic systems, and human health and wellbeing, particularly for Indigenous communities whose lives are intertwined with salmon (Garibaldi & Turner, 2004; Janetski et al., 2009; Marushka et al., 2019; Schindler et al., 2003). Therefore, salmon research must take a multi-faceted ecosystem level approach and investigate species and stocks who are often overlooked but contribute greatly to crucial ecosystem services (Borja et al., 2020). In order to properly manage such complex species, scientists have to gain understanding into the stressors salmon face at each point in the life cycle.
to quantify major bottlenecks in survival (Beamish, 2017). For example, the early marine phase has been shown to mediate salmon cohort survival through significant size-selective mortality.

1.3  **Salmon life history and early marine migration**

Pacific salmon are semelparous, anadromous fish, meaning they are born in freshwater, migrate to the ocean to grow and mature, and return to spawn in the same freshwater system and then die. Although there are always exceptions to these general trends of salmon, such as the freshwater-only kokanee salmon (same species as sockeye, *O. nerka*), and the iteroparous and anadromous salmonid, steelhead, who spawns multiple times, with multiple marine migrations (Quinn, 2018). Different species and types of salmon have different life histories, where species spend various amounts of time in freshwater, estuaries, and the ocean and return to spawn at different times of year. Pink and chum salmon are both species who migrate to the ocean shortly after fry emerge from the gravel where they were born, and chum salmon spend a lot of time rearing in estuary environments (Levings, 2016). In comparison, sockeye, chinook and coho salmon spend months to years in freshwater. Although, ocean-type sockeye tend to migrate into the marine environment around the same time as pink and chum (Groot & Margolis, 1991).

The life cycle timing of pink and chum salmon in southern British Columbia includes spawning in fall and migrating toward the ocean environment in early spring (Quinn, 2018). Pink salmon are the only salmon species who have obligate two-year life cycles, with genetically distinct odd-year and even-year stocks (Oke et al., 2019). Chum salmon on the other hand, have more flexible life histories, living around 3 to 4 years or longer, depending on the ocean
conditions. The first few months at sea are an important life phase of salmon, where populations will experience significant mortality and individuals must grow quickly enough to survive this period (Beamish et al., 2003). Pink salmon survival in Alaska has been shown to be higher for faster growing and larger pink salmon, mediated by ocean conditions and size-selective predation (Cross et al., 2008, 2009; Malick et al., 2011; Miller et al., 2012; Moss et al., 2005). Chum salmon growth in the North Pacific has also been linked to environmental conditions, zooplankton abundance, and density-dependent competition (Agler et al., 2013; Honda et al., 2017; Saito et al., 2009; Yasumiishi et al., 2016). Salmon likely have to grow to certain sizes at given phases in the life cycle in order to feed successfully on larger prey, compete with other individuals, evade predators, and be resilient against diseases (Beamish & Mahnken, 2001). The juvenile phase in particular has been shown to be a bottleneck in the survival of salmon, and when there is not a sufficient amount of high-quality food available this can result in low adult returns (Beamish et al., 2012; Farley et al., 2007). In addition to the survival factors listed above, the first summer at sea for salmon may influence their fat reserves and resilience in subsequent bottlenecks in survival, such as the first winter at sea, which tends to have poor food availability.

1.4 Salmon feeding and competition in the ocean

In the Fraser River, British Columbia’s largest salmon bearing river, sockeye salmon abundance and survival dropped to such low levels in 2009 that a national inquiry was launched (Cohen, 2012). While there has been much attention given to sockeye salmon early marine phase research, there has been less of a focus on co-migrating pink and chum salmon as competitors that may affect sockeye salmon survival. Sockeye salmon feed very similarly to pink salmon,
also consuming zooplankton as their main prey (Brodeur, 1990). Pink salmon have been shown to outcompete other species, and in years of high abundance or poor food availability, adult pink salmon are hypothesized to be at least partly responsible for declines in sockeye salmon and other species (Batten et al., 2018; Ruggerone & Nielsen, 2004; Ward et al., 2017). Thus, pink salmon should be a priority species for salmon conservation scientists to study. Chum salmon are another intriguing species as they coexist with other salmon by prey switching, limiting competition, and tracking ecosystem productivity (Azuma, 1995). There is potential for chum salmon to compete with other species as well, as chum salmon also occur in high abundance, in part due to significant hatchery populations in the Pacific. Both pink and chum salmon have not been declining as steadily as sockeye and chinook, and this may be due to competitive advantages or adaptive strategies to cope with changing conditions.

The species of salmon can be separated by differences in their feeding biology. Pink, chum, and sockeye are salmon who tend to be more planktivorous predators, whereas chinook, coho and steelhead feed more on fish (Brodeur, 1990). Since pink and chum salmon are planktivorous feeders who overlap in time and space, they compete for a limited pool of prey resources (Bailey et al., 1975; Perry et al., 1996). Adult pink salmon have been shown to have detrimental effects on the growth and survival of chum salmon on multiple occasions (Beacham, 1993; Minicucci, 2018). Chum salmon have evolved strategies to adapt to these challenges posed by food limitation, and they have specialized larger stomachs to consume higher amounts of gelatinous prey (Welch, 1997). However, there is scarce literature on competition between juvenile pink and chum salmon with stomach content analysis or quantifying the conditions when and where prey switching occurs (Beamish et al., 2010; Gulbransen, 2014). Aside from
observing *Oikopleura* spp. in juvenile chum salmon diets, the tendency of chum to prey switch to gelatinous zooplankton has been noted in adults, but not in juveniles (Brodeur, 1990; Healey, 1991). This research was initiated by a need to fill this knowledge gap through utilization of high spatial and temporal resolution of juvenile pink and chum salmon diets in a highly dynamic migration area.

Interspecific competition will possibly increase with climate change and increasing temperatures that cause shifts in food web structure, resulting in lower quality prey for salmon. In cooler conditions, diatoms dominate phytoplankton communities, leading to a more efficient food web and large zooplankton, whereas in warm conditions, smaller phytoplankton dominate, which leads to abundant microzooplankton and lower trophic efficiency (Costalago et al., 2020). In B.C., zooplankton communities also fluctuate from northern large, lipid-rich copepods in cool conditions to southern smaller, lipid-poor copepods in warmer conditions (Mackas et al., 2001). As oceans warm and salmon metabolism increases while prey size and quality decreases, further understanding salmon interactions in poor feeding conditions is crucial to predict their survival.

### 1.5 Study region

The study region encompasses the traditional coastal water ways of the Kwakwaka'wakw Nations’ territories, whose stewardship actively cares for the environment and salmon in this area, as they have since time immemorial (Cullon, 2013; Gwixsisälas, 2016). Juvenile salmon annually migrate through this area, which is now known as “the Discovery Islands and Johnstone Strait” region, from May to July (Figure 1.1), where they encounter a diversity of habitats and
highly variable ocean conditions (Johnson et al., 2018). The Discovery Islands region is influenced by coastal freshwater inputs where zooplankton communities and their phenology is related to the seasonally stratified and productive Strait of Georgia (Mahara et al., 2019). Most of these salmon originate from the Fraser River (except odd-year juvenile pink salmon), and experience good feeding in the Strait of Georgia (DFO, 2020; Osgood et al., 2016). However, years of poor foraging in the Strait of Georgia have been hypothesized to negatively impact salmon survival (Beamish et al., 2012), potentially from cumulative effects of food limitation in subsequent areas (McKinnell et al., 2014), but juvenile salmon diet research is limited beyond the Strait of Georgia.

After the Discovery Islands, salmon then enter the less productive Johnstone Strait with low seasonality, where phytoplankton are light-limited due to tidal mixing promoting a constant “winter state” (Mahara et al., 2019; McKinnell et al., 2014). Furthermore, an underwater sill between Discovery Islands and Johnstone Strait limits water mass mixing between regions and Johnstone Strait tends to be more influenced by Queen Charlotte Strait waters of higher salinities and lower temperatures, as well as unique zooplankton communities (Khangaonkar et al., 2017). These two regions of juvenile salmon migration provide a dynamic study area to compare in-depth species interactions under different physical and biological settings, relevant to our understanding of how salmon respond to other complex areas along the migration route. Comparing competitive pressures and foraging strategies under poor and good feeding conditions has the potential to provide insights into fundamental salmon biology and common responses to ecosystem effects throughout their lives.
1.6 Study aims

This study analyzed 312 juvenile pink and chum salmon stomachs from the Discovery Islands and Johnstone Strait and quantified diets, trophic niches, and interspecific competition. Each chapter has a different focus, Chapter 2 analyzed diets spatially along the migration route, and Chapter 3 had a temporal/seasonality focus in 2015 and 2016 (Figure 1.1; Figure 1.2). Both of the thesis chapters investigated foraging strategies of juvenile pink and chum salmon under contrasting ocean conditions and prey availability to describe their species-specific adaptations.

The Chapter 2 aims were to (a) quantify and compare juvenile pink and chum salmon diets and trophic niches in areas of contrasting foraging conditions; (b) assess the foraging success of juvenile pink and chum salmon in the Discovery Islands and Johnstone Strait, southern B.C.; and (c) describe the potential interspecific competition between juvenile pink and chum salmon under contrasting feeding conditions. Chapter 3 aimed to a) quantify juvenile pink and chum salmon diets and their seasonal and interannual interactions in southern coastal B.C.; b) describe how salmon species condition and foraging success vary over time; and c) compare juvenile salmon size with zooplankton prey sizes consumed across regions and years. Overall, this thesis investigated juvenile pink and chum salmon diets and species interactions in response to large shifts in ocean and foraging conditions during their early marine migration.
1.7 Figures

Figure 1.1 Combined thesis study sites in Discovery Islands and Johnstone Strait. Chapter 2’s spatial sites are shown as circles, and Chapter 3’s temporal sites are marked by X’s. Note: D07 samples in mid-June 2016 are included in both chapters, shown by the circle with an X.
Figure 1.2 Conceptual diagram of thesis aims to compare juvenile pink and chum salmon diets under good and poor feeding conditions in stratified (“STRAT.”) and mixed ocean conditions. Stratified waters only occur in southern Discovery Islands, but other listed conditions occur in both Discovery Islands and Johnstone Strait regions, according to previous research. Species interactions of salmon are included in both chapters, with Chapter 2 focusing on spatial dynamics and Chapter 3 on temporal dynamics. The chapters build off each other, as Chapter 3 includes both spatial and temporal components.
Chapter 2: Juvenile pink and chum salmon divide prey resources in response to poor foraging conditions

2.1 Introduction

Pacific salmon (*Oncorhynchus* spp.) are irreplaceable to the cultures, food security and ecosystems within the Pacific Northwest, migrating from freshwater to the Pacific Ocean then returning to their natal habitats, thereby bringing important nutrients into multiple environments (Marushka et al., 2019; Quinn, 2018; Wyllie de Echeverria & Thornton, 2019). While pink (*O. gorbuscha*) and chum salmon (*O. keta*) currently have the highest abundance and biomass (respectively) of all salmon species in the North Pacific, there have been regional declines of these salmon stocks in British Columbia (Malick & Cox, 2016; Ruggerone & Irvine, 2018). Commercial fisheries for salmon have decreased in response to declining stocks and traditional harvest for many B.C. First Nations have also been greatly reduced (Garner & Parfitt, 2006; Healey, 2009). Despite ongoing research on salmon, predictions of adults returning to spawn are highly variable, often lower than expected, and salmon fisheries have become increasingly difficult to manage (Beamish 2017).

Chum and pink salmon are species who leave freshwater soon after fry emerge, heading straight towards the estuary and the ocean at a relatively small size (Groot & Margolis, 1991). Salmon juveniles must contend with the physiological challenges of smoltification, multiple potential predators, and a new foraging environment (Levings, 2016). Mortality for salmon juveniles can be high, and research has shown that growth during their early marine phase is an
important determinant of the cohort strength during their first winter at sea and the likelihood of adult survival (Beamish & Mahnken, 2001).

Prey availability and salmon foraging behaviour are important factors for the rapid growth of salmon during their early marine life (Brodeur, 1990). Patchiness of zooplankton in the ocean leads to relatively generalist salmon feeding (Osgood et al., 2016). However, there are energetic trade-offs and decisions regarding effort required to capture prey, leading to species-specific trophic niches (Gill, 2003). Indeed, salmon species have unique foraging behaviour and preferences, allowing them to portion available prey resources (Healey, 1991). For example, pink, chum and sockeye salmon are planktivorous during early marine life, with often high dietary overlap, whereas chinook and coho salmon are more piscivorous than the other species (Daly et al., 2019; Osgood et al., 2016).

Pink and chum diets vary in response to prey availability, size, intra- and interspecific competition (Beamish et al., 2003). Small pink and chum salmon often forage in the nearshore coastal environment, consuming prey such as harpacticoids (Godin, 1981; Healey, 1979), shifting to larger calanoids, decapods, Oikopleura, amphipods, and euphausiids as salmon size increases (Manzer, 1969; Perry et al., 1996). Pink and chum salmon therefore have the potential to compete for food or occupy different trophic niches to reduce competition. Niche can be defined as a combination of the conditions that allow a given species to satisfy their minimum requirements for survival and the impact of that species on ecosystem processes (Chase & Leibold, 2003). Therefore, the “trophic niche” of a salmon species can be identified as prey resources consumed to meet energetic demands and the effect of salmon foraging on the
zoooplankton community and other species (Jenkins, 2011). Essentially, trophic niche is an organism’s role within the food web; it can be dynamic over time and coexisting species cannot occupy the same niche as this leads to competitive exclusion (Hardin, 1960). Previous studies have shown that prey availability and climate forcing may influence competition and trophic niches of juvenile pink and chum salmon. It has been observed that when under poor feeding conditions, juvenile pink and chum salmon tend to have high diet overlap by competing for the same resources (Gulbransen, 2014; Jenkins, 2011).

Adult pink salmon in the ocean are an example of dominant competitors for food resources (Ruggerone & Nielsen, 2004). They actively feed on crustacean zoooplankton and in high abundance years can cause trophic cascades in plankton communities (Batten et al., 2018). Emerging studies on competition have shown adult pink salmon to negatively affect the growth and survival of other salmonids, herring, sea birds, and killer whales (Beamish et al., 2010; Pearson et al., 2012; Ruggerone et al., 2019; Springer et al., 2018). Adult chum salmon, on the other hand, have more flexible feeding strategies, with the tendency to prey shift towards gelatinous zoooplankton in response to competition or limited food resources (Johnson & Schindler, 2009; Tadokoro et al., 1996). Chum salmon have a substantially larger stomach than other salmon, which enables them to specialize on large gelatinous prey to meet their energetic requirements (Welch, 1997). While these foraging trends for pink and chum salmon have been shown in adults, similar research is limited for outmigrating juveniles.

The zoooplankton communities migrating salmon encounter are largely supported by bottom-up processes such as ocean mixing, nutrients, temperature, salinity, and phytoplankton
productivity (Mackas et al., 2001). In southern British Columbia, the majority of pink and chum salmon originate from the Fraser River and the juveniles migrate northward through the Strait of Georgia, a seasonally stratified and productive region (DFO, 2020; Harrison et al., 1983). North of the Strait of Georgia are the complex and tidally mixed areas of the Discovery Islands and Johnstone Strait, which differ in oceanographic properties and zooplankton communities (Khangaonkar et al., 2017; Mahara et al., 2021). Specifically, the Discovery Islands are characterized as warmer and fresher, with small zooplankton and meroplankton dominating, relative to Johnstone Strait, which is cooler and more saline, with higher proportions of larger calanoid copepods (Mahara et al., 2021). Recent studies have hypothesized these regions to be a “trophic gauntlet” for juvenile salmon, and sockeye salmon have indeed been demonstrated to be food limited in these tidally mixed waters, with gut fullness < 0.5% of their body weight (James et al., 2020; McKinnell et al., 2014). Salmon exit Johnstone Strait into Queen Charlotte Strait, where they may be able to forage successfully and recover from the food shortages experienced in Discovery Islands and Johnstone Strait (McQueen & Ware, 2006). Therefore, salmon are able to survive this challenging route of Discovery Islands and Johnstone Strait since it is book-ended with productive feeding conditions in the northern Strait of Georgia and Queen Charlotte Strait. Since pink and chum salmon have similar foraging and migration patterns to sockeye, they are also exposed to the trophic gauntlet, potentially increasing competition for resources and affecting juvenile growth and survival (Healey, 1991).

The conditions salmon encounter in this region of B.C. are representative of environments encountered by early marine phase juvenile salmon in other regions of the Northeast Pacific (Brodeur et al., 2007). For example, Southeast Alaska has a similar coastal
oceanography, with inlets, channels, archipelagos, and high amounts of tidal mixing that can influence salmon diets (Weingartner et al., 2009). In Icy Strait, Southeast Alaska, juvenile pink and chum salmon diets comprised calanoid copepods, euphausiids, *Oikopleura* spp. and amphipods (Orsi et al., 2004; Sturdevant et al., 2002), but to vary in response to ocean conditions such as temperature, salinity and wind (Fergusson et al., 2020). Therefore, not only does the Discovery Islands and Johnstone Strait region represent an important section of the salmon migration route, but it is a microcosm of coastal conditions experienced by juvenile pink and chum salmon along the Northeast Pacific coast. Salmon therefore migrate through a complex coastal ocean with patchy foraging conditions, which may cumulatively impact survival. Further research is needed on how salmon respond to this spatial variability and how these conditions may fluctuate under shifting ocean conditions, to gain a more holistic and integrated understanding of salmon ecology.

This study addressed a knowledge gap in the foraging biology of juvenile pink and chum salmon across good and poor feeding conditions in tidally mixed waters during their coastal outmigration. Specifically, this study aimed to (a) quantify and compare juvenile pink and chum salmon diets and trophic niches in areas of contrasting foraging conditions; (b) assess the foraging success of juvenile pink and chum salmon in the Discovery Islands and Johnstone Strait, southern B.C.; and (c) describe the potential interspecific competition between juvenile pink and chum salmon under contrasting feeding conditions. The prediction was that low prey availability would lead to juvenile pink and chum salmon competition.
2.2 Methods

2.2.1 Field sampling

The Hakai Institute’s Juvenile Salmon Program was established in 2015 as a collaboration between the Hakai Institute, the University of British Columbia, Simon Fraser University, the University of Toronto and Salmon Coast Field Station. This ongoing program annually samples juvenile salmon as they migrate through the Discovery Islands and Johnstone Strait during the main outmigration period (May to July). The objective of the program was to improve understanding of the early marine phase of Pacific salmon, particularly the factors contributing to salmon health and survival (Hunt et al., 2018). This study focused on 2016, which had the largest spatial sampling coverage in an effort to resolve the primary migration pathways through the region. The previous year, 2015, had similar spatial sampling coverage but there was an expected and observed lower pink abundance, due to their biennial life patterns.

In the Discovery Islands, 12 sites were sampled in 2016, and in Johnstone Strait, 10 sites were sampled, to provide coverage of all possible salmon migration routes through these regions (Hunt et al., 2018). Sample coverage extended from the northern Strait of Georgia, multiple routes in the Discovery Islands, through Johnstone Strait to the beginning of Queen Charlotte Strait. For this study, 6 sites (three from each region) were selected in order to obtain a sample size of 10 pink and 10 chum per set (n = 120 total), focusing on the central pathway of Discovery Islands through Okisollo Channel (Figure 2.1), as the other sites did not achieve sufficient sample sizes of pink and chum salmon. The entire length of the sample area encompasses 140
km, with the distance between sites ranging from 15 to 30 km and the distance between the two regions being around 50 km. Samples for this analysis were selected from mid-June (Table 2.1) to align with the peak out-migration of salmon, determined as the date when 50% of the total catch for a species over the season had migrated through the area (Johnson et al., 2019). The peak outmigration was June 10\textsuperscript{th}, 2016 for both juvenile pink and chum salmon and average peak outmigration date for 2015-2019 was June 17\textsuperscript{th} for pink and June 14\textsuperscript{th} for chum (Table A.1).

Salmon were captured from a small research boat using a purse seine net with bunt dimensions of 27 m × 9 m with 13 mm mesh and tow area dimensions of 46 m × 9 m with 76 mm mesh. Once arrived at a site, weather and sea state were recorded, followed by a visual survey of salmon surface activity. The purse seine net was set on a targeted school of fish and loosely cinched up to facilitate collection while keeping salmon in the water to limit stress. A maximum of 10 pink and 10 chum were sampled per set due to logistical constraints, and the remaining salmon were counted and released (Hunt et al., 2018). Retained fish were individually euthanized with tricaine methane sulfonate (MS-222) on removal from the seine net, lengths and weights recorded, and preserved at -196 °C with liquid nitrogen in a dry shipper until the salmon samples were stored in the -80 °C freezer at the lab. Salmon were collected under DFO license number ‘XR 92 2016’ with approval from UBC’s Animal Care Committee (Protocol A19-0025).

A YSI instrument (model #15B102233 and 15C100324) was used to measure temperature and salinity at the surface and 1-meter depth recorded while salmon were held for processing in the net. These depths were chosen as the salmon were sampled near surface. After purse seine set, zooplankton were sampled aboard the research vessel with a 50 cm diameter ring
net with 250 μm mesh net, towed horizontally at the surface for one minute or until clogged. A General Oceanics flowmeter was attached to the zooplankton net to calculate volume filtered for sample tows. Zooplankton collected were then preserved in 4% formaldehyde for future analysis.

2.2.2 Zooplankton and salmon stomach content analysis

In the lab, zooplankton samples were poured over sieves and separated into 250 μm, 1000 μm and 2000 μm size fractions before being weighed and analyzed. Wet weights were measured to the nearest 0.1 mg on an analytical balance, with non-gelatinous and gelatinous groups weighed separately. If necessary, each size fraction of zooplankton was subsampled with a Motodo plankton splitter. Zooplankton were identified to life stage and the finest taxonomic resolution possible, each group was then enumerated and measured with an ocular micrometer.

Wet weight and fork length were recorded for juvenile salmon before dissection to remove their stomachs, which were preserved in 95% ethanol. Prior to analysis, salmon stomachs were removed from ethanol and soaked for 30 minutes in tap water to reduce the brittleness of the sample. The stomach was then dissected open and the food contents removed. The entire food bolus was weighed on an analytical balance and wet weight recorded to the nearest 0.1 mg. The bolus was then placed on a petri dish with water added, and prey rearranged by species, size, life stage and digestive state. Digestive states were defined as 1) fresh prey, intact, 2) semi-fresh prey, with lost appendages or color, 3) semi-digested prey, only identifiable to group, and 4) fully digested prey, unidentifiable. If prey could not be identified to species, it was identified to the most detailed taxonomic group possible, e.g., Ctenophora and Cnidaria jellyfish, collectively
grouped as “gelatinous” hereafter. For each prey group, minimum and maximum lengths were measured with an ocular micrometer, individuals were counted, and the group wet weight recorded to nearest 0.1 mg. If a stomach sample had over 1,000 prey of similar size, a \( \frac{1}{4} \) subsample was processed, after all the large and/or rare prey present were recorded and removed. Stomach contents were preserved in vials of 95% ethanol for storage and possible DNA analysis.

2.2.3 Data analysis

The spatial variation in prey composition was analyzed using a multivariate approach. Prior to the analysis, rare taxonomic prey categories (occurring in less than three stomachs) were combined into higher level groupings, ignoring “digested food.” Fish stomach content wet weight was multiplied by 1.54 to correct weights for water loss after storage in ethanol (James, 2019). Relative prey biomass for each stomach (% of total wet weight) was calculated and arcsine square root transformed before calculating Bray-Curtis dissimilarity. The dissimilarity matrix was used for non-metric multidimensional scaling (NMDS) ordination and agglomerative hierarchical clustering (AHC). Outlier samples excluded from the NMDS ordination were determined from single clusters in the AHC that had > 95% dissimilarity to all other samples.

In addition to the multivariate statistics, various indices were calculated from the raw data. Gut fullness indices (GFI) were calculated for each fish, expressed as percent body weight:

\[
GFI = \left( \frac{\text{food bolus weight}}{\text{fish weight}} \right) \times 100
\]

Fulton’s condition factor \( K \) comparing length-weight relationships of salmon was calculated as:

\[
K = 100,000 \times \frac{\text{fish weight}}{\left( \text{fish fork length} \right)^3}
\]
Weight was measured in grams and fork length in millimetres, $K = 1$ is average condition, $> 1$ is relatively healthy, and $< 1$ is poor condition (Beamish et al., 2012; Jones et al., 1999). Condition for study fish ($n = 212$) was analyzed with a two-way ANOVA to find differences in regions (DI vs. JS) and species (pink vs. chum), after reciprocal transformation (Keppel & Wickens, 2004). The Schoener percent similarity index (PSI) for species diet overlap was calculated for each site:

$$\text{PSI} = [\Sigma \text{(minimum prey}_{ip}, \text{prey}_{ic})] * 100$$

Where prey$_{ip}$ was the proportion by weight of prey $i$ in pink salmon stomachs and prey$_{ic}$ was the proportion by weight of prey $i$ in chum salmon stomachs (Chipps & Garvey, 2006; Krebs, 2013). The minimum value of prey$_{ip}$ or prey$_{ic}$ is taken then summed with the subsequent prey groups. Empty stomachs with no identifiable prey were excluded from the multivariate calculations but were included in the calculation of the above indices. A two-way ANOVA was also calculated to compare the percentage of empty stomachs for each species and six sites, to compare significant differences between regions and salmon species. Prey taxonomic detail was used in analyses, but for summary tables and figures prey that contributed $< 10\%$ to the weight of diets were grouped as ‘other’. Diet richness was determined by cumulative prey curves for pink and chum stomachs. Analysis was done in R (v4.0.2.), with vegan v2.5-6 (Oksanen et al., 2019; R Core Team, 2020).

### 2.3 Results

#### 2.3.1 Environmental conditions and zooplankton

The environment of Discovery Islands was characterized as warmer and fresher and Johnstone Strait was colder and more saline (Table 2.1). The site nearest the northern Strait of
Georgia, D07, had high freshwater influence (salinity = 24.9) and warmest temperature (17°C), potentially indicative of stratified conditions (Table 2.1; Figure 2.1). The other Discovery Islands sites (D09 and D11) were cooler (< 12°C) and saltier (> 28.5‰), indicating that they were in the tidal mixing zone. Johnstone Strait sites were consistently cold and saline due to mixing, with surface temperatures ranging from 9.9 to 10.4°C and salinities from 30.9 to 32.2‰ (Table 2.1).

Different zooplankton communities by biomass (wet weight) characterized Discovery Islands and Johnstone Straight waters, with more zooplankton in Discovery Islands (326 mg/m³ on average) compared to Johnstone Strait (139 mg/m³; Table 2.1). The zooplankton biomass throughout this area were mostly composed of small zooplankton, in the 250 μm size fraction (mean 197 mg/m³) or gelatinous zooplankton from the 2000 μm size fraction (mean 48 mg/m³). At D07, there were similar amounts of small (250 μm: 130 mg/m³) and gelatinous (2000 μm: 117 mg/m³) zooplankton biomass, whereas D09 only had zooplankton in the 250 μm size fraction (569 mg/m³). At D11 and J06, there were similar amounts of 250 μm (29-31 mg/m³) and 2000 μm gelatinous (56-57 mg/m³) zooplankton, while at J08 the composition was dominated by small 250 μm zooplankton (109 mg/m³; Table 2.1). At sites D11, J06, and J08, there were 1000 μm and 2000 μm non-gelatinous zooplankton, but the biomass never exceeded 10 mg/m³ (Table 2.1).

The zooplankton community composition varied regionally in both the Discovery Islands and Johnstone Strait. While calanoids mainly dominated zooplankton counts across the region, the highest proportions of calanoids (59.3-77%) were observed at J06 and J08 in Johnstone Strait (Table 2.2). Conversely, the Discovery Islands were characterized by a higher proportional abundance of *Oikopleura* spp. (8.6-10.9%) compared to Johnstone Strait (< 3%). High numbers
of bivalve veliger larvae were observed at D07 (30.3%) and a dominance of small cyclopoid copepods at J02 (54.4%; Table 2.2). There were often high amounts of ‘other’ prey, which included small zooplankton such as barnacle larvae and cladocerans.

2.3.2 Salmon diet composition

At the first DI site location D07, near the northern Strait of Georgia, chum salmon had predominately consumed Oikopleura spp. (91% of diet by weight), whereas pink salmon diets were more diverse including calanoid copepods (19.8%), decapod larvae (28.4%) and ‘other’ small prey (21.1%; Table 2.3). Further north, at the Discovery Islands sites D09 and D11, both salmon species continued to consume calanoids and Oikopleura spp., in different proportions: where chum salmon had a high contribution of Oikopleura (44.2-64.6%) and pink salmon a higher contribution of calanoids (30.2-57.2%; Figure 2.2). At site D09, pink salmon had consumed 25.1% harpacticoid copepods and 12.3% insects, which indicated nearshore feeding.

At the first Johnstone Strait site (J06) chum salmon diets were comprised almost entirely by gelatinous prey (96.2%), while pink salmon diets had a high contribution of nearshore prey, such as harpacticoids (19.3%) and arachnids (16.7%; Table 2.3; Figure 2.2). At Johnstone Strait site J08, chum salmon diets still had a high contribution of gelatinous prey (76.1%) but, in addition, had higher amounts of large calanoid copepods (15.7%), while pink salmon predominantly ate calanoids (85.5%). There was a complete diet shift at the most northerly site (J02), where both salmon species consumed calanoids (pink 61.9%, chum 18.7%), chaetognaths (pink 5.5%, chum 21.3%) and euphausiids (pink 29.6%, chum 53.5%; Table 2.3; Figure 2.2).
The NMDS plot demonstrated that differences in diet composition of salmon was largely influenced by differences between the two regions (Figure 2.3). Within each region, differences were apparent between both site and salmon species. In the Discovery Islands, juvenile salmon diets had a higher degree of separation between species than between sites. In contrast, Johnstone Strait showed a clear relationship between species and site. The most southern Johnstone Strait site, J06 had high species-specific diet dissimilarity, at J08 species separated to a lesser degree, and at J02 (Queen Charlotte Strait), dissimilarity between species was the lowest (Figure 2.3).

The cluster analysis largely supported the NMDS results (Figure 2.4). Diets from Johnstone Strait and Discovery Islands mostly separated at the ~ 85% level of dissimilarity. In the Discovery Islands, sites tended to group together within clusters, and with a few exceptions, chum salmon diets were in one cluster with less than 50% dissimilarity to one another (Figure 2.4). Pink salmon in the Discovery Islands within D09 and D11 were highly variable, spread over multiple clusters, which also had overlap with J06 and similarity to site J08. Conversely, D07 (near the northern Strait of Georgia) pink salmon group together within one cluster (< 60% dissimilarity), with the exception of one outlier cluster with 96% dissimilarity. In Johnstone Strait, the separation between sites was more distinct. There was one cluster for both pink and chum diets in J02, near Queen Charlotte Strait (< 60% dissimilarity). Conversely, for the other Johnstone Strait sites pink and chum salmon clustered separately. At J08, diets had < 55% dissimilarity within species, but 82% between species. At J06, there was high dissimilarity within pink salmon diets (> 79%), while chum diets had < 55% dissimilarity (Figure 2.4).
2.3.3  *Salmon biology, gut fullness, and condition*

Pink and chum salmon samples collected for analysis were shown in Table 2.1, with length and weight information in Table 2.4. Mean (± SE) fork length was 103.4 ± 0.3 mm for chum salmon and 105.1 ± 0.2 mm for pink salmon in the Discovery Islands. In Johnstone Strait, chum salmon mean fork lengths were 118.8 ± 0.3 mm and pink salmon, 113.4 ± 0.2 mm. Wet weight (mean ± SE) of juvenile salmon was also lower in Discovery Islands (10.5 ± 0.1 g pink; 10.9 ± 0.1 g chum), compared to Johnstone Strait (14.1 ± 0.1 g pink; 17.4 ± 0.1 g chum). Juvenile pink salmon condition was poor throughout most of the region, with a mean K value of < 1 at all sites except J02, near Queen Charlotte Strait (Figure 2.5). Chum salmon were in significantly better condition (F\(_{1,114}=17.7\), p = 0.0001) with a mean K of > 1 at each end of the study area, D07 and J02, and poorer condition in other sites, with high variability (Figure 2.5). Both species had significantly higher condition in Johnstone Strait (F\(_{1,114}=13.0\), p = 0.0005).

Gut fullness was consistently low throughout the Discovery Islands and Johnstone Strait, with the exception of full and distended stomachs at the last site, in southern Queen Charlotte Strait (Figure 2.6). Gut fullness indices (GFI) for both species were generally below 0.5% body weight throughout the Discovery Islands, and J06, the most southerly Johnstone Strait site. At the mid-Johnstone Strait site J08, the GFI increased to ~ 1% body weight (pink 1.13% ± 0.06, chum 1.28% ± 0.04). At J02, GFI increased to ~ 7% body weight GFI at site J02 (pink 7.46% ± 0.19, chum 6.20% ± 0.11). Microplastics and other non-digestible objects (glass, a rock) were found in 10% of all juvenile pink stomachs (5% of all salmon), in all Discovery Islands sites and J06, sites with the lowest GFI. No chum salmon were found to have eaten any non-food objects.
Empty stomachs were found throughout the Discovery Islands and the first Johnstone Strait site (Table 2.4). Empty stomachs were recorded for pink salmon at D07 (20%) and J06 (40%), and for chum salmon at D09 (30%) and D11 (30%). There were no sites where empty stomachs occurred for both pink and chum salmon simultaneously. By region, in the Discovery Islands 7% of pink salmon and 20% of chum salmon stomachs were empty, while in Johnstone Strait, no empty stomachs were recorded for chum salmon, compared to 13% for pink salmon. Ten percent of all juvenile salmon stomachs analysed in this study were found empty. Percentage of empty stomachs did not differ by species ($F_{1,8}=0.00$, $p = 1.0$) or region ($F_{1,8}=0.55$, $p = 0.5$).

2.3.4 Diet overlap between pink and chum salmon

Dietary overlap between pink and chum salmon was relatively low and consistent in the Discovery Islands and shifted from low to high levels in Johnstone Strait (Figure 2.6). At the first site of the migration route, D07, dietary overlap reached 24.9%. This increased to 33.0% at D09 and then decreased to 21.7% at D11. The lowest dietary overlap, 4.8%, was observed at J06 (Figure 2.6). Dietary overlap at mid-Johnstone Strait J08 was 14.1% and the final site near the entrance to Queen Charlotte Strait J02 had the highest diet overlap of 59.8%. In summary, the Schoener overlap index showed consistently low to modest diet overlap between juvenile pink and chum salmon at all sites, with the exception of J02 (Figure 2.6).

The dietary richness or number of taxa found in the stomachs, demonstrated that pink salmon had a broader range of prey in the diets than chum salmon at every location (Figure 2.7). The site with the highest prey richness for both salmon species was the most northerly site, J02,
and the lowest prey richness occurred at site J06 for chum salmon, and D11 for pink salmon. Johnstone Strait generally had higher diet richness than Discovery Islands, likely due to calanoid diversity. Overall, the pink salmon diets were about twice as rich as chum salmon (Figure 2.7).

2.4 Discussion

This study examined juvenile pink and chum salmon stomachs to characterize diets during the 2016 peak outmigration through the Discovery Islands and Johnstone Strait routes. Contrasting ocean conditions were observed in the temperature and salinity properties of the regions and the zooplankton biomass was higher in the Discovery Islands than Johnstone Strait, as previously demonstrated by James et al. (2020). The regional differences in oceanography and zooplankton resulted in clear diet separation for both pink and chum salmon in the two regions of study. The dietary overlap between pink and chum salmon varied from low to high overlap of prey composition in relation to stomach fullness, with low overlap when fullness was low, indicating resource partitioning. These specific points are discussed in more detail below.

2.4.1 Pink and chum salmon niches and competition

Diet composition of salmon species and their competitive interactions shifted quite dramatically along the migratory route. In waters with strong tidal mixing, pink and chum salmon had low stomach fullness and showed prey and niche partitioning, with chum occupying a gelatinous plankton feeding niche and pink feeding on meroplankton, generally close to the littoral. The exception was the northern most site of J02 which was shown to be a foraging hot
spot for juvenile pink and chum salmon, with high diet overlap between species and the highest diet richness. Chum salmon diets were characterized by *Oikopleura* spp. in the Discovery Islands and Cnidaria in Johnstone Strait, but switched to euphausiids at the entrance to Queen Charlotte Strait (J02). Pink salmon diets were variable and characterized by decapod larvae in southern Discovery Islands, harpacticoid and calanoid copepods in both areas, and also euphausiids at J02.

Zooplankton biomass was low throughout Discovery Islands and Johnstone Strait in June 2016, when juvenile pink and chum salmon were migrating through these regions. Most of the zooplankton samples in this study had a biomass of $< 250 \text{ mg/m}^3$, with all samples $< 600 \text{ mg/m}^3$, compared to the productive Strait of Georgia, with winter minimum values of around 4,000 mg/m$^3$ and average summer peaks which can reach 9,000 mg/m$^3$ (Mackas et al., 2013). The zooplankton community composition observed in net tows was not closely reflected in the stomach contents. Contributing to this is that surface net tows were unable to capture all relevant salmon prey, such as epibenthic harpacticoid copepods, or fish and euphausiids that are able to avoid zooplankton nets. However, the zooplankton captured did include *Oikopleura* in the Discovery Islands and calanoid copepods in Johnstone Strait, which were reflected heavily in the dietary compositions. The most representative way of capturing available prey, was through the diets themselves, viewing salmon as “plankton sampling gear” for the ideal prey type and size.

Differences in zooplankton prey composition have implications for juvenile salmon diet quality. Prey quality is an important factor for juvenile salmon diets and growth during the early marine phase, and fatty acid contents is a good measure of prey quality. Recent research in the Strait of Georgia on zooplankton quality found large copepods, euphausiids, chaetognaths, and
hyperiid amphipods to have high fatty acids contents (Costalago et al., 2020). In comparison, meroplankton, small zooplankton, and gelatinous zooplankton were lower in nutritional content, and poorer quality prey (Boldt, 2001). Therefore, both the amount of food consumed by salmon and the prey types are important for salmon growth and survival (Weil et al., 2020). In this study, salmon consumed higher quality prey (euphausiids, large calanoids, and chaetognaths) at the most northern site near Queen Charlotte Strait and lower quality prey throughout the other sites.

The trophic niche of juvenile salmon in the Discovery Islands and Johnstone Strait can also be related to the habitat niche of each species, with pink salmon foraging more in the nearshore and chum salmon in the pelagic environment. Each sampling set captured salmon likely travelling within the same school(s), however nearshore prey items were found more frequently and in higher proportions in pink salmon diets, including higher prey richness of harpacticoids, insects, arachnids, barnacle larvae, cumaceans, caprellid and gammarid/corophiid amphipods. Pink and chum salmon may consume smaller or lower quality prey when better prey is not available since they need to constantly feed in order to achieve growth rates of up to 3.5-7% body weight per day (Beamish et al., 2003; LeBrasseur & Parker, 1964). Since gelatinous prey are often lower in nutritional content than other zooplankton, chum salmon have evolved larger stomachs than other salmon to consume more biomass of jellyfish to benefit off that specific prey source (Welch, 1997). Therefore, it seemed pink and chum salmon were genetically predisposed to littoral and gelatinous niches, respectively, when food was scarce. However, niche switching occurred when foraging conditions improved and higher quality prey, such as large calanoids and euphausiids, became more readily available. This adaptive flexibility of the trophic and habitat niches of juvenile salmon could be an area for future research and should be
investigated further. This should include niche flexibility of other species, in other areas, at different life phases, and compared across seasons and years, to better understand the cost and benefits and to provide a framework for inclusion in life-history models of salmon species.

Pink salmon consumption of microplastic pieces, glass, and rocks may have also reflected nearshore feeding. These foreign objects were found in 5% of all salmon stomachs analyzed (10% of pinks), at sites D07, D09, D11 and J06, the sites with empty stomachs. The objects were likely too small (0.3-2.8 mm) to block digestive tracts, but foreign items may have been mistaken for food in poor feeding conditions when prey encounters were lower. Further research is needed on whether plastic debris is more common in this area or there is less consumption of plastics by salmon in areas with improved zooplankton feeding opportunities. Other studies have found Chinook salmon to have consumed microplastic fibers (Collicutt et al., 2019), none of which were present in this study. The microplastic pieces in salmon stomachs in the Discovery Islands and Johnstone Strait were irregularly shaped, a shape that has been shown to impact the fitness of other fish species (Choi et al., 2018). This study suggests that plastic consumption may be an emerging threat and greater in areas of poor foraging, which may cumulatively impact salmon.

2.4.2  *Feast or famine: salmon feeding and condition*

Juvenile pink and chum salmon were found to have extreme values of stomach fullness in the Discovery Islands and Johnstone Strait, relative to other locations along the coastal migration routes in the Pacific Northwest. For example, juvenile pink and chum mean gut fullness was found to be 2-4% body weight (BW) in the nearby Broughton Archipelago in 2003 and 2006.
(Gulbransen, 2014), 1% BW in northern B.C. in 2000-2002 (Brodeur et al., 2007), 1-4% BW in Southeast Alaska in 2001 (Sturdevant et al., 2002), and 1.7-1.9% BW in the eastern Gulf of Alaska (Daly et al., 2019). Comparatively, in this study juvenile pink and chum salmon gut fullness averaged < 0.5% BW in the first five sites (0.35% pink; 0.40% chum; sites: D07, D09, D11, J06, J08) and > 6% BW in Queen Charlotte Strait (7.5% pink; 6.2% chum; site: J02).

Therefore, the results of this study indicate the area of Discovery Islands and Johnstone Strait as a prolonged migratory challenge for juvenile salmon, with significantly poor feeding conditions. Previous research demonstrated that juvenile sockeye salmon experience similarly poor foraging success, indicating that this is not confined to pink and chum salmon (James et al., 2020). Future research is recommended to quantify the challenges for other species, such as herring, chinook and coho salmon, as these conditions are expected to impact their growth and survival as well.

The foraging refuge at the confluence between Queen Charlotte Strait and Johnstone Strait may help juvenile salmon meet their energetic demands for outmigration after a period of food limitation and poor food quality. The same location was found to be productive for juvenile sockeye salmon in 2015 (James et al., 2020), however, chum salmon had lower stomach fullness (~1%) elsewhere in Queen Charlotte Strait in 2015 (unpublished data). Therefore, there was likely a physical oceanographic front, where mixed and stratified water masses meet, at the confluence of Johnstone Strait and Queen Charlotte Strait, where upwelled zooplankton accumulated to form a “hot spot” (Franks, 1992; Perry et al., 1983). If ocean conditions change and these refuge areas become unproductive, this may have devastating effects on salmon survival (Beamish et al., 2012; McKinnell et al., 2014). If juvenile salmon experience an extended starvation period of two weeks, they may not be able to fully recover (Kuzmenko et al.,
It is possible these unique hot spots are instrumental to salmon cohort survival, and more research along the coast is needed to characterize these small-scale features.

The migration time to pass through these regions was around 11 days for sockeye salmon (James et al., 2020), and pink and chum are possibly comparable but have not been studied yet. According to peak outmigration dates in the Discovery Islands and Johnstone Strait, they may take an average of 22 days to migrate across this region (Table A.1). In this study, salmon size differed between regions, as Johnstone Strait is further north than Discovery Islands. However, chum salmon lengths spanned a wide range, which potentially indicated longer residence periods or multiple migrating stocks. Further studies on the stock migration timing and pathways of pink and chum salmon in this area are required to investigate benefits and costs of quick or long migrations on salmon health in dynamic areas of food gauntlets and hot spots.

In addition to stomach fullness being low for migrating juvenile salmon in the Discovery Islands and Johnstone Strait, Fulton’s condition factor K was also low throughout both regions. There was a higher condition factor for D07 chum salmon that indicated good feeding in the northern Strait of Georgia, even though stomach fullness was low at this site. The difference in K between pink and chum salmon conditions at D07 may also indicate differing residence times in the Strait of Georgia, with pink salmon moving more quickly through the area. The good condition (for chum salmon) in D07, poor feeding and condition in other Discovery Islands and Johnstone Strait sites, followed by good feeding and condition in Queen Charlotte Strait for pink and chum salmon, was mirrored by the study done on juvenile sockeye salmon in the same area in 2015, which found food limitations and similar foraging hot spots (James et al., 2020).
Another study on the growth of juvenile salmon found that pink and chum salmon experienced poor growth in Johnstone Strait and Queen Charlotte Strait areas during the 2012 – 2014 outmigration (Journey et al., 2018). It may be speculated that this low growth occurred due to poor feeding opportunities for juvenile pink and chum salmon in this area, though their foraging ecology had not been analyzed until this current study. This study confirms that the low growth through the region can be attributed to poor foraging conditions. Furthermore, 2012 – 2014 were cooler years than 2015 – 2016, suggesting these limitations may persist despite shifts in climate.

In other areas with similar coastal conditions, pink salmon were found to be nearshore foragers upon small crustaceans, while chum salmon often prey switch from crustacean to gelatinous plankton (Godin, 1981; Tadokoro et al., 1996). Previous studies have found harpacticoid and calanoid copepods as primary prey items for both pink and chum salmon (Chebanova et al., 2018; Godin, 1981; Healey, 1979). Recently, a study that was conducted simultaneously to this one showed that sockeye salmon diets were dominated by *Oikopleura* spp. in the Discovery Islands (James, 2019), which is similar to what was observed here for chum salmon. Furthermore, larger calanoids were dominant sockeye (James, 2019) and pink salmon prey in Johnstone Strait. Therefore, when all three species are compared, pink and chum have the lowest overlap in both the Discovery Islands and Johnstone Strait regions. This is supported by previous research that investigated dietary overlap among these species, which found that pink salmon diets tend to be more similar to sockeye than chum salmon (Daly et al., 2019).
2.4.3 *Species competition or coexistence?*

Juvenile pink and chum salmon had similar diets when prey availability was high but utilized different foraging strategies under low prey availability, indicating resource partitioning. Through most study sites, chum salmon appeared to occupy a gelatinous predator niche, while pink salmon switched to the littoral niche utilizing nearshore insects, harpacticoids and amphipods. These niche strategies shifted with zooplankton prey availability, where at the Queen Charlotte Strait site with ~ 7% body weight stomach fullness, both species fed similarly. Therefore, pink and chum salmon were both observed to consume similar and likely higher quality prey, such as euphausiids and large calanoids, in regions of high prey availability but clearly portioned the resource space when prey was limited. This strategy would be expected to limit potential competition between the two species but is not a dynamic that has previously been explored in nearshore coastal environments for juvenile salmon.

There was an interplay between species-specific differences in diet and the prey available for juvenile salmon at each location within the Discovery Islands and Johnstone Strait. It appears that chum salmon tended to specialize on gelatinous prey, *Oikopleura spp.* in the Discovery Islands and Cnidarians in Johnstone Strait, with overall low prey richness. Whereas pink salmon were more generalist feeders with higher prey richness. Other research has also demonstrated chum salmon’s tendency to specialize whereas pink salmon feed more broadly (Graham, 2020).

In poor foraging conditions juvenile pink and chum salmon were likely competing for limited resources and therefore employed species-specific foraging strategies. Chum salmon
have been shown to adapt and switch prey in response to inter-specific competition with pink salmon at the adult phase (Kaga et al., 2013; Tadokoro et al., 1996). This study indicated that chum salmon prey switching may occur as early as the juvenile stage. The specialization under poor foraging conditions was reflected in the low prey richness, low stomach fullness and low dietary overlap between pink and chum salmon along the Discovery Islands and Johnstone Strait route. In contrast, the site at Queen Charlotte Strait had the opposite trend, with high prey richness, high gut fullness and high dietary overlap between species, indicating a lack of competition likely due to high prey availability (Graham, 2020). It appears that in periods of limited food resources during early marine migration salmon behaviour is highly dynamic.

2.4.4 Future directions

One limitation of this study is knowledge of the potential effect of predators on salmon distribution and foraging behaviour, since prey choice is mediated by energetic trade-offs and predation risk in foraging habitats. Predators may cause salmon to shelter in certain habitats and forage only during certain time intervals. Currently, little is known about predators of juvenile salmon in this area and it is unclear to what extent predators may affect salmon. Studies have shown satiation to affect predation risk, more so in pink salmon than chum salmon, with prolonged foraging in hungry salmon increasing predator exposure risk (Magnhagen, 1988). Sea lice infection has also been shown to increase levels of “boldness” of juvenile salmon toward predator exposure in order to capture prey, in both pink and chum salmon (Krkošek et al., 2011). Sea lice loads have been demonstrated to be high in the study area, which has also been an active Atlantic salmon farming location (Brookson et al., 2020). While it is not possible to assess the
role of predation in the distribution and foraging behaviour of salmon in this study, mortality needs to be considered in future studies. Predation may be mediated by the ocean conditions, through the effects on foraging success, size and condition of salmon (Tucker et al., 2016).

This research study focused on a snapshot of juvenile salmon feeding in June 2016 and the next step is to investigate trends with seasonal and interannual components. The dynamics of each of these regions may shift over time, especially the Discovery Islands which was naturally more variable due to morphology and freshwater influence. This study characterized salmon species interactions in good and poor foraging scenarios, but other factors may have contributed, such as stock-specific feeding differences or competition with other species (e.g., herring, other salmonids). More accurate descriptions of these regions require a longer time series on salmon feeding during the outmigration period and across years, and this is the focus of the next chapter.

2.5 Conclusions

In the Discovery Islands-Johnston Strait corridor, juvenile pink and chum diets and feeding intensity were influenced by the availability of prey and the overlap between salmon species. While it is intuitive that zooplankton prey determines diet composition, it is somewhat counterintuitive that competition would decrease with increased diet similarity between salmon species. When high quality food becomes scarcer, it seems juvenile salmon have strategies to fall back on, where pink salmon focus efforts in nearshore environments and chum salmon shift to planktonic gelatinous prey. These salmon species could potentially be used as ecosystem
indicators, where pink salmon track changes in the zooplankton community as generalist predators and chum salmon indicate the overall feeding conditions available for other species.

The diversity of conditions encountered by salmon migrating through the Discovery Islands-Johnston Strait corridor highlighted the ability of both species to coexist by utilizing different trophic niches, allowing them to partition the prey resources. Since pink salmon had the potential to outcompete other species for high quality prey such as large calanoid copepods, chum salmon deployed a different strategy in order to survive. Salmon species occupied distinct trophic niches and this relationship shifted across the migration route relative to the environmental conditions, foraging intensity, prey types and density.

On their northward migration, salmon passed through warm and fresh surface waters as they entered the Discovery Islands, before encountering tidally mixed waters with a high prevalence of meroplankton and *Oikopleura* prey. Subsequently, they migrated into the cool and saline surface waters of Johnstone Strait, where juveniles shifted to consumption of mainly jellyfish (chum) and calanoids (pink), maintaining species specific diets. Finally, at the end of this challenging section of their migration, salmon found improved foraging conditions where upwelled coastal water provided for large amounts of euphausiids and chaetognaths. Salmon therefore experienced a suite of coastal conditions within this region, where poor feeding opportunities were bookended by good prey availability, which likely supported salmon survival. In this “trophic gauntlet” area, future monitoring is justified, as poor feeding in the Strait of Georgia or Queen Charlotte Strait could devastate a cohort of juvenile salmon along this route.
2.6 Tables

Table 2.1 Sampling details for study: Site IDs for the Discovery Islands and Johnstone Strait, sampling date, number of pink and chum salmon stomachs analyzed, temperature (Temp.), salinity (Sal.) and size fractionated and total zooplankton biomass.

<table>
<thead>
<tr>
<th>Site</th>
<th>Date</th>
<th>Pink (#)</th>
<th>Chum (#)</th>
<th>Temp (°C)</th>
<th>Salin. (%)</th>
<th>250 μm</th>
<th>1000 μm</th>
<th>2000 μm</th>
<th>Total</th>
</tr>
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<td>8.4</td>
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<td>-</td>
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</table>

*Note:
* A large amount of phytoplankton was captured at D09 and biomass was skewed.
* Biomass data are missing for J02.
Table 2.2 Zooplankton relative abundance (expressed as percent) at each site, summarized by the main groups.

<table>
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<tr>
<th></th>
<th>D07</th>
<th>D09</th>
<th>D11</th>
<th>J06</th>
<th>J08</th>
<th>J02</th>
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<td><strong>Amphipoda</strong></td>
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<td>-</td>
<td>-</td>
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<tr>
<td><strong>Calanoida</strong></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Small (&lt;2mm)</td>
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<td>31.3</td>
<td>46.3</td>
<td>55.8</td>
<td>76.5</td>
<td>36.8</td>
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<td><em>Oikopleura</em> spp.</td>
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<td>9.4</td>
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<td>0.6</td>
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<td>-</td>
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<td>-</td>
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</tr>
<tr>
<td>Balanomorpha</td>
<td>20.9</td>
<td>6.4</td>
<td>9.2</td>
<td>8.8</td>
<td>4</td>
<td>1.8</td>
</tr>
<tr>
<td>Cladocera</td>
<td>2.8</td>
<td>18.1</td>
<td>3.1</td>
<td>2.1</td>
<td>3.4</td>
<td>0.3</td>
</tr>
<tr>
<td>Zooplankton Eggs</td>
<td>0.9</td>
<td>-</td>
<td>0.2</td>
<td>1.1</td>
<td>8.3</td>
<td>1.3</td>
</tr>
<tr>
<td>Echinodermata</td>
<td>-</td>
<td>0.3</td>
<td>-</td>
<td>-</td>
<td>0.2</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 2.3 Diet composition summary by average relative wet weight (expressed as percent) of the main groups of prey for pink (PI) and chum (CU) salmon at each site.

<table>
<thead>
<tr>
<th></th>
<th>D07 PI</th>
<th>D09 PI</th>
<th>D11 PI</th>
<th>J06 PI</th>
<th>J08 PI</th>
<th>J02 PI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amphipoda</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hyperiidea</td>
<td>0.2</td>
<td>0.3</td>
<td>1.0</td>
<td>-</td>
<td>0.1</td>
<td>2.6</td>
</tr>
<tr>
<td>Senticaudata</td>
<td>10.5</td>
<td>5.6</td>
<td>0.9</td>
<td>-</td>
<td>1.8</td>
<td>-</td>
</tr>
<tr>
<td>Calanioda</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small (&lt;2mm)</td>
<td>3.9</td>
<td>1.2</td>
<td>2.9</td>
<td>0.7</td>
<td>30.1</td>
<td>15.3</td>
</tr>
<tr>
<td>Large (&gt;2mm)</td>
<td>15.9</td>
<td>1.4</td>
<td>27.3</td>
<td>19.7</td>
<td>27.1</td>
<td>20.7</td>
</tr>
<tr>
<td>Euphausiidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adults</td>
<td>-</td>
<td>-</td>
<td>0.2</td>
<td>1.2</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Larvae</td>
<td>0.4</td>
<td>0.1</td>
<td>1.5</td>
<td>3.7</td>
<td>1.2</td>
<td>0.3</td>
</tr>
<tr>
<td>Decapoda</td>
<td>28.4</td>
<td>0.1</td>
<td>3.7</td>
<td>1.6</td>
<td>0.2</td>
<td>-</td>
</tr>
<tr>
<td>Insecta/Arachnida</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
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<td>Insecta</td>
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<td>12.3</td>
<td>0.4</td>
<td>5.4</td>
<td>-</td>
<td>0.4</td>
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<tr>
<td>Arachnida</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>16.7</td>
<td>-</td>
</tr>
<tr>
<td>Harpacticoida</td>
<td>0.2</td>
<td>25.1</td>
<td>-</td>
<td>1.5</td>
<td>19.3</td>
<td>-</td>
</tr>
<tr>
<td>Gelatinous</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cnidaria</td>
<td>-</td>
<td>3.7</td>
<td>0.4</td>
<td>2.6</td>
<td>-</td>
<td>9.8</td>
</tr>
<tr>
<td>Ctenophora</td>
<td>-</td>
<td>1.6</td>
<td>-</td>
<td>-</td>
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<td>86.4</td>
</tr>
<tr>
<td>Oikopleura spp.</td>
<td>18.4</td>
<td>91.9</td>
<td>15.3</td>
<td>64.6</td>
<td>19.9</td>
<td>44.2</td>
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<td>Chaetognatha</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>5.3</td>
<td>-</td>
</tr>
<tr>
<td>Other</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyclopoida</td>
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<td>0.5</td>
<td>0.8</td>
<td>0.1</td>
<td>0.7</td>
<td>1.3</td>
</tr>
<tr>
<td>Bivalvia</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Pteropoda</td>
<td>9.5</td>
<td>0.4</td>
<td>0.2</td>
<td>0.1</td>
<td>-</td>
<td>13.1</td>
</tr>
<tr>
<td>Polychaeta</td>
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<td>0.5</td>
<td>1.0</td>
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<td>5.5</td>
</tr>
<tr>
<td>Actinoptyrgii</td>
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<td>0.8</td>
<td>4.6</td>
<td>7.2</td>
<td>0.1</td>
</tr>
<tr>
<td>Balanomorpha</td>
<td>4.2</td>
<td>0.1</td>
<td>2.4</td>
<td>1.6</td>
<td>0.4</td>
<td>3.8</td>
</tr>
<tr>
<td>Cumacea</td>
<td>-</td>
<td>0.3</td>
<td>-</td>
<td>3.0</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Object</td>
<td>-</td>
<td>0.4</td>
<td>3.0</td>
<td>0.1</td>
<td>0.1</td>
<td>-</td>
</tr>
</tbody>
</table>

40
Table 2.4 Salmon biological data including wet weight (WW), fork length (FL), gut fullness index (GFI), showing mean and standard error, the number of empty stomachs, and percent dietary overlap between pink and chum salmon at each site.

<table>
<thead>
<tr>
<th>Site</th>
<th>Species</th>
<th>Salmon FL (mm)</th>
<th>Salmon WW (g)</th>
<th>GFI</th>
<th>Empty (#)</th>
<th>Diet Overlap</th>
</tr>
</thead>
<tbody>
<tr>
<td>D07</td>
<td>Pink</td>
<td>108.9 ± 0.6</td>
<td>11.8 ± 0.2</td>
<td>0.13 ± 0.02</td>
<td>2</td>
<td>24.9</td>
</tr>
<tr>
<td></td>
<td>Chum</td>
<td>103.7 ± 0.6</td>
<td>11.3 ± 0.2</td>
<td>0.23 ± 0.01</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>D09</td>
<td>Pink</td>
<td>103.9 ± 0.5</td>
<td>9.6 ± 0.2</td>
<td>0.38 ± 0.02</td>
<td>0</td>
<td>33.0</td>
</tr>
<tr>
<td></td>
<td>Chum</td>
<td>104 ± 0.5</td>
<td>10.1 ± 0.2</td>
<td>0.3 ± 0.03</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>D11</td>
<td>Pink</td>
<td>102.6 ± 0.7</td>
<td>10.2 ± 0.2</td>
<td>0.1 ± 0.01</td>
<td>0</td>
<td>21.7</td>
</tr>
<tr>
<td></td>
<td>Chum</td>
<td>102.9 ± 1.6</td>
<td>11.3 ± 0.5</td>
<td>0.02 ± 0.01</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>J06</td>
<td>Pink</td>
<td>114.1 ± 0.4</td>
<td>13.9 ± 0.2</td>
<td>0.03 ± 0.01</td>
<td>4</td>
<td>4.8</td>
</tr>
<tr>
<td></td>
<td>Chum</td>
<td>120 ± 0.8</td>
<td>16.8 ± 0.4</td>
<td>0.19 ± 0.01</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>J08</td>
<td>Pink</td>
<td>113.2 ± 0.5</td>
<td>13.3 ± 0.2</td>
<td>1.13 ± 0.06</td>
<td>0</td>
<td>14.1</td>
</tr>
<tr>
<td></td>
<td>Chum</td>
<td>114.4 ± 0.5</td>
<td>14.9 ± 0.2</td>
<td>1.28 ± 0.04</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>J02</td>
<td>Pink</td>
<td>113 ± 1</td>
<td>15 ± 0.5</td>
<td>7.46 ± 0.19</td>
<td>0</td>
<td>59.8</td>
</tr>
<tr>
<td></td>
<td>Chum</td>
<td>122.4 ± 1</td>
<td>20.5 ± 0.4</td>
<td>6.2 ± 0.11</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>
2.7 Figures

Figure 2.1 Map of salmon survey stations in the Discovery Islands and Johnstone Strait. Inset map (left) shows the British Columbia coast with the study region highlighted in red.
Figure 2.2 Average relative biomass of the main prey groups for juvenile pink (top) and chum salmon (bottom), at each site along the migration route. The ‘Other’ group includes prey such as cyclopoids, fish, polychaetes and pteropods.
Figure 2.3 Non-metric multidimensional scaling (NMDS) ordination of juvenile pink and chum salmon diet composition. Each point represents one salmon stomach, colored by site, where open circles represent pink and filled circles, chum. “Stress” indicates how well the distances between points were retained when displayed in two-dimensions and for this plot, stress was 0.17.
Figure 2.4 Cluster analysis of juvenile pink and chum diet composition (average linkage clustering and Bray-Curtis dissimilarity).
Figure 2.5 Boxplot of pink and chum salmon condition factor K across the study sites. Box plots show the mean (black bar), interquartile range (boxes), 1.5*inter-quartile range (whiskers), and points indicate extreme values of salmon condition. The red dotted line separates fish in good condition (high weight to length ratio, > 1) and in poor condition (low weight to length, < 1).
Figure 2.6 Gut fullness index (GFI) of juvenile pink and chum salmon. Box plots show the mean (black bar), interquartile range (boxes), 1.5*inter-quartile range (whiskers), and points indicate extreme values of salmon GFI. The overlaid dark red line indicates dietary overlap between pink and chum salmon (secondary y-axis).
Figure 2.7 Cumulative prey taxonomic richness curves for juvenile pink and chum, salmon at each site location. Note: All sampling events included 10 salmon, but not all stomachs had prey in them (n = 12 empty stomachs total).
Chapter 3: Salmon trophic interactions shift with prey phenology and migration timing

3.1 Introduction

The early marine phase for pink and chum salmon is incredibly important, as these species spend less time in freshwater systems, compared to sockeye, chinook or coho (Groot & Margolis, 1991). Research has shown the early marine phase to be a likely bottleneck in survival of chinook and coho salmon, mediating individual and cohort success during the first ocean winter (Beamish et al., 2004; Duffy & Beauchamp, 2011). Understanding the fundamental biology of salmon during this crucial early marine life phase is therefore essential to properly manage these species. However, modern research is somewhat more limited on the early marine feeding ecology and survival of sockeye, pink and chum salmon in British Columbia (Beamish et al., 2003). A number of studies of pink and chum diets were conducted in British Columbia prior to the 2000’s, identifying copepods, larvaceans, amphipods and fish as important in diets (Landingham et al., 1998; Manzer, 1969; Osgood et al., 2016) and food limitation in southern and northern B.C. (Healey, 1991; Perry et al., 1996). However, more research is needed on pink and chum foraging responses to shifting coastal conditions in B.C., to better predict adaptive responses under climate change.

Researchers in other areas of the North Pacific continue to study pink and chum diets (Armstrong et al., 2005; Bollens et al., 2010; Chebanova et al., 2018; Moss et al., 2009; Nagata et al., 2007) and survival trends (Agler et al., 2013; Cross et al., 2008; Honda et al., 2017; Malick
et al., 2011; Miller et al., 2012; Saito et al., 2009; Yasumiishi et al., 2016). Foraging conditions experienced by juvenile salmon is expected to vary spatially across the north east Pacific due to the wide range of oceanographic conditions (Mueter et al., 2005), seasonally due to plankton production cycles (Schweigert et al., 2013; Tommasi et al., 2013), and interannually due to longer term climate driven changes in ocean conditions (von Biela et al., 2019). Pink and chum salmon are two species of salmon who spend most of their life cycle in the marine environment and juveniles must grow quickly to avoid size-selective predation risks. Whether or not pink and chum salmon achieve sufficient growth in the early marine phase is an important question that remains to be answered in potentially food limited migration pathways. Early marine growth of salmon is determined largely by prey quality and quantity, which varies significantly across multiple spatial scales, due to variable productivity regimes and coastal conditions (Malick et al., 2015). Another important factor is how zooplankton phenology and salmon migration timing interact to influence salmon foraging success. This may be compounded by potential competitive interactions between species, which will be explored during salmon outmigration in this study.

The prey which salmon encounter in different habitats along the migration route depends on bottom-up processes that drive productivity, such as temperature, salinity, mixing, and nutrients. The ocean environment in northern latitudes is characterized by clear seasonal cycles of summer surface layer stratification and extensive phytoplankton growth. Differences in ocean mixing, temperature, freshwater inputs and nutrient levels vary on multiple spatial and temporal scales. The previous chapter of this study found major differences in zooplankton consumed by juvenile pink and chum salmon across the dynamic migration route of the Discovery Islands and Johnstone Strait. Productive areas such as the Strait of Georgia have been shown to positively
impact salmon feeding (Harrison et al., 1983; Osgood et al., 2016). Similarly, productivity may be enhanced in areas where mixed and stratified waters meet, due to the “fertilization effect” when nutrient depleted stratified waters are replenished (Mahara et al., 2021). However, areas such as Johnstone Strait with deep tidal mixing, cause phytoplankton to be mixed below the photic zone and hence be light limited, preventing the development of a significant seasonal spring bloom (McKinnell et al., 2014; Thomson, 1976). The zooplankton communities are characterized by euphausiids and calanoid copepods in the Northern Strait of Georgia, meroplankton in the mixed areas within the Discovery Islands and small < 2 mm copepods in Johnstone Strait (Mahara et al., 2021). These habitat mosaics of differing productivity regimes may have large effects on juvenile salmon health by mediating short-term prey availability. These regional productivity differences may also shift over time due to climate change, impacting cumulative foraging experience of outmigrating salmon.

The prey available to juvenile salmon is further mediated by zooplankton phenology. Seasonal timing can affect both the quantity and the size of prey available to migrating juvenile salmon. Over time, evolution has selected for spring outmigration run timing that coincides with ideal foraging conditions, as genetic lineages of fish migrating through optimal zooplankton prey fields will have higher survival than earlier or later migrating counterparts (Asch et al., 2019; Schweigert et al., 2013). However, climate change may alter seasonal cycles, which can lead to a mismatch of predators and prey (Edwards & Richardson, 2003). Spring bloom timing has been shown to be a stronger predictor of salmon survival than overall mean chlorophyll-a values (Malick et al., 2015), and salmon migrations in Auke Creek, Alaska have shifted earlier for both juveniles and spawning adults (Kovach et al., 2013). Normally, phytoplankton blooms are
followed in succession by increased amounts of herbivorous small zooplankton, and then by expansion of the omnivorous and carnivorous zooplankton populations. However, when the onset of phytoplankton bloom timing shifts or the community composition is dominated by small phytoplankton, smaller, short-lived zooplankton likely benefit and larger zooplankton with fixed life spans may decline (Mackas et al., 2007). Pink and chum salmon tend to migrate slightly earlier than sockeye and chinook, and therefore are vulnerable to potential mismatches in bloom timing affected by the warming environment.

The size of salmon in relation to size of their prey is another important factor in foraging success and this is influenced by zooplankton phenology as well as salmon size at ocean entry and growth rate during the first few months at sea (James et al., 2020; Moss & Beauchamp, 2007). The ideal size of prey for juvenile salmon depends on salmon size and mouth gape, therefore large prey may be available in the water column but unavailable as a prey choice for certain salmon. Conversely, if only small zooplankton are available, it may not be energetically sustainable as prey for larger salmon.

An additional prey parameter is that of their quality as dietary items. Prey quality can be inferred through the lipids or fatty acid compositions essential to the nutrition of predators. Generally, small zooplankton (< 2 mm) and jellyfish are low in nutritional quality, whereas euphausiids, polychaetes, chaetognaths, insects, fish, and large copepods species are known as prey of a higher quality (Boldt, 2001; Costalago et al., 2020). Quality, size, and quantity of prey can all have significant impacts on salmon growth and survival, through impacting fish condition and physiological fitness to survive in competitive conditions.
Salmon are broadly opportunistic feeders, and their diets are incredibly variable over time (Boldt & Haldorson, 2003; Lazhentsev & Maznikova, 2015; Murphy et al., 1988). Therefore, prey choice and interspecific competition can potentially rapidly shift spatially and temporally. Juvenile pink and chum salmon diets in the Broughton Archipelago were shown to shift between high and low overlap due to ocean conditions and prey availability (Gulbransen, 2014). Chapter 2 of this study demonstrated that interspecific competition and trophic niches differed spatially due to differences in foraging opportunities. Competition between species leading to trophic niche separation may be caused by low productivity or high densities of salmon, or a combination of both. For example, chum salmon growth has been observed to decrease as a result of high densities of pink, chum, and sockeye salmon, and competitive interactions may be exacerbated by periods of poor food availability (Debertin et al., 2017; Morita & Fukuwaka, 2020). Furthermore, adult pink salmon in the Gulf of Alaska have demonstrated feeding effects on zooplankton standing stocks causing trophic cascades (Batten et al., 2018) and quantifiable effects on other species, including chum salmon. However, to date the competitive interactions between pink and chum salmon have largely been studied in adults and less so among juveniles. Many prior research studies on juvenile pink and chum salmon have described diet composition without in-depth comparisons between species and analysis of prey switching tendencies of chum salmon. Chapter 3 will address this knowledge gap by investigating the persistence of the interaction dynamics observed spatially in Chapter 2 over the seasonal cycle and between years.

Previous studies in coastal British Columbia have shown Discovery Islands to be very seasonally and tidally dynamic, whereas Johnstone Strait is more consistent with minimal
seasonality (Mahara et al., 2021). Until the current study, there has been limited research on juvenile pink and chum salmon for the entirety of the outmigration period in tidally mixed waters. Other studies in comparable tidally mixed waters are Southeast Alaska, however studies sampled monthly or only studied chum salmon (Orsi et al., 2004; Sturdevant et al., 2002, 2012). In these areas, pink and chum salmon diet overlap also varied and prey switching occurred, shifting mainly between euphausiids, larvaceans (Oikopleura) and calanoids (Fergusson et al., 2020; Sturdevant et al., 2002). Another study investigated juvenile pink and chum diets in the Broughton Archipelago in 2003 and 2006 from April to May (salmon fork length range: 25 - 70 mm), and found interannual variation in dietary overlap between the species (Gulbransen, 2014). While the Broughton Archipelago is located close to the strong tidal currents of Johnstone Strait, the freshwater influence leads to stratified surface waters in the archipelago, that will likely influence salmon diets differently (Pearsall, 2008). Therefore, more research is required to fully explore the intricacies of juvenile pink and chum salmon interactions in oceanographically dynamic regions during their early marine phase, especially as this may be further complicated by competition with co-migrating juvenile sockeye.

This study will investigate the seasonal dynamics of the trophic ecology of juvenile pink and chum salmon and the zooplankton community composition dynamics during their early outmigration. The main research question of this study is: how did pink and chum salmon respond to shifts in prey availability during their outmigration? This study aims to a) quantify juvenile pink and chum salmon diets and their seasonal and interannual interactions in southern coastal B.C.; b) describe how salmon species condition and foraging success vary over time; and c) compare juvenile salmon size with zooplankton prey sizes consumed across regions and years.
3.2 Methods

3.2.1 Field sampling

The Hakai Institute’s Juvenile Salmon Program was established in 2015 as a collaboration between the Hakai Institute, the University of British Columbia, Simon Fraser University, the University of Toronto and Salmon Coast Field Station. This ongoing program annually samples juvenile salmon as they migrate through the Discovery Islands and Johnstone Strait during the main outmigration period (May to July). The objective of the program was to improve understanding of the early marine phase of Pacific salmon, particularly the factors contributing to health and survival (Hunt et al., 2018). This study focused on 2015 and 2016, which had good seasonal coverage of pink and chum salmon from late May to around early July.

During 2015 and 2016, 12 and 10 sites were sampled in Discovery Islands and Johnstone Strait, respectively, to provide coverage of all possible salmon migration routes through these regions (Hunt et al., 2018). While each site was sampled weekly, included in this study were bi-weekly sampling events. For this study, 2 sites, one from each region, were selected (the distance between the sites was ~ 95 km), in order to obtain a sample size of 10 pink and 10 chum per set (Figure 3.1). However, 2015 was lower in pink salmon abundance due to their biennial life pattern and the absence of Fraser River pink salmon (n = 212 total). Samples for this analysis were selected from late May, early/mid-June, and late June or early July (Table 3.1) to capture the early, peak, and late stages of salmon out-migration, respectively (Johnson et al., 2019).
Salmon were captured from a small research boat using a purse seine net with bunt dimensions of 27 m × 9 m with 13 mm mesh and tow area dimensions of 46 m × 9 m with 76 mm mesh. Once arrived at a site, weather and sea state were recorded, followed by a visual survey of salmon surface activity. The purse seine net was set on a targeted school of fish and loosely cinched up to facilitate collection while keeping salmon in the water to limit stress. Up to 30 sockeye, 10 pink and 10 chum salmon were retained, and the remaining salmon were counted and released (Hunt et al., 2018). All retained fish were individually euthanized with tricaine methane sulfonate (MS-222) upon removal from the seine net, lengths and weights recorded, and preserved at -196 °C with liquid nitrogen in a dry shipper until the salmon samples were stored in the -80 °C freezer at the lab. All salmon were collected under DFO license number ‘XR 42 2015’ and ‘XR 92 2016’ with approval from UBC’s Animal Care Committee (Protocol A19-0025).

A YSI instrument (model #15B102233 and 15C100324) was used to measure temperature and salinity at the surface and 1-meter depth, recorded while salmon were held for processing in the net. Once the purse seine set had been complete, zooplankton were sampled with a 50 cm diameter ring net with 250 μm mesh net, towed horizontally at the surface. A General Oceanics flowmeter was attached to the zooplankton net to calculate volume filtered for each tow. Zooplankton collected were then preserved in 4% formaldehyde for future analysis.

3.2.2 Zooplankton and salmon stomach content analysis

In the lab, zooplankton samples were poured over sieves and separated into 250 μm, 1000 μm and 2000 μm size fractions before being weighed and analyzed. Wet weights were measured
to the nearest 0.1 mg on an analytical balance, with non-gelatinous and gelatinous groups weighed separately. If necessary, each size fraction of zooplankton was subsampled with a Motodo plankton splitter. Zooplankton were identified to life stage and the finest taxonomic resolution possible, each group was then enumerated and measured with an ocular micrometer.

Wet weight and fork length were recorded for juvenile salmon before dissection to remove their stomachs, which were preserved in 95% ethanol. Prior to analysis, salmon stomachs were removed from ethanol and soaked for 30 minutes in tap water to reduce the brittleness of the sample. The stomach was then dissected open and the food contents removed. The entire food bolus was weighed on an analytical balance and wet weight recorded to the nearest 0.1 mg. The bolus was then placed on a petri dish with water added, and prey rearranged by species, size, life stage and digestive state. Digestive states were defined as 1) fresh prey, intact, 2) semi-fresh prey, with lost appendages or color, 3) semi-digested prey, only identifiable to group, and 4) fully digested prey, unidentifiable. If prey could not be identified to species, it was identified to the most detailed taxonomic group possible, e.g., *Oikopleura* spp. For each group, minimum and maximum lengths were measured with an ocular micrometer, individuals were counted, and the group wet weight recorded to nearest 0.1 mg. If a stomach sample had over 1,000 similarly sized prey, a ¼ subsample was processed, after all of the large and/or rare prey present were recorded.

3.2.3 **Data analysis**

The temporal variation in prey composition was analyzed using a multivariate approach. Prior to the analysis, rare taxonomic prey categories (occurring in less than three stomachs) were
combined into higher level groupings, ignoring “digested food.” Fish stomach content wet weight was multiplied by 1.54 to correct weights for water loss after storage in ethanol (James, 2019). Relative prey biomass for each stomach was calculated and arcsine square root transformed before calculating Bray-Curtis dissimilarity. The dissimilarity matrix was used for non-metric multidimensional scaling (NMDS) ordination and agglomerative hierarchical clustering (AHC). For the NMDS plot, taxonomic group vectors were overlaid as arrows to visualize the direction and magnitude of prey driving differences in samples, which were calculated by a modified BIO-ENV method (Clarke & Ainsworth, 1993). Indicator value (INDVAL) analysis was performed on clusters at the 65% dissimilarity level to determine prey species differences between clusters (Dufrêne & Legendre, 1997). The transformed data were input into two-way crossed analysis of similarity (ANOSIM) to compare region and species diets during outmigration, and similarity percentages (SIMPER) analysis was calculated separately for pink and chum to determine which prey taxa drove differences between sites.

The diet composition was also calculated according to prey size classes (< 1, 1-2, 2-5, 5-10 and > 10 mm) for each salmon sample, only taking into consideration fresh (DS1) prey items. Digested zooplankton were excluded since reliable lengths could not be measured when the prey was degraded, crustaceans were often broken, and soft-bodied prey were especially poor quality. Relative biomass was calculated for each salmon then averaged by each sample date, region, and species to create a prey size bar graph similar in layout to the taxonomic diet composition figure. Average fresh prey size was compared to salmon size (fork lengths) for each species, region and year through linear models, where the mean prey size per stomach was weighted by the biomass.
In addition to the multivariate statistics, various indices were calculated from the raw data. Gut fullness indices (GFI) were calculated for each fish, expressed as percent body weight:

\[ \text{GFI} = \left( \frac{\text{food bolus weight}}{\text{fish weight}} \right) \times 100 \]

Fulton’s condition factor \( K \) comparing length-weight relationships of salmon was calculated as:

\[ K = 100,000 \times \frac{\text{fish weight}}{(\text{fish fork length})^3} \]

Weight was measured in grams and fork length in millimetres, \( K = 1 \) indicates average condition, > 1 means relatively healthy, and < 1 poor condition (Beamish et al., 2012; Jones et al., 1999).

Condition of study fish (\( n = 212 \)) were analyzed with a multi-way ANOVA to investigate any interactions and differences between years, regions, and species, after reciprocal transformation to meet the assumptions of normality and homogeneity of variance (Keppel & Wickens, 2004).

The Schoener percent similarity index (PSI) for species diet overlap was calculated for each date:

\[ \text{PSI} = \left[ \sum (\text{minimum prey}_p, \text{prey}_c) \right] \times 100 \]

Where prey\(_p\) was the proportion by weight of prey \( i \) in pink salmon stomachs and prey\(_c\) was the proportion by weight of prey \( i \) in chum salmon stomachs (Chipps & Garvey, 2006; Krebs, 2013).

The empty stomachs (those with no identifiable prey) in this study were excluded from the multivariate dissimilarity calculations but were included in the calculation of the above indices.

The prey taxonomic detail was retained in analyses, but for summary tables and figures, ‘other’ was prey grouped together that does not contribute substantially to diets (< 10% weight), e.g., mysids, amphipods, cyclopoids, harpacticoids, bivalve larvae, pteropods, and polychaetes, etc.

Diet richness was determined through cumulative prey curves for juvenile pink and chum salmon stomachs. All analyses were performed in R (v4.0.2.), using the vegan package v2.5-6 (Oksanen et al., 2019; R Core Team, 2020), except ANOSIM, calculated in PAST (Hammer et al., 2001).
All of the above data analyses were calculated on the 212 salmon used in the study (95 pink salmon and 117 chum salmon samples total). However, average peak migration timing and salmon size (fork lengths) for pink and chum was also determined for all samples collected by the Hakai Juvenile Salmon Program, for 2015-2019 (n = 5765 for migration, n = 2650 for size). Outmigration peak was assumed to be the point when 50% of salmon passed through the area, which was calculated for each species and year, see Johnson et al. (2019) for more information.

3.3 Results

3.3.1 Environmental conditions and zooplankton

In the Discovery Islands, the temperature and salinity of the surface waters were variable during the salmon outmigration periods, and warm and fresh compared to Johnstone Strait in both 2015 (mean ± standard error: 15.8 ± 0.6 °C, 27.2 ± 0.4 ‰) and 2016 (15.5 ± 0.7 °C, 25.8 ± 0.3 ‰; Table 3.1). In contrast, the surface temperature and salinity of Johnstone Strait remained consistently colder and more saline during the salmon outmigration periods in 2015 (10.4 ± 0.2 °C, 28.8 ± 0 ‰) and 2016 (10.3 ± 0.2 °C, 31 ± 0.2 ‰). The zooplankton biomass was overall more than two-fold higher in 2016 than in 2015 in both regions, 853 ± 72 mg/m³ vs 338 ± 59 mg/m³ (Table 3.1). The zooplankton biomass composition by size class was dominated by either the 250 μm or 2000 μm size fraction. The latter was dominated by gelatinous zooplankton. In 2015, the Discovery Islands had low overall zooplankton biomass, with the exception of a single peak on June 5th, 2015 reaching 1245 mg/m³. The Discovery Islands had more 1000 μm size fraction biomass in mid-season in both years (72-89 mg/m³), compared to Johnstone Strait,
which had less 1000 μm zooplankton through the study period (0.5-16 mg/m³; Table 3.1). The biomass of non-gelatinous zooplankton from the 2000 μm size fraction was very low throughout both regions and years (0.2-8 mg/m³; Table 3.1). Therefore, zooplankton biomass differed by year and region, with overall low biomass in 2015, and large contributions of gelatinous zooplankton in Johnstone Strait and small zooplankton in Discovery Islands in 2016.

In the Discovery Islands, there was a high prevalence of cladocerans captured early and mid-season in both 2015 and 2016 (ranging from 32.3-75.1% of total abundance), shifting to more numerous calanoid composition in mid-June (40.1-52.9%; Table 3.2). In Johnstone Strait, calanoids (15.4-59.6%) and zooplankton eggs (25.1-77.7%; Table 3.2) were the two main types of zooplankton in 2015 and late June 2016. Cladocerans (27.3%) and ‘other’ (Cyclopoida, 15.8% and Pteropoda, 10.8%) were also prominent in early June 2016 in Johnstone Strait (Table 3.2).

3.3.2 Salmon diet composition

In late May and early June 2015 in the Discovery Islands, juvenile pink and chum salmon both consumed Oikopleura spp. (16.9-97.7% of diet by weight for pink; 59.3-79.3%, chum). Early in the season in 2015, diets were quite diverse and included Balanomorpha barnacle larvae (0.2-43.6% pink; 2-14.7% chum), cladocerans (0.2-22.3% pink; 2.9-3.6% chum), and juvenile fish (sand lance, Ammodytes hexapterus, 20.4% chum), as well as small amounts of Calanoida, Decapoda, and ‘other’ taxa (Figure 3.2; Table 3.3). Later in June 2015, the Discovery Islands salmon diets shifted and both species consumed Calanoida (53.4% pink; 33.4% chum), Chaetognatha (39.3% pink; 46.4% chum), and chum consumed Euphausiidae (10%; Figure 3.2).
The 2016 diets of salmon in the Discovery Islands were comprised of different prey than in 2015. *Oikopleura* spp. were still common prey in 2016 for both pink (18.2-27.7%) and chum (34.4-91%) salmon throughout the outmigration season (Figure 3.2; Table 3.3). However, in late May 2016, Euphausiidae eggs were the main prey type (44.2% pink; 55.3% chum), and in early June, Echinodermata larvae were the most dominant prey for pink salmon (36.1%; chum, 6.8%; Figure 3.2). Finally, in mid-June 2016, chum salmon diets were dominated by *Oikopleura* (91%) and pink salmon diets shifted to Decapoda (28.3%), ‘other’ (29.1%, e.g., Amphipoda, Pteropoda, Cyclopoidea, see Table 3.3) and Calanoida (19.8%). In Johnstone Strait, pink and chum diets were consistent in the main groups of prey consumed in 2015 and 2016, chum salmon primarily fed on gelatinous prey (68.4-96.5%) and pink salmon on calanoids (63.3-99.4%; Figure 3.2).

The clear prey partitioning in Johnstone Strait was also reflected in the NMDS ordination of diets, where pink and chum salmon occupied separate groups (Figure 3.3). Furthermore, the NMDS showed variable diets, particularly for pink salmon, in the Discovery Islands. Pink salmon in the Discovery Islands had the greatest spread in the ordination and could not be characterized by a single prey type, but were influenced by ‘other’, meroplankton (Decapoda, Echinodermata and Balanomorpha larvae), Cladocera, and Euphausiidae eggs (Figure 3.3). The grouping of chum salmon in the Discovery Islands was mostly driven by *Oikopleura* spp. diets, however, there was one unique diet event, defined by abundant Chaetognaths (June 13, 2015).

The cluster analysis revealed the same trends, with diet composition separated by region and further subdivided by salmon species and date (Figure 3.4). The separation between pink and chum was strongest in Johnstone Strait. In the Discovery Islands, there were seven subclusters:
two outlier clusters of chum salmon (May 2015), three pink salmon clusters separated by date, one comprising both salmon species in May 2016, and one comprising chum salmon clustered regardless of date (Figure A.1). The other main cluster included mostly Johnstone Strait samples with some occurrences of Discovery Islands diet similarity as well (Figure A.2). The five subclusters in the Johnstone Strait included: chum salmon for most dates, chum salmon in mid-June 2016, pink salmon in early June 2016, both species from Discovery Islands (mid-June 2015), and most pink salmon. Outside of these two main clusters, there were also more extreme outliers (~ 95% dissimilarity), a pink salmon in Johnstone Strait (mid-June 2016), a pink salmon in Discovery Islands (mid-June 2016), and chum salmon in Discovery Islands (mid-June 2016; Figure 3.4). Regardless of site, pink salmon diets had higher within-group variability than chum.

The indicator value analysis revealed the prey species characterizing each subcluster. Small prey defined the pink salmon diets in the Discovery Islands, such as barnacle nauplii, cladocerans, echinoderm larvae and euphausiid eggs (Table A.2). Chum salmon in the Discovery Islands also consumed euphausiid eggs, as well as *Ammodytes hexapterus* and *Oikopleura* spp. In Johnstone Strait, chum salmon mainly consumed *Cnidaria*, along with *Acartia longiremis*, with the exception of mid-June 2016 being characterized by Ctenophora prey. Pink salmon diets in Johnstone Strait were characterized entirely by copepods, mainly *Calanus marshallae*, except early June 2016, when pink consumed *Pseudocalanus, Tortanus discaudatus*, and *Harpacticus*. The unique pink and chum diets of Discovery Islands on June 13, 2015 grouped with Johnstone Strait and were defined by *Tomopteris septentrionalis*, chaetognaths, and *Calanus pacificus* prey.
The two-way analysis of similarity (ANOSIM) revealed a strong difference in the diet compositions by region (R = 0.71, p = 0.001), and a moderate significant difference by species (R = 0.43, p = 0.001). The similarity percentage (SIMPER) analysis determined that the top three prey driving differences between regions in pink salmon diets were *Calanus marshallae* (12% dissimilarity) and digested calanoids (5%) in Johnstone Strait, and *Oikopleura* spp. (9%) in Discovery Islands. Other important prey in the SIMPER analysis for pink salmon were other calanoid species in Johnstone Strait, i.e., *Calanus pacificus, Aetideus divergens, Pseudocalanus* spp. and *Epilabidocera longipedata*. The characteristic prey for pink salmon in the Discovery Islands were meroplankton and small zooplankton, e.g., barnacle nauplii and cyprids (*Balanus crenatus* and *B. glandula*), brachyuran larvae and echinoderm larvae, euphausiid eggs and cladocerans (see Table 3.4 for more details). The main prey types of chum salmon driving these differences by region were *Oikopleura* (explained 23% of dissimilarity) in the Discovery Islands, as well as Cnidaria (29%) and *Calanus marshallae* (5%) in Johnstone Strait (Table 3.4).

3.3.3 Diet diversity and overlap between juvenile salmon

Pink salmon had higher diet diversity than chum salmon in both regions and years (Figure 3.5). The difference between species diet richness was more pronounced in 2016, with pink salmon consuming over 20 types of taxa more than chum salmon throughout both regions. There was a higher difference between regional diet diversity in 2015, where Discovery Islands had high richness for both species (80 taxa) and Johnstone Strait had low diet richness (40 taxa). Comparing within species diets, Discovery Islands had higher observed richness than Johnstone Strait, with the exception of 2016 pink salmon, when regions had similar richness (Figure 3.5).
Dietary overlap between juvenile pink and chum salmon was highly variable throughout the study period and regions. In the Discovery Islands in 2015, overlap increased from 22.4% on May 21st to 60.5% on June 13th, and decreased in 2016, from 80.8% to 24.9% (May 19th to June 16th; Figure 3.6). Overall, mean diet overlap between salmon species was higher in Discovery Islands (48.1-53.9%) than Johnstone Strait (9.9-16.7%), and higher for both in 2015 (Table 3.5).

3.3.4 Salmon health

Salmon gut fullness indices (GFI) were consistently low in Johnstone Strait during 2015 (mean GFI: pink salmon 0.45%; chum salmon 0.63%) and 2016 outmigration (pink salmon 0.56%; chum 0.99%; Table 3.5). In the Discovery Islands, GFI was highly variable over time, having a mean of between 0.89-3.02% and 0.13-3.29% for pink in 2015 and 2016 respectively, and 1.73-3.28% and 0.23-3.92% for chum salmon in the same years (Figure 3.6). Chum salmon generally had slightly higher mean GFI than pink salmon, and in 2015 Discovery Islands, chum salmon also had higher variation in the GFI.

Empty stomachs were not very prevalent in this study, 4% of all juvenile salmon had no food items present in the stomachs (n = 8, Table 3.5). Empty stomachs were more common for pink salmon (6% of pink stomachs; n = 6) than chum salmon (2% of chum stomachs; n = 2). The distribution of empty stomachs also differed between species, with empty pink salmon stomachs occurring in each region but only in 2016, and chum salmon having empty stomachs only in the Discovery Islands. For the 212 salmon in this study, condition factor K was higher in 2015 than in 2016 (Figure 3.7). The 3-way ANOVA on condition revealed significant differences by year.
(p < 0.001), species (p = 0.01), and interaction of species and year (p = 0.013), but region was not significant (p = 0.84). Species differed in condition significantly in 2016 (p < 0.001), but not in 2015 (p = 0.8). For 2015, both species had average condition in both regions (mean 1.02 K), but in 2016, pink were in much poorer condition (0.9-0.93) than chum (0.96-0.97; Table 3.5).

There was a total of 25 microplastics or other objects (macroplastic, glass) found in 8.5% of all the salmon stomachs included in this study (n = 18 salmon). These foreign objects were consumed by both pink and chum salmon, mostly in the Discovery Islands (at least one for each date except June 16th, 2016), compared to Johnstone Strait (mostly from July 5th, 2016). The size of the plastics/objects ranged from 0.3 mm to 5.8 mm, and included two pieces of glass, 11 micro-plastic fibers, 9 hard microplastic pieces, 1 microplastic film, 1 microplastic clothing tag fastener and 1 macroplastic piece that was likely a broken straw piece. Furthermore, the macroplastic found in a juvenile pink salmon stomach in the Discovery Islands, constituted 41.1% of the “prey” biomass and appeared to be larger than the fish’s sphincter (Figure A.3).

3.3.5 Salmon and prey size

The size of juvenile salmon prey varied across regions, species, season and years, but the dominant size class by weight was often 2-5 mm (Figure 3.8). Chum salmon consumed larger or similar sized prey in the Discovery Islands compared to pink salmon, and smaller or similar prey in Johnstone Strait (although “gelatinous” was excluded due to the digested nature of the prey). There were interannual differences in prey size consumed by both species, where 2015 included generally larger prey than 2016, this difference was especially pronounced in the Discovery
Islands. Size increased somewhat across the outmigration season in Discovery Islands in both 2015 and 2016, however Johnstone Strait prey size classes were consistent without seasonality.

The seasonal trend in prey size was correlated with an increase in salmon size in the Discovery Islands and this predator-prey relationship was most apparent for chum (Figure 3.9). In the Discovery Islands in 2015, pink salmon had a moderate relationship to prey size ($y = -12.4 + 0.16x$, $R^2 = 0.55$, $p < 0.001$), and chum had a strong correlation ($y = -16.2 + 0.21x$, $R^2 = 0.71$, $p < 0.001$; Figure 3.9). For the Discovery Islands in 2016, there was a moderate relationship of chum and prey size ($y = -2.5 + 0.05x$, $R^2 = 0.46$, $p < 0.001$), but not pink ($y = 0.6 + 0.01x$, $R^2 = -0.03$, $p = 0.64$). In Johnstone Strait, there was no relationship between salmon and prey size in 2015 for pink ($y = 2.0 + 0.01x$, $R^2 = -0.01$, $p = 0.40$) or chum ($y = -3.2 + 0.05x$, $R^2 = -0.02$, $p = 0.47$). In Johnstone Strait in 2016, there was a weak but significant size effect for pink salmon ($y = -2.8 + 0.05x$, $R^2 = 0.34$, $p = 0.001$), but not chum salmon ($y = 4.9 - 0.01x$, $R^2 = 0.03$, $p = 0.20$).

The size of salmon also differed between years, regions and species, in 2015 the salmon were larger than in 2016, larger in Johnstone Strait since it is further along the migration route, and chum salmon were generally slightly larger than pink salmon (Table 3.5). Compared to more recent years (2017-2019), 2015 salmon were still relatively large and 2016 salmon, small (Figure 3.10). Migration timing was comparable between 2015 and 2016 for pink and chum salmon, with 2016 being slightly earlier than 2015 and pink salmon generally a little bit later than chum salmon (Table A.1). Compared to other years of migrating pink and chum, 2015 and 2016 were early migrants, with peak outmigration of June 10th, 2016 for both species, and June 17th, 2015 for pink salmon (average peak migration) and June 12th, 2015 for chum salmon (2 days early).
3.4 Discussion

This study quantified juvenile pink and chum salmon diets, interactions, condition, and predator-prey size relationships, seasonally and interannually in the salmon outmigration period. It was found that diets and species interactions were variable in the Discovery Islands but were consistent in Johnstone Strait. Salmon condition was significantly higher in 2015 relative to 2016, likely due to the presence of larger and more nutritious prey in the Discovery Islands in June 2015. The spatial patterns in foraging observed in Chapter 2 were reflected across the outmigration season, when juvenile pink and chum salmon fed on similar prey during periods of high food availability and partitioned resources when food was limited.

3.4.1 Oceanographic seasonality and prey phenology

The two regions of Discovery Islands and Johnstone Strait were very different from each other, in seasonality of oceanographic conditions and diet composition of pink and chum salmon. Waters in the Discovery Islands region increased in temperature and became fresher as the season progressed, although, later in 2015, there was also a drop in temperature and increased salinity, which potentially indicated a mixing event due to wind (James, 2019). Johnstone Strait had low temperatures and high salinity, but 2015 had slightly fresher surface water than 2016.

While the zooplankton samples showed some seasonal shifts from barnacle larvae and cladocerans to calanoid copepods in Discovery Islands, there was low interannual variability. Zooplankton biomass appeared higher in 2016 relative to 2015, although, small zooplankton and
gelatinous zooplankton dominated in the Discovery Islands and Johnstone Strait, respectively. These findings were comparable to a concurrent study that included more frequent weekly sampling (James, 2019). However, a more detailed analysis of zooplankton communities in Discovery Islands in 2015 and 2016, found a ten-fold higher prevalence of meroplankton and delayed spring phytoplankton and zooplankton bloom timing in 2016 (Mahara et al., 2019).

Zooplankton communities captured by horizontal net tows did not quite match what was found in juvenile salmon diets. While taxa proportions found in diets differed from those in the zooplankton samples, overall trends were comparable. In 2016, euphausiid eggs and echinoderm larvae were captured in the Discovery Islands zooplankton tows. Johnstone Strait had calanoid copepods throughout, as well as zooplankton eggs and cladocerans, though fish may have been too large to consume such small prey. Since salmon may feed beyond the surface waters and for a longer period than the snapshot of zooplankton sampling, there was likely a mismatch between zooplankton sampled and salmon diets. Therefore, in the current study, horizontal net tows were considered supplemental, and diets were used to assess feeding conditions and prey availability.

### 3.4.2 Seasonality of salmon diet composition

In the Discovery Islands diets, prey appeared to shift seasonally from small zooplankton and meroplankton, such as barnacles and cladocerans, to *Oikopleura*, and later in 2015, to larger calanoids, chaetognaths and euphausiids. However, in 2016 the Discovery Islands dietary composition had less of a shift, with larval and egg stages of zooplankton remaining dominant throughout the season, including a high prevalence of euphausiid eggs, echinoderm larvae, and
decapod larvae, as well as *Oikopleura*. Prey composition in Johnstone Strait had less seasonality than Discovery Islands, and also appeared to be more variable in 2016. Overall, the Discovery Islands diets of pink and chum juveniles were mostly comprised of meroplankton and *Oikopleura* spp., respectively. In Johnstone Strait, juvenile pink and chum salmon diets were dominated by calanoids and gelatinous prey, respectively. These spatial patterns in diet composition remained relatively constant over time, affording the findings of Chapter 2, where salmon species’ unique trophic niches were robust throughout both the season and years.

While Johnstone Strait had relatively low seasonal and interannual variability, the taxonomic composition of prey did shift over time, especially in 2016. The most dominant prey types were Cnidaria for chum salmon and *Calanus marshallae* and *C. pacificus* for pink salmon. In Johnstone Strait, pink salmon consumed a higher diversity of smaller calanoids in 2016, e.g., *Pseudocalanus*, *Tortanus discaudatus* and *Aetideus divergens*, especially early June 2016. Chum salmon prey shifted to Ctenophora in mid-June 2016, coinciding with lower gut fullness values. Overall, 2016 included more diet composition outliers. The clear preference for gelatinous prey by chum juveniles compared to pink in Johnstone Strait agreed with Chapter 2 and published literature describing chum salmon as gelatinovorous species and pink salmon as generalist foragers, strategies suggested to limit inter-species competition (Brodeur, 1990; Graham, 2020).

Juvenile salmon dietary overlap varied greatly across regions and dates and may be used to infer potential competition between species. It was noted in this study that in the Discovery Islands overlap depended on prey types available, and the high overlap coincided with periods of high foraging success (judged from GFI values). This was clearly the case during late 2015 and
early 2016, when both species consumed similar and high-quality prey. Conversely, during periods of poor feeding conditions in the Discovery Islands, chum salmon specialized on *Oikopleura* spp. and pink salmon on small, nearshore meroplankton. Similarly, in Johnstone Strait, pink specialized on calanoid copepods and chum salmon consumed almost exclusively gelatinous prey, which resulted in negligible diet overlap throughout outmigration in both years.

### 3.4.3 Interannual variability in prey size

Prey size was considerably larger in 2015 relative to 2016, particularly in the Discovery Islands. The Discovery Islands had a seasonal trend of increasing prey size compared to the more consistent Johnstone Strait. The seasonal trend in the Discovery Islands was correlated with an increase in salmon size, potentially indicating a size-based shift to larger prey. While no size trend was evident in Johnstone Strait, suggesting larger prey were not available there, which was also reflected in the zooplankton tow samples. The interannual variation in size may have been due to the delayed spring bloom in 2016, potentially limiting succession of large zooplankton and leading to an abundance of meroplankton in the Discovery Islands (Mahara et al., 2019). Prey size had a stronger relationship with salmon size in 2015 in the Discovery Islands, and for chum salmon this trend was more prevalent. Therefore, it appears that larger salmon may only have an advantage when large prey are available, and the absence of large prey through most of the area and time period is likely responsible for the poor feeding. Small prey may have a compounding effect on salmon growth, as small prey both provide less energy and require more energy to capture, compared to a few larger prey items (Gill, 2003; Moss & Beauchamp, 2007).
In the Discovery Islands-Johnstone Strait corridor, chum salmon appear to have more beneficial foraging strategies, since they consume larger and higher quality prey than pink salmon when available and tend to specialize on abundant gelatinous zooplankton when ideal food is scarcer. This led to a significant difference in condition between chum and pink salmon in 2016, the year with lower condition than 2015. The gelatinous foraging strategy of chum salmon may be beneficial when either productivity and food supplies are generally low or when density dependent interactions between salmon is high. Future research can use abundant chum salmon as broad ecosystem indicators, and generalist pink salmon to reveal available prey taxa.

3.4.4 *Salmon health implications*

Salmon condition did not vary significantly between regions, but stomach fullness was at times higher in the Discovery Islands than in Johnstone Strait, where it remained consistently low. However, condition was higher in 2015 than 2016 in both regions, which indicating better feeding in 2015. Stomach fullness appeared to somewhat increase across 2015 in the Discovery Islands, as did prey quality, since calanoids and chaetognaths have higher caloric and fatty acid contents than small prey (Boldt, 2001; Costalago et al., 2020). Whereas, in 2016, both prey size and quality remained low throughout and stomach fullness decreased considerably across the season in the Discovery Islands, which may have depressed salmon health. This may have been due to a mismatch in prey development and outmigration timing. Pink and chum juveniles in 2016 migrated about one week earlier than the 2015-2019 average migration date. Furthermore, the spring bloom was around 6 weeks later in 2016, although the zooplankton community composition appeared consistent despite this shift (Mahara et al., 2019). This interannual
variability demonstrated the importance of salmon migration timing and zooplankton community succession on juvenile salmon health and should be investigated further with climate shifts.

The low stomach fullness and poor food quality reflected in small prey sizes, appeared to be manifested in the low salmon condition in the Discovery Islands and Johnstone Strait, and may have negative impacts on salmon survival and returns (Duffy & Beauchamp, 2011; Tucker et al., 2016). Smaller sized zooplankton have low fatty acid and lipid content that is likely not sufficient for small migrants such as pink and chum salmon during this early marine phase (Costalago et al., 2020; Litz et al., 2017). Therefore, regions of significantly improved feeding further north (e.g., site “J02”, Chapter 2) are likely crucial to salmon survival, to recover from areas with consistently poor or variable foraging conditions along the migration route. Foraging hotspots warrant more research to understand how critical habitat may vary with climate change.

There were anomalously warm conditions in 2015 and 2016, due to the warm “blob” in the North Pacific, which originated in 2014, which was compounded by a strong El Niño in 2016 (Bond et al., 2015; Jackson et al., 2018). These warm ocean conditions may have influenced the earlier spring bloom timing, poor feeding and depressed condition of juvenile salmon in 2016. Pink salmon condition was significantly lower than chum salmon condition in 2016, and when adult pink salmon returned to the Fraser River in 2017, they had experienced one of the poorest returns on record of less than 5 million, compared to the average of 12.4 million (DFO, 2018). These generalist foragers are potentially more vulnerable to the zooplankton prey availability relative to chum salmon, who employ an opportunistic specialist strategy, and take advantage of large and nutritious prey when it becomes available and rely on gelatinous when it is necessary.
Cooler years in this migration area may improve conditions regarding zooplankton community composition and phenology timing with salmon migration, although future research is needed.

Microplastics were not the focus of this study but they were found in 8.5% of juvenile salmon stomachs, and a macroplastic was found to be > 40% weight of a pink salmon stomach. The 6 mm macroplastic had the shape, color and texture of a broken straw piece and appeared larger than the sphincter could potentially pass, which would likely reduce survival for that fish. Recent studies indicate plastic debris ingestion and entanglement as a widespread and increasing threat to the survival of salmon and other fish species (Myers et al., 2013; Savoca et al., 2021). Therefore, improvements in waste management to prevent marine plastic pollution is urgently needed in order to limit these threats to salmon health (Harris et al., 2021; Konecny et al., 2018).

3.5 Conclusions

Juvenile pink and chum salmon diets were highly dynamic and reflected prey preference, availability, and quantity, which shifted seasonally and interannually during their outmigration. Environmental drivers such as temperature regulated the prey size and community composition, which influenced salmon foraging strategies, stomach fullness, and interspecific competition. These trends were most apparent in the Discovery Islands, when prey size and quality increased across the 2015 season and salmon species had high diet overlap and were in healthy condition. Compared to 2016, when warm El Niño conditions initiated an early spring bloom, which caused a mismatch of small prey, insufficient for salmon to achieve full stomachs and build fat reserves.
In 2015, there were zooplankton community compositions that better aligned ideal prey size (2 to 5mm) with migrating juvenile salmon, and in mid-June, pink and chum salmon diets consisted of higher quality prey. More research is needed to determine whether high-quality prey timing is synchronized with salmon peak outmigration in mid-June in other years. This resulted in pink and chum salmon being fatter and in better condition as compared to 2016. There was a potential mismatch of prey in 2016, with small zooplankton available through the season and low gut fullness throughout, except late-May when early migrants fed on euphausiid eggs. This was comparable to juvenile sockeye salmon diets in the same time and place (James, 2019), therefore it reflected feeding conditions available to other planktivores and higher trophic levels.

Zooplankton availability for juvenile salmon is largely driven by bottom-up effects and timing of migration and plankton blooms is critically important for salmon survival to adulthood. However, in the context of climate change, salmon migration timing may shift since they utilize temperature cues, and plankton bloom timing may also shift from weather and freshet conditions. Therefore, salmon interactions under differing scenarios of zooplankton community timing are needed to further understand how salmon may cope and adapt to challenging early life histories. Juvenile pink and chum experience food-limitation in southern British Columbia and the species have evolved strategies to coexist by either utilizing generalist or specialist feeding, respectively. Further studies on multiple species interactions during salmon outmigration is recommended to comprehend challenges and strengths of different species in response to environmental hardship.
### Tables

Table 3.1 Sampling details for study: Site ID for the Discovery Islands (D07) and Johnstone Strait (J07), sampling date and year, number of pink and chum salmon stomachs analyzed, temperature (Temp.), salinity (Sal.) and size fractionated and total zooplankton biomass. The 2000 μm size fraction biomass values were divided by non-gelatinous (Non-Gel.) and gelatinous (Gel.) zooplankton.

<table>
<thead>
<tr>
<th>Site</th>
<th>Date</th>
<th>Year</th>
<th># Pink</th>
<th># Chum</th>
<th>Temp. (°C)</th>
<th>Sal. (%)</th>
<th>250 μm</th>
<th>1000 μm</th>
<th>Non-Gel.</th>
<th>Gel.</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>D07</td>
<td>May 21</td>
<td>2015</td>
<td>7</td>
<td>8</td>
<td>15.7</td>
<td>27.8</td>
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<td>No</td>
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</table>

Zooplankton Biomass (mg/m³)
Table 3.2 Zooplankton relative abundance (expressed as percent) by major groups.

<table>
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<th></th>
<th>Discovery Islands (D07)</th>
<th>Johnstone Strait (J07)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>May</td>
<td>June</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Calanoida</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small (&lt;2mm)</td>
<td>2</td>
<td>13.5</td>
</tr>
<tr>
<td>Large (&gt;2mm)</td>
<td>-</td>
<td>-</td>
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<tr>
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<td>43.1</td>
<td>54.2</td>
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<td>Decapoda</td>
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<td>Balanomorpha</td>
<td>32</td>
<td>25.3</td>
</tr>
<tr>
<td>Echinodermata</td>
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<td>2.6</td>
</tr>
<tr>
<td>Zooplankton Eggs</td>
<td>3.4</td>
<td>0.5</td>
</tr>
</tbody>
</table>

Gelatinous

|                |        |        |          |         |         |
| Cnidaria       | 0.2    | 1.3    | 0.3      | 0.1     | -       | 0.8     | 1.3      | 0.2     | -       | -       | 0.5     | 0.1     |
| Oikopleura spp.| 8.4    | 1.8    | 3.2      | 1.1     | 10.4    | 12.2    | 10.9     | 3.2     | -       | 0.5     | 0.4     | 0.9     |
| Chaetognatha   | -      | -      | -        | -       | -       | -       | -        | -       | -       | -       | 0.3     | 0.3     |

Other

|                |        |        | 0.5      | 1.3    | 0.3    | 11.4    | 1.4      | 3       | 7       | 0.5     | 3.7     | 0.6     | 15.8    | 0.2     |
| Cyclopoida     | -      | -      | -        | -      | -      | -       | -        | -       | -       | -       | -       | -       | -       |
| Harpacticoida  | -      | -      | -        | -      | -      | -       | -        | -       | -       | -       | -       | -       | -       |
| Euphausiidae   | -      | -      | 0.3      | -      | 0.1    | -       | -        | 0.7     | 0.8     | 0.5     | 3.6     | -       |
| Amphipoda      | -      | -      | -        | -      | -      | -       | 0.2      | -       | -       | -       | -       | -       | -       |
| Pteropoda      | 2.4    | 0.2    | 0.3      | 36.5   | 0.4    | 0.4     | 0.9      | -       | -       | 0.2     | 10.8    | 0.9     |
| Bivalvia       | 1.3    | 1.8    | 1.7      | 0.6    | 1      | 0.6     | 2.1      | 0.1     | 0.2     | -       | 0.4     | -       |
| Polychaeta     | 0.2    | -      | -        | 0.1    | 0.4    | -       | -        | -       | -       | -       | -       | -       |
| Bryozoa        | -      | -      | 1.2      | 0.3    | 0.1    | -       | 0.4      | 2.3     | -       | 0.6     | -       | 1.7     |
Table 3.3 Diet composition summary (% wet weight) of juvenile pink (PI) and chum (CU) salmon by date and year.

<table>
<thead>
<tr>
<th></th>
<th>Discovery Islands (D07)</th>
<th>Johnstone Strait (J07)</th>
<th>Discovery Islands (D07)</th>
<th>Johnstone Strait (J07)</th>
</tr>
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<td>June 13</td>
<td>June 02</td>
</tr>
<tr>
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<td>PI</td>
<td>CU</td>
<td>PI</td>
<td>CU</td>
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<td>Calanoida</td>
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<td></td>
<td></td>
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<tr>
<td>Small (&lt;2mm)</td>
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<td>-</td>
<td>2.7</td>
</tr>
<tr>
<td>Large (&gt;2mm)</td>
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<td>0.1</td>
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<td></td>
<td></td>
<td></td>
</tr>
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<td>Eggs</td>
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</tr>
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<td>Adults</td>
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<tr>
<td>Ctenophora</td>
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<td>-</td>
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Table 3.4 SIMPER results of prey taxa driving differences between regions of A) pink salmon diet composition and B) chum salmon diet composition (by transformed relative wet weights).

Group classification is included to the left of species or highest taxonomic resolution of prey, DI is relative biomass in the Discovery Islands, and JS is relative biomass in Johnstone Strait.

Average is the average contribution to dissimilarity and Sum is the cumulative contribution of prey to region dissimilarity, only taxa contributing to 70% of dissimilarity were included.

### A) Pink salmon SIMPER results

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<th>Groups</th>
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<th>DI</th>
<th>JS</th>
<th>Average</th>
<th>Sum</th>
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<td>60.39</td>
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<td>0.00</td>
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### B) Chum salmon SIMPER results

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<th>JS</th>
<th>Average</th>
<th>Sum</th>
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<td>4.88</td>
<td>60.37</td>
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<td>65.46</td>
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<td>Eggs</td>
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<td>0.00</td>
<td>4.01</td>
<td>69.72</td>
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<td><em>Eukrohnia hamata</em></td>
<td>6.53</td>
<td>0.47</td>
<td>2.93</td>
<td>72.84</td>
</tr>
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</table>
Table 3.5 Summarized salmon biological data for 2015-2016 in DI-JS: fork length (FL), wet weight (WW), condition factor K, gut fullness (GFI), number of empty stomachs, diet overlap of species, and richness (number of prey taxa), expressed as mean ± standard deviation.

<table>
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<tr>
<th>Species</th>
<th>Site</th>
<th>Year</th>
<th>Fish FL (mm)</th>
<th>Fish WW (g)</th>
<th>Condition (K)</th>
<th>GFI (%BW)</th>
<th># Empty</th>
<th>Overlap</th>
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<td>2015</td>
<td>94.5 ± 8.2</td>
<td>8.3 ± 2.3</td>
<td>1 ± 0.07</td>
<td>1.33 ± 0.96</td>
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<tr>
<td>Chum</td>
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<td></td>
<td>100.2 ± 11.3</td>
<td>10.3 ± 3.3</td>
<td>1 ± 0.11</td>
<td>2.5 ± 1.42</td>
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<td>2016</td>
<td>91.2 ± 16.9</td>
<td>7.6 ± 3.7</td>
<td>0.93 ± 0.08</td>
<td>1.3 ± 1.69</td>
<td>2</td>
<td>48.4</td>
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<tr>
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<td></td>
<td>89.3 ± 15.9</td>
<td>7.4 ± 3.8</td>
<td>0.97 ± 0.09</td>
<td>1.62 ± 1.92</td>
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<td>J07</td>
<td>2015</td>
<td>130.2 ± 9.1</td>
<td>22.6 ± 4.9</td>
<td>1.01 ± 0.06</td>
<td>0.45 ± 0.54</td>
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<td>16.8</td>
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<tr>
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<td></td>
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<td>23.9 ± 4.4</td>
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</tr>
<tr>
<td>Pink</td>
<td></td>
<td>2016</td>
<td>118.7 ± 9.6</td>
<td>15.5 ± 4.4</td>
<td>0.9 ± 0.07</td>
<td>0.56 ± 0.61</td>
<td>4</td>
<td>9.9</td>
</tr>
<tr>
<td>Chum</td>
<td></td>
<td></td>
<td>120.9 ± 13.4</td>
<td>17.6 ± 6.5</td>
<td>0.96 ± 0.05</td>
<td>0.99 ± 0.66</td>
<td>0</td>
<td></td>
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</tbody>
</table>
Figure 3.1 Map of sampling sites for Discovery Islands (D07) and Johnstone Strait (J07) during May to July 2015-2016. Inset map (left) shows B.C. coast with study location in red.
Figure 3.2 Diet composition of major prey groups by relative biomass of juvenile pink (“PI”, outlined in pink) and chum (“CU”, outlined in dark green) salmon during outmigration in 2015-2016 at the Discovery Islands site D07 and Johnstone Strait site J07.
Figure 3.3 Non-metric multidimensional scaling (NMDS) ordination plot of diet composition of pink (open circles) and chum (filled circles) salmon in Discovery Islands (red) and Johnstone Strait (blue) during outmigration (May to July) of 2015 and 2016. Vectors were overlaid to show direction and magnitude of the main taxonomic prey groups driving dissimilarity, overlapping labels not shown (Euphausiidae, Balanomorpha, Echinodermata, Cladocera, Decapoda).
Figure 3.4 Cluster dendrogram of temporal diet data, with outliers in grey and main clusters colored by region (details in appendix).
Figure 3.5 Cumulative prey curves for Discovery Islands (red) and Johnstone Strait (blue) juvenile pink (open circles) and chum salmon (closed circles) during 2015 and 2016.
Figure 3.6 Gut fullness indices (GFI) for juvenile pink and chum salmon in DI-JS, 2015-2016. Box plots show the mean (black bar), interquartile range (boxes), 1.5*inter-quartile range (whiskers), and points indicate extreme values of salmon GFI. The overlaid dark red line indicates dietary overlap between pink and chum salmon (secondary y-axis).
Figure 3.7 Juvenile salmon condition during outmigration in 2015-2016 for Discovery Islands and Johnstone Strait combined. Box plots show the mean (black bar), interquartile range (boxes), 1.5*inter-quartile range (whiskers), and points indicate extreme values of salmon GFI. The red dotted line separates fish in good condition (high weight relative to length, > 1) and fish in poor condition (low weight relative to length, < 1). Significant differences are indicated by ** p < 0.01, *** p < 0.001 and **** p < 0.0001.
Figure 3.8 Juvenile salmon diet composition by prey size class (mm). Only digestive state 1 “fresh” zooplankton prey were included to calculate mean relative biomass by date and species. For each sampling event, “PI” is pink on the left, and “CU” is chum on the right.
Figure 3.9 Predator and prey size relationships by species, date and region. A) chum salmon predator prey relationships, colored by sampling date (light is early season and dark is late season) and B) pink salmon predator prey relationships, colored by sampling date.
Figure 3.10 Fork length frequency distributions of A) all pink and chum salmon collected throughout 2015-2019 and B) study salmon in 2015-2016.
Chapter 4: Conclusion

4.1 Knowledge gap of juvenile pink and chum salmon competition

The health of salmon populations, as recognized keystone species in marine, freshwater and terrestrial environments, is related to the health and wellbeing of humans and ecosystems. Pink and chum salmon are two species who are severely underappreciated, in the scientific and fisheries communities, despite their importance to ecosystems and Indigenous peoples’ wellness. Sockeye, chinook and coho salmon have high economic value as well as conservation interest, whereas modern pink and chum salmon have received far less research and are less valued by fishers overall. However, pink and chum salmon are the most abundant and the least threatened of the salmon. Understanding the strategies that make them successful can provide important insights into the declines of other salmon, and their interactions with other salmon species may potentially be a contributing factor in those related declines. They bring a substantial amount of nutrients to terrestrial environments and apex predators, and they hold high importance in both the pre-contact and modern diets of Indigenous peoples. In particular, chum and pink salmon are well suited for preservation as winter food sources, due to their low oil content, as a result of shorter freshwater migrations relative to other salmon species (O’Neill et al., 2014). Chum and pink salmon are therefore immensely valuable to the Haida, Kwakwaka’wakw, Heiltsuk, WSÁNEĆ/Saanich, and many other First Nations (Cannon & Yang, 2006; Cullon, 2013; Haggan et al., 1999; Paul, 2006; White (Xanius), 2006). This research aims to emphasize the ecological role of pink and chum salmon as co-migrants with the “iconic” sockeye salmon and immense value as study subjects for juvenile salmon biology. Pink and chum salmon foraging strategies
provided insights into how adaptability during their early migration is necessary for survival and hopefully this project can help to shift our perspectives.

4.2 Diets of juvenile pink and chum salmon in contrasting foraging conditions

This study investigated juvenile pink and chum salmon diets and feeding strategies across the Discovery Islands and Johnstone Strait migration pathway from May–July in 2015 and 2016. Firstly, Chapter 2 analyzed diets along the migration route during the peak outmigration (mid-June) in 2016 and identified extended areas of poor feeding conditions and prey availability where resource partitioning between salmon species occurred. Chapter 3 investigated interannual variability of diets within the regions during the outmigration period, which described varying species interactions depending on the zooplankton community succession. Specifically, both species had greater foraging success in 2015 compared to 2016, when the prey size in the Discovery Islands was larger later in the 2015 season, and in other areas and times, prey was small. Therefore, the spatial (Chapter 2) and temporal (Chapter 3) data chapters reflect juvenile pink and chum salmon diets shifting with prey availability, where species will differ in prey types to limit their competition (Figure 4.1). Pink salmon were more generalist feeders, with high diet diversity and variability, and frequently consumed calanoids throughout the two regions, as well as nearshore prey and meroplankton. Conversely, chum salmon relied heavily on the gelatinous prey available in both regions, except when prey switching during improved foraging conditions, when they consumed large crustaceans. Overall, this study found that species-specific foraging behaviour in response to competitive pressures persisted across time and space in poor feeding conditions; and in good feeding conditions, larger salmon benefitted in seasonally
dynamic Discovery Islands and all salmon successfully foraged in the zooplankton hot spot near Queen Charlotte Strait (Figure 4.1).

4.3 Trophic interactions of pink and chum salmon during outmigration

The relationships between juvenile pink and chum salmon appear to fluctuate with the changing ocean conditions along their coastal outmigration. These species coexist by utilizing different strategies, either resource partitioning or complete trophic niche separation when food availability is low, and species consume the same resources when food is more plentiful. The separation of trophic niches for pink and chum salmon is a strategy to limit competition and share the environmental space to survive under challenging conditions in the early marine period. Pink salmon tended to consume the higher quality prey whenever possible, actively seeking out calanoids, even in the Discovery Islands where calanoids were rarer than in Johnstone Strait. Conversely, chum salmon in Johnstone Strait preyed upon lower quality jellyfish, however chum salmon have evolved strategies to benefit off this prey more than other salmonids. For example, chum salmon have larger, thicker stomachs and more pyloric caeca to aid in quick digestion, and thus, chum salmon may rely on an under-utilized niche to meet energy demands (Azuma, 1995).

The sympatric coevolution of Pacific salmonids led to 6 anadromous species with diverse life histories, feeding strategies and distributions, persisting today in spite of many challenges. Salmon species adapted behavioural and physiological differences to occupy distinct habitats, trophic niches or migration timing from one another, through evolutionary selection processes. The anadromous life cycle of salmon through complex habitats with cumulative stressors poses
challenges to salmon scientists and conservationists aiming to understand these elusive species. Despite these logistical hurdles, Pacific salmon are well-studied overall, with researchers filling knowledge gaps and intellectual niches on each phase and aspect of salmon species life histories.

Salmon provide unique case studies for investigating sympatric evolution and ecology of marine animals through dynamic areas and how species interactions shift with conditions encountered. This study demonstrated the tendency of chum salmon to fill the gelatinous predator niche under food limitation as early as the juvenile phase, with pink salmon relying on smaller zooplankton. One question to research in the future includes, where does this leave juvenile sockeye salmon? Sockeye salmon may compete with pink salmon in years of high abundance if occupying similar niches, distinct from chum, coho, chinook and steelhead, which may influence sockeye survival.

Furthermore, one theory that has not yet been explored, is that perhaps chum salmon are preying upon the easier to catch jellyfish while also benefiting off the jellyfish’s captured prey. In most of the chum salmon stomachs with jellyfish present in this study, calanoid prey, such as *Acartia longiremis*, were often inside the jellyfish, thereby increasing the quality of prey eaten. Future experiments could be done on chum salmon prey selection, to determine under exactly what concentrations of jellyfish and calanoids will they consume which and determine if chum salmon actively select jellyfish that have calanoids inside their tentacles, using them as a capture system. While this has not yet been shown for calanoids, some hyperiid amphipods are found exclusively living commensally or parasitically on jellyfish and are consumed by salmon (Weil et al., 2020). Further research or meta-analyses should investigate pink and chum salmon diets under differing conditions, since previous work underappreciated the gelatinous prey of chum, likely due to difficulty identifying soft-bodied prey, often classified as “other” (Graham, 2020).
The foraging strategies utilized by juvenile pink and chum, encompassing both generalist and specialist zooplankton consumption, indicate that these species can be used as ecosystem samplers to track environmental changes. The juvenile salmon stomach fullness reflected the changes in prey availability and foraging opportunities during coastal outmigration, and diet composition gave more detailed information. Therefore, juvenile pink and chum salmon diets can be utilized to study the foraging conditions available to other species such as sockeye salmon or herring and find any hot spots and gauntlets. Both pink and chum salmon prey groups and quality of prey tended to match stomach fullness and fish condition, where small meroplankton or gelatinous prey indicated their poor feeding and conversely, large calanoid, euphausiid and chaetognath prey demonstrated improved conditions. Thus, future ecosystem modelling research should incorporate species-specific salmon diet data.

4.4 Lessons and calls to action

In Indigenous worldviews, salmon are often seen as supernatural beings who provide us with teachings on how to be in a meaningful relationship with the world around us (CHN, 2011). It seems that the lessons to be learned from chum and pink salmon specifically, is to be adaptable and resilient, utilize strengths to better coexist with others, and be active in getting what we need. The entire life cycle of salmon is all about giving back to the next generations through spawning and sacrificing their lives to enhance natal habitats with energy they spent their lives gathering. Salmon hold a wealth of information that scientists are constantly trying to gain knowledge from, but reciprocity to that which sustains them is an important reminder to us to give back to salmon.
For complex species who are up against human and environmental pressures at each life phase, the science is intertwined with management and we must save salmon to sustain our ecosystems.

Therefore, one recommendation to improve salmon survival in significantly poor feeding conditions in the Discovery Islands and Johnstone Strait regions is coastal habitat restoration. Special consideration should also be given to the pollution and open-net pen aquaculture in the region, where juvenile salmon are negatively affected by pollution and sea lice from fish farms. The impacts of plastic pollution on fish are still emerging in the literature, but this study found a relatively high occurrence of micro- and macro-plastic in juvenile salmon stomachs (Figure A.3). However, the negative effects of sea lice and pathogens such as piscine orthoreovirus (PRV) on juvenile salmon have been well documented (Morton et al., 2017), with increased parasite loads decreasing the foraging success of sockeye salmon (Godwin et al., 2017). Given that industry releases untreated effluent into salmon migration pathways and underreports sea lice data (Godwin et al., 2020; Price et al., 2013), continued research is required to quantify the impacts on the health of wild salmon. While this thesis study did not focus on sea lice, the findings did clearly demonstrate general food limitations of juvenile salmon in this region. Alternative to the costly and uncertain nature of restoration, one cost-effective method to protect salmon and habitats is to limit further damaging development projects and industry (Walsh et al., 2020).

Climate change will further exacerbate these impacts during every phase of the salmon life cycle. Therefore, if salmon stocks are to continue to survive into the future generations, intervention is urgently required to halt the cumulative pressures that provide critical barriers to salmon health. Since salmon must contend with stressors in both freshwater (droughts, high
temperatures, dams, habitat loss, pollution) and the ocean, each phase of the life cycle is important for determining resilience in subsequent phases and understanding each phase is crucial for salmon management. As temperatures increase, the food web structure and salmon distribution and metabolic needs shift. Understanding the fundamental biology and ecology of salmonids is needed to help preserve the biodiversity and productivity of salmon stocks, for them to be resilient in a rapidly changing environment. Once we gain an understanding of what salmon require to survive through their arduous migrations, we can better predict how stocks may fluctuate and implement adaptive management strategies. In order to accomplish this gigantic task of amassing salmon knowledge into conservation action, collaboration across disciplines and groups is necessary to collate complex knowledge systems. Often, salmon are studied in isolated systems, with limited impact into preserving these species. Therefore, everyone should be engaged in salmon conservation, from citizens to policy makers. As salmon scientists, we have a responsibility to pass on what we know to the next generation and ease stressors salmon face so they may flourish and keep contributing to coastal ecosystems. Furthermore, major effort should be made to slow the rate of the changing climate, thus giving salmon more time to adapt.

In addition to preventing or reversing damaging conditions for juvenile salmon, there is also a need to improve survival and ease the competitive pressures that exist for salmon species. Another recommendation is to restore eelgrass foraging grounds as salmon habitats, especially in the Discovery Islands, where nearshore invertebrates were very important juvenile salmon prey. Eelgrass habitats in this area have decreased over the past several decades (Cullis-Suzuki, 2007; Nahirnick et al., 2020), and restoration would provide habitat for salmon and invertebrate prey, such as harpacticoids. Specifically, the area on Quadra Island near Heriot Bay docks, has had
eelgrass beds decrease in size, biomass, and quality of eelgrass habitat (Cullis-Suzuki, 2007). Other areas in Discovery Islands and Johnstone Strait showed positive responses to restoration efforts, e.g., Campbell River and Salmon River (Levings & MacDonald, 1991; Pellett, 2011). This study revealed considerable amounts of harpacticoid copepods in the diets of pink salmon, as well as other invertebrates typically found in eelgrass habitats, such as gammarid amphipods. Other studies have found juvenile pink and chum salmon in eelgrass habitats had diverse diets, dominated by harpacticoid copepods, and had high gut fullness (Kennedy et al., 2018; Zahner, unpublished data). Habitat restoration would also benefit species other than salmon, as eelgrass communities support diverse fish assemblages with shelter and food (Chalifour et al., 2019).

Furthermore, a study found that the traditional harvesting methods employed by the Kwakwaka’wakw peoples stimulated growth of healthy eelgrass, and restoration efforts should be co-developed with these Nations whose traditional territories encompass this part of the salmon migration route (Alfred, 2010; Cullis-Suzuki, 2007). Traditional knowledge of the pre-colonization habitats would provide in-depth insights into the best locations to restore eelgrass habitats and other conservation efforts. Therefore, Indigenous sovereignty in this area would benefit both science and conservation, and lead to an increase in healthy systems that support salmon within this challenging food-limited area. Both salmon and eelgrass have shown phenomenal resilience and responses to restoration efforts, which provides a lot of hope for salmon, who continue to uphold the foundations of our society.
4.5 Figures

Figure 4.1 Conceptual diagram of combined thesis results on juvenile salmon diet variability.

Stratified surface conditions from the southern Discovery Islands (D07) are labelled as “Strat.”

Mixed ocean conditions with poor feeding are represented by sites D09, D11, J06, J08, and J07.

Whereas the good feeding conditions in mixed waters represented J02, northern Johnstone Strait.

Diet overlap between species and predator-prey ratios revealed that size was an important factor in stratified conditions, large fish ate larger prey, and species separated niche under poor feeding.

No species or size differences were found at the migration route terminus feeding hot spot.
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Appendix

Table A.1 Peak outmigration timing of pink and chum salmon calculated as the date when 50% of fish have passed through the area of Discovery Islands and Johnstone Strait, 2015–2019, as well as average values for both regions and years.

<table>
<thead>
<tr>
<th>Species</th>
<th>Region</th>
<th>2015</th>
<th>2016</th>
<th>2017</th>
<th>2018</th>
<th>2019</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pink</td>
<td>DI</td>
<td>June 05</td>
<td>May 30</td>
<td>June 27</td>
<td>June 01</td>
<td>June 01</td>
<td>June 06</td>
</tr>
<tr>
<td>Chum</td>
<td></td>
<td>June 02</td>
<td>May 30</td>
<td>June 15</td>
<td>June 01</td>
<td>June 03</td>
<td>June 04</td>
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<tr>
<td>Pink</td>
<td>JS</td>
<td>June 30</td>
<td>June 23</td>
<td>July 06</td>
<td>June 22</td>
<td>July 05</td>
<td>June 29</td>
</tr>
<tr>
<td>Chum</td>
<td></td>
<td>June 23</td>
<td>June 23</td>
<td>July 01</td>
<td>June 22</td>
<td>June 30</td>
<td>June 25</td>
</tr>
<tr>
<td>Pink</td>
<td>Average</td>
<td>June 17</td>
<td>June 10</td>
<td>July 01</td>
<td>June 11</td>
<td>June 18</td>
<td>June 17</td>
</tr>
<tr>
<td>Chum</td>
<td></td>
<td>June 12</td>
<td>June 10</td>
<td>June 23</td>
<td>June 11</td>
<td>June 16</td>
<td>June 14</td>
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</table>
Table A.2 Indicator value (Ind. val.) analysis for temporal (Chapter 3) clusters. Clusters were defined by site, species and dates, with “+” symbol denoted that other samples were also present as well. “Pink/Chum” means both species were well represented within that cluster and “2015/2016” indicated that multiple sampling dates were in the cluster. Only significant values are shown (p < 0.05).

<table>
<thead>
<tr>
<th>Cluster</th>
<th>Site</th>
<th>Species</th>
<th>Dates</th>
<th>Prey Group</th>
<th>Prey Taxa</th>
<th>Ind. val.</th>
<th>p value</th>
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<td></td>
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<td></td>
</tr>
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<td>1</td>
<td>J07</td>
<td>Pink</td>
<td>2016-06-20</td>
<td>Calanoida</td>
<td><em>Aetides diversgens</em></td>
<td>0.7686</td>
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<td>2</td>
<td>D07</td>
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<td>2016-06-16</td>
<td>Amphipoda</td>
<td><em>Senticaudata</em></td>
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<td>2016-06-16</td>
<td>Insecta</td>
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<tr>
<td>3</td>
<td>D07</td>
<td>Chum</td>
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<td>15</td>
<td>J07+</td>
<td>Pink+</td>
<td>2015/2016</td>
<td>Calanoida</td>
<td><em>Calanus marshallae</em></td>
<td>0.3618</td>
<td>0.001</td>
</tr>
</tbody>
</table>
Figure A.1 Discovery Islands subcluster for temporal (Chapter 3) juvenile salmon diets, labelled and colored with survey date.
Figure A.2 Johnstone Strait subcluster for temporal (Chapter 3) juvenile salmon diets, labelled and colored with survey date.
Figure A.3 Micrograph of a blue macroplastic (5.8 mm) found in a juvenile pink salmon stomach in the Discovery Islands, before the stomach contents were removed.